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THE RUTGERS HYBRID DOGWOOD: NAMING AND GENETIC DIVERSITY  
ANALYSIS

By

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And approved by

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## ABTRACT OF THE THESIS

The Rutgers Hybrid Dogwood: Naming and Genetic Diversity Analysis

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Big-bracted dogwoods (*Cornus* spp.) are popular landscape trees in the United States, accounting for \$30 million in sales annually. This group of dogwoods is comprised of the Florida dogwood (*C. florida*), the Asian dogwood (*C. kousa*) and the Pacific dogwood (*C. nuttallii*). They are beloved for their four season appeal: floral bract display in the spring, attractive green foliage in the summer, striking autumn colors in the fall and exfoliating bark in the winter. These trees are the focus of a big-bracted dogwood breeding program at Rutgers University, which started in the 1960s under the helm of Dr. Elwin Orton. His focus was to develop new pink or red-bracted varieties of *C. kousa* and red-bracted dwarf varieties of *C. florida*. In order to accomplish these breeding goals, Dr. Orton created the first inter-specific hybrids between *C. florida* × *C. kousa* and *C. kousa* × *C. nuttallii*. These hybrids have since become an important staple in the horticultural trade known for their vigor, enhanced disease tolerance and improved ornamental qualities. Part of this study was to formally name and describe these hybrids in order to facilitate scientific and horticultural communication. The *C. florida* × *C. kousa* hybrids

were formally named *Cornus* × *rutgersensis* in honor of Rutgers University and the *C. kousa* × *C. nuttallii* were named *Cornus* × *elwinortonii* in honor of Dr. Elwin Orton. Only a handful of these hybrids were fertile potentially creating a genetic bottleneck in the Rutgers germplasm collection when they were used in breeding. Big-bracted dogwoods are highly heterozygous and sensitive to inbreeding depression requiring the breeding program to maintain high levels of genetic diversity within its breeding lines. Genetic diversity levels in the Rutgers breeding program are unknown. This study sought to elucidate the level of genetic diversity in 276 Rutgers University dogwood accessions and 59 from the University of Tennessee by using eleven simple sequence repeat molecular markers. Results showed that five consensus groups were found: *C. florida* group, *Cornus* × *rutgersensis* group, *Cornus* × *elwinortonii* group, *C. kousa* inter-specific hybrid group and Pink-bracted *C. kousa* group. It was found that genetic diversity is high across the entire germplasm collection tested; however, limited genetic diversity exists within the *Cornus* × *rutgers* and *Cornus* × *elwinortonii* groups. This information will be important in the future of the Rutgers and other breeding programs allowing breeders to make more genetically distant crosses to help maintain high levels of genetic diversity.

**Keywords:** *Cornus*, tree breeding, molecular markers, Kousa dogwood, Florida dogwood, botany

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## Literature Review

### Introduction

The circumboreal genus *Cornus* L. consists of approximately 60 morphologically diverse species comprising 10 subgenera (Fan and Xiang, 2003; Xiang et al., 2006). Species found in this genus occupy various ecological niches and can range from small herbaceous forms like *C. canadensis* to tall-statured trees like *C. nuttallii*. This recently declared monophyletic genus is found in the order Cornales that contains the families Cornaceae and Hydrangaceae (Xiang et al. 2006). Hydrangaceae, the family containing the well-known ornamental shrub hydrangea (*Hydrangea spp*), native to Asia and North American, is found in Cornales and is considered the sister clade to Cornaceae.

The *Cornus* genus includes the economically and horticulturally important big-bracted (BB) dogwoods, which comprise three subgenera: *Cynoxylon*, *Discocrania* and *Syncarpea* (Xiang et al. 2006). The defining characteristics of this monophyletic clade include small- to medium-sized flowering trees that display large, showy petaloid bracts which are located under tight multi-flower inflorescences. The most well known species of this clade in North America is *C. florida* L. subgenus *Cynoxylon*. Also in this subgenus is another native North American tree *C. nuttallii* Audobon ex Torr. & A.Gray. or the Pacific dogwood named after the Pacific northwest region where it is commonly found. The Kousa dogwood, *C. kousa* Buerger ex Miq., is native to most parts of eastern Asia and is the most commonly found landscape BB-dogwood in Asia. *Cornus kousa* includes the subspecies *C. kousa* ssp. *chinensis*. BB-dogwoods also include the species *C. capitata* subgenus *Syncarpea*, *C. elliptica* subgenus *Syncarpea*, *C. multinervosa* subgenus

*Syncarpea*, *C. disciflora* subgenus *Discocrania* and multiple subspecies of *C. hongkongensis* subgenus *Syncarpea*.

Many dogwood species, especially the BB-dogwoods, are commonly used as horticultural specimens. *C. florida* and *C. kousa* are considered ideal landscape trees because of their four season appeal: attractive “flowers” in the spring, attractive foliage and form in the summer, vivid autumn color and exfoliating bark in the winter. Not only is *C. florida* an important species in horticulture, it is also an important understory tree in eastern and southern deciduous forests of North America. *C. kousa* is an important species in deciduous forests of Japan, China, Korea and other eastern Asian countries as well as being an important ornamental species found throughout Europe and the eastern US. *C. nuttallii* is a native tree in the Pacific northwest of North America, an area that lacks the dramatic seasonal changes as eastern Asia and the northeast US. However, this species is also a prized ornamental tree having larger flowers than *C. florida* and *C. kousa*, attractive foliage and exfoliating bark.

With the popularity of *C. florida* as an ornamental landscape tree, a Rutgers BB-dogwood breeding program began in 1965 under the helm of ornamental tree breeder Dr. Elwin R. Orton Jr. He received his doctorate degree in plant genetics from the University of Wisconsin completing his thesis work on basic corn genetics. He was first hired at Rutgers University in 1960 with the specific goal of developing improved hybrids between American holly (*Ilex opaca*) and the European holly (*I. aquifolium*) to combine the glossy foliage and excellent fruit display of European holly with the cold hardiness of

the American species. After unsatisfactory results, he turned his attention to other *Ilex* spp. and also began working on dogwoods. At the onset of the program, Dr. Orton's goals were to develop red- or pink-bracted varieties of *C. kousa* and *C. nuttallii* and to develop red-bracted, dwarf varieties of *C. florida* (Orton, 1970). He quickly realized the narrow genetic base of *C. kousa* in the US at the time and the huge potential for inter-specific hybrids (Orton, personal communication). He was the first person to create hybrids between these three species (Dirr, 2009) and employed various techniques to accomplish this. All three species flower at different times, so by manipulating chilling times, temperatures, and daylengths in greenhouses and cold-rooms, he was able to get the flowering times to overlap.

After nearly 30 years of breeding, Dr. Orton released his first cultivars, today famously known as the Stellar Series®, a group of *Cornus* × *rutgersensis* Mattera et al. hybrids (Orton, 1993a-e; Orton, 1991). Because cultivar name recognition is a major aspect in ornamental horticulture, Orton insisted on patenting and trademarking the hybrids developed in his program, a new practice at the time (Hanrahan, 2013). He believed that in order to continue the breeding program long term, royalties should be collected from the sale of the patented plants and revenue returned to the university. Following an approach that has since become common in the nursery trade, most of the Rutgers' dogwoods have a 'coded' patent name such as 'KN30-8' and an attractive trademark name such as Venus®. This practice allows for the trademark owner to continue collecting royalties on the use of the name of the cultivar even after the patent expires in 20 years. In some cases, a 20 year period of patent protection is a short timeframe for a

new tree cultivar to garner enough sales to recuperate the financial investment to develop it. While a plant patent expires, trademark names can be protected indefinitely. Using the trademark name when marketing and licensing RU cultivars increases the name recognition in industry. This system of naming forces nurseries to use an unrecognized name (the ‘coded’ cultivar name: ‘Rutnut’) when propagating and selling the cultivar after patent expires, instead of the trademark name the industry has grown accustomed to, unless a fee is paid to the owner of the trademark.

### **Dogwood Phylogeny, Ecology and Horticulture**

The *Cornus* genus consists of four main subgroups: Blue or white fruited dogwoods (BW); Cornelian cherries (CC); Big-bracted dogwoods (BB); and Dwarf dogwoods (DW; Fan et al., 2003; Xiang et al., 2006). The BW subgroup, made up of ten subgenera, is characterized by having paniculate or corymbose cymes; small bracts; globose or subglobose fruit that is white, blue or black in color; and a chromosome number of  $n=10$  or 11. The CC subgroup, made up of three subgenera, is characterized by umbellate cymes; modified non-petaloid bracts; oblong red fruit; and a chromosome number of  $n=9$  or 10. The DW group, made up of a single subgenera, is characterized by small corymbose cymes; petaloid bracts; red globose fruit; herbaceous and rhizomatous; and a chromosome number of  $n=11$  or 12. Lastly the BB subgroup, characterized by capitular cymes consists of three subgenera: *Discocrania* (Harms) Wangerin, *Cynoxylon* Raf. and *Syncarpea* (Nakai) Xiang. *Discocrania* is a subgenus characterized by having four modified, non-petaloid bracts and red oblong fruit and consists of one to two species found in Central and South America. *Cynoxylon* is a subgenus characterized by four or

six modified, petaloid bracts and red oblong fruits ( $n = 11$ ). *Cynoxylon* includes *C. florida* and *C. nuttallii*. A subspecies designated *C. florida* ssp. *Urbiniiana*, found in northeastern Mexico, is unlike most *C. florida* species with the petaloid bracts fused at the tip.

*Syncarpea*, the last subgenus, is characterized by four large petaloid bracts and compound multi-stone red fruits ( $n = 11$ ). *Syncarpea* consists of 4-12 species including *C. kousa* and is found exclusively in eastern Asia. (Fig. 1; Fan et al., 2003; Xiang et al., 2006).

*Cornus florida*, the most well known of the BB-dogwoods, is native to eastern North America with some populations stretching as far south and west as Texas and northern Mexico. Being an integral component of the understory canopy in deciduous mesic hardwood-forests, *C. florida* is an important native ecological species. It is known as a “calcium-pumping” species and can extract calcium from lower soil depths and concentrate it in their leaves (2-3.5% v/v) and fruit (8% of total calcium in the tree) making it an important player in calcium recycling – making it accessible to birds, snails and mammals (Nation, 2007; Thomas, 1969; Rossell et al., 2001) The understory of *C. florida* has been associated with significantly higher levels of land snail diversity and density when compared to other native understory species (Nation, 2007). The ability of dogwood leaves to decompose rapidly makes high levels of calcium available in the upper soil layers (Hepting, 1971; Rhoades et al., 2011) The high concentration of calcium in the leaves is one of the main sources of calcium for lactating white-tail does (*Odocoileus virginianus*) in the early spring (Halls et al., 1969; Li et al., 2009; Mitchell et al., 1988).

*Cornus florida* flowers in the early spring (April-May), with between 15-30 inconspicuous, perfect protandrous flowers held on a capitate inflorescence that is subtended by four floral-like bracts ranging in color from white to pink to dark red (Figure 2). Flowering lasts between 2-7 days, representing a fairly narrow-range for pollen flow to occur. The major pollinators of *C. florida* in Tennessee are halictid and adrenid bees, while various other insects species such as cerambycid beetles play minor roles in pollination (Rhoades et al., 2011).

The bright orange or red fruit, which are single-seeded drupes, develop throughout the summer and ripen in the fall (September- October). The fruit containing 16.7% crude fat and 10% crude protein represent an important food source for migratory and overwintering birds such as wild turkey (*Meleagris gallopavo*) and northern cardinals (*Cardinalis cardinalis*; Mitchell et al., 1988; Servello and Kirkpatrick 1987; Stiles, 1980).

*Cornus florida* is also an important plant in horticulture. It is a prized small- to medium ornamental tree (5-20m, occasionally reaching 30m) used by homeowners, businesses and botanical gardens as a container specimen or landscape centerpiece for its four season appeal: Spring – striking floral bract display; Summer – attractive foliage and form; Fall – Bright fruit display and striking autumn color; and Winter – interesting, exfoliating bark (Fact sheets). In Spring, the ornamental floral bract color peaks a few days before true flowering and drops several weeks after. *C. florida* bract color ranges from pale to cream colored white to white with pink accents to pale pink and finally to



dark-red (Fig. 2). There are over 100 cultivars, some with very unique characteristics such as dwarf habits or yellow fruit color (normally orange-red; Santamayor and McArdle, 1985)

Short list of cultivars: ‘Sweetwater Red’, ‘Spring Song’, ‘Mystery’, ‘Cloud 9’, ‘Cherokee Chief’, ‘Cherokee Princess’, ‘Cherokee Sunset’, ‘Prosser’, ‘Jean’s Appalachian Snow’, ‘Appalachian Blush’, ‘First Lady’ and ‘Barton’ (Santamayor and McArdle, 1985)

The Kousa dogwood (*C. kousa*) is native to Korea, China, Japan, Taiwan, Sikkim and Bhutan and is reportedly naturalized in New York, New Jersey, Connecticut and Hawaii (Flora of China; Biota of NA Project). In its native range, *C. kousa* grows in mixed woodlands, stream sides and valleys between the elevations of 400 and 2,200m (eFloras, 2008; Fulcher et al., 2012).

In North America, *C. kousa* flowers in the late spring and early summer (May-June), about one month after *C. florida*. Inconspicuous, perfect flowers (15-40) are fused in a capitate inflorescence that is subtended by four showy floral bracts, usually white (Figure 2). Bracts are narrower than the bracts of *C. florida* and end in an acuminate apex. *C. kousa* is pollinated by halictid bees and scarab, cerambycid and cantharid beetles in North America (Rhoades et al., 2011). The difference in inflorescence structures between *C. kousa* and *C. florida* (fused vs. free flowers) leads to a major difference in fruit structure. *C. kousa* fruit, which ripens to a bright orange or red color in the fall, is a multi-seeded compound fruit with an appearance similar to a spherical raspberry, which is unlike the

single-seeded drupes of *C. florida*. These fruits have edible pulp, some with flavors similar to an apple and mango and are sometimes used to make wine. *Cornus kousa* is a popular ornamental landscape tree in Japan, Korea and China and has been gaining significant popularity in North America. It is considered by many to be the Asian parallel to *C. florida*. Its four-season appeal is similar to that of *C. florida*: Spring – striking floral-bract display; Summer – attractive foliage and form; Fall – bright fruit display and striking autumn color; Winter – exfoliating bark (Gilman and Watson, 1993a). With similar tree size (8-20m) and climatic ranges (USDA Hardiness zones 4-8; Daly, 2012) and only a slightly more upright appearance than *C. florida*, *C. kousa* shares many of the same horticultural uses as *C. florida*. Kousa dogwood has a longer floral-bract display than *C. florida* typically lasting around a month (Gilman and Watson, 1993b). Floral-bracts are almost exclusively white but rarely light-pink trees do exist.

Short list of cultivars: ‘Chinensis’, ‘Lustgarten’, ‘Gold Star’, ‘Milky Way’, ‘Moonbeam’ and ‘Rochester’ (Santamayor and McArdle, 1985)

*Cornus nuttallii*, the Pacific dogwood, is the second BB-dogwood native to North America. Like its common name indicates, its native range includes the lowlands of southwestern British Columbia (Canada) to the mountains in southern California (Edson et al., 1994; Keir et al., 2011). A disjunct population also exists in northern Idaho (Keir et al., 2011). *C. nuttallii* is commonly found as an understory tree in douglas-fir (*Pseudotsuga menziesii*) forests and occasionally giant sequoia (*Sequoiadendron giganteum*) forests (Franklin et al., 2002). Like *C. florida*, it flowers in early spring

before the emergence of leaves. Tightly packed inconspicuous flowers (50-100) are held on a compact capitate inflorescence that is subtended with 4-7 showy white floral-bracts. Clusters of single-seeded drupes ripen to a bright red color in the fall.

*C. nuttallii*, while being an ecologically important component to western mesic forests, is also used as a small to medium sized ornamental landscape tree. Being native to the Pacific Northwest it has low cold-tolerance and therefore has a much more limited role in horticulture than *C. florida* and *C. kousa*. Its ornamental appeal is derived from its floral bract display, unique form and exfoliating bark. In full sun situations this species tends to be multi-stemmed creating both bushy and upright unique forms. Unlike both *C. florida* and *C. kousa*, which typically have four bracts, *C. nuttallii* has between 4-7 floral bracts, usually with 5 or more. Bract color is usually only white.

Short list of cultivars: ‘Goldspot’ and ‘Corigo White Giant’ (Santamayor and McArdle, 1985)

### **Propagation, Breeding and Breeding Challenges**

Big-bracted dogwood cultivars are normally single genotypes that are clonally propagated by chip or t-budding on seedling rootstocks. Both *C. florida* and *C. kousa* seedlings can be used as rootstocks depending on what is being budded and the nursery’s preference. Rootstocks are usually grown for a year before budding occurs. Budding generally occurs in August with buds remaining dormant that winter. In the following Spring, growth from the bud is forced and the rootstock is pruned back. The scion grows

throughout the summer and is trained to a single leader if needed. Plants are then dug up in the winter or early spring (one year later in Tennessee, two years later in Oregon), the roots are washed and sold as “liners” to grow-on nurseries that either plant them directly into the field or into containers. Field grown dogwoods are cultivated for several seasons and then dug up, ball and burlapped and sold to retail outlets or landscape firms. Container grown liners are grown for 1-2 more seasons before being sold.

The dogwood breeding program at Rutgers University, which started in the late 1960s, has had many goals throughout the years. At first, the program only focused on improving the aesthetic quality of dogwoods, but disease resistance was added as an important breeding objective soon after, when disease pressure from introduced pathogens began affecting both nursery growers and homeowners. The first major disease to spur this change in objectives was dogwood anthracnose, caused by the ascomycete fungus *Discula destructiva* Redlin. This fungus, a member of the family Valsaceae, causes dark necrotic spots on the leaves and eventually spreads to the twigs. It can infect multiple species of dogwoods but aggressively kills *C. florida* and *C. nuttallii* (Holzmueller et al., 2006). It was first introduced to the US in 1976 and an epidemic spread throughout the US with mortality rates of *C. florida* as high as 86% in Connecticut between 1977 and 1987 (Britton, 1994; Holzmueller 2006). Based on genetic studies that indicate a narrow genetic base of this fungus in the US, it is believed that *D. destructiva* was introduced from Asia to the US sometime in the early-mid 1970s and was reported on *C. nuttallii* in the Pacific northwest in 1976 and on *C. florida* in the eastern coast of the US in 1978 (Hibben and Daughtrey, 1988; Trigiano et al., 1995; Redlin, 1991).

In some reports, dogwood anthracnose had a mortality rate as high as 90% on *C. florida* in the eastern US (Holzmueller et al., 2006). While both North American BB native species are highly susceptible, *C. kousa* displays high levels of tolerance or resistance to this disease. It is believed that *D. destructiva* and *C. kousa* occur sympatrically in Asia suggesting that these species co-evolved giving *C. kousa* increased levels of tolerance to this fungal disease (Britton, 1994; Holmes & Hibben, 1989; Holzmueller et al., 2006). The spread of this fungus throughout North America and the devastation left in its wake spurred Dr. Orton to begin evaluating germplasm for and developing new dogwood anthracnose resistant cultivars. Creating hybrids between the two native dogwoods and *C. kousa* represented the most efficient way to introgress resistance and tolerance traits, which some might consider has the best overall aesthetic attributes.

A second devastating disease, powdery mildew, reached epidemic levels in 1994. Caused by the ascomycete fungi *Erysiphe pulcrha* Cooke & Peck and *Phyllactinia guttata* (Wellr:Fr) Lev., this disease caused tens of millions of dollars worth of losses to nursery growers within the first years of its epidemic (Li et al., 2009). While typically not lethal to older, established trees, powdery mildew can dramatically decrease aesthetic value and can only be prevented by expensive fungicide applications. This additional cost is something many homeowners, landscapers and botanical gardens will not consider for ornamental trees. Powdery mildew not only makes long-term care of established trees in the landscape more difficult but it is lethal to young seedling trees, the protection of which in the nursery setting spurs a significant increase in overhead cost. Pre-epidemic cost per acre for disease management and control for dogwood nursery production was

approximately \$120/ha/year. Post-spread of powdery mildew, the same costs are now estimated at \$1975/ha/year, an increase of more than 1,500% mainly due increased fungicide regimens (Li et al., 2009).

Similar to studies on dogwood anthracnose, genetic studies *E. pulchra* indicate a narrow genetic base suggesting a single introduction event into North America (Li et al., 2009). Both *C. florida* and *C. nuttallii* show varying levels of susceptibility, while *C. kousa* is generally resistant (Li et al., 2009). It is likely that Kousa dogwoods co-evolved with *E. pulchra* and naturally acquired increased levels of resistance to this disease (Li et al., 2009). Fortunately, because of this fact, Dr. Orton and the program at RU was poised to handle this new introduction of a disease organism.

There currently exists very few *C. florida* cultivars that are resistant or tolerant to powdery mildew. Only four known cultivars ('Jean's Appalachian Snow', 'Kay's Appalachian Mist', 'Karen's Appalachian Blush' and 'Appalachian Joy'), all white-bracted varieties, display resistance to powdery mildew (Li et al., 2009), and this resistance may not hold up uniformly across all regions (Molnar, personal communication, 2016). The very popular pink-bracted cultivar 'Cherokee Brave' was once considered resistant but resistance seems to have broken down or was not widely tested (Hagan et al., 1998; Windham et al., 2005). The *Cornus* × *rutgersensis* cultivars 'Rutgan' Stellar Pink®, 'Rutfan' Stardust®, 'Rutdan' Galaxy®, 'Rutcan' Constellation®, 'Rutban' Aurora® and 'Rutlan' Ruth Ellen® all display moderate to high levels of

resistance (Lie et al., 2009; NC). However, studies have shown that resistance does vary depending on location (Ranney et al., 1995).

At the time of this publication, the program at Rutgers has released 15 cultivars: 8 *Cornus* × *rutgersensis* hybrids, 3 *Cornus* × *elwinortonii* hybrids, 3 *C. florida* and 1 *C. kousa* cultivar (Table 1). Recent releases include the cultivar *Cornus* × *rutgersensis* ‘KF111-1’ Hyperion® in 2011 and *Cornus* × *elwinortonii* ‘KN144-2’ Rosy Teacups® in 2013, both highly tolerant to powdery mildew (Figure 3; Figure 4). In 2008, Dr. Orton retired but his ornamental tree-breeding work was continued by Dr. Thomas Molnar with a focus remaining on breeding big-bracted dogwoods.

Currently the Rutgers program contains an estimated 5,000 advanced generation hybrids in the field undergoing evaluation and selection, many with complicated and/or incomplete pedigree records. To support and bolster breeding efforts, there is an essential need to clarify and confirm known pedigree records, as well as to identify male parents of important accessions derived from open-pollination events. The level of genetic diversity in the germplasm collection is unknown and may potentially be low in some breeding lines due to only a few F<sub>1</sub> inter-specific hybrids being fertile and them subsequently being used as the foundation of later breeding efforts. This level of genetic diversity needs to be assessed to support future success of the program especially in terms of avoiding a narrowing of the *Cornus* spp. gene pool.

Achieving plant-breeding goals can take many selections across multiple generations. For BB-dogwoods, a single generation can take 3-5 years to flower when grown from seed and from this time another 3-10+ years to make proper ornamental evaluations including clonal propagation and testing in multiple locations. Thus, significant improvements can take a breeder an entire lifetime. This can easily be seen when examining the dogwood breeding history at Rutgers. It took nearly 30 years for the first hybrid cultivars, known as the Stellar Series®, to be fully evaluated, patented and released.

Challenges with tree breeding go beyond generation times. The large size of trees limits the population size that can be grown and makes field maintenance challenging.

Germplasm storage is expensive especially because collections are stored as living material usually in the field. Long-term storage of seeds is frequently not possible due to decreasing seed viability over time (Reed, 2005), and the outcrossing nature negates the benefits of this mode of germplasm storage. Pathogen screening is also a challenge for tree species since many environmental factors influence disease spread and severity.

Dogwoods, like many tree species, are highly heterozygous, self-incompatible (gametophytic) and extremely sensitive to inbreeding (Orton, personal communication; Reed, 2004).

Intra- and inter-specific hybrids have long been used in breeding to create novel, vigorous offspring. Hybrids are especially important in horticulture and ornamental tree breeding where genetic bases can sometimes be narrow, generation times are very long, and where novel phenotypes are desired by the nursery and landscape industry as well as



homeowners and other clientele. The creation of inter-specific hybrids allowed Dr. Orton to introgress novel bract shape, bract color and leaf shape and color into a population. The difficulty in creating inter-specific hybrids is three-fold: temporal isolation, spatial isolation and genetic incompatibility. In the dogwood breeding program, spatial isolation was overcome by inter-planting the different species in the same fields and greenhouses. The two main hurdles Dr. Orton faced were temporal isolation and genetic incompatibility.

To overcome temporal isolation Dr. Orton applied two techniques. By manipulating greenhouse temperatures and utilizing cold rooms, *C. kousa*, *C. florida* and *C. nuttallii* could be made to have overlapping flowering times. While dogwood pollen does not store well (Craddock et al., 2000), Dr. Orton managed to store enough pollen to make successful inter-specific crosses (personal communication). *C. florida*, *C. kousa* and *C. nuttallii* all have very similar genome sizes approximately 1.58pg, 1.92pg and 1.70pg respectively, and are all considered to be closely related (Shearer and Ranney, 2013). Even with these similarities, Dr. Orton faced many challenges when trying to recover hybrid offspring. He made 1000s of hand crosses, and although there are seed viability issues (many hybrid seeds failed to germinate), through his persistence he obtained viable seeds and grew them on for evaluation. He also found that many hybrid offspring were sterile, therefore limiting the number of viable F<sub>1</sub> hybrid parents to continue breeding, although not being of consequence when deciding to release new cultivars (all of his releases are sterile except Rosy Teacups® and Hyperion®). Since only a few fertile F<sub>1</sub>

hybrids were used to breed later generations of crosses, it is unknown at this time if a genetic bottleneck is present in some of the breeding lines at Rutgers.

Current industry and homeowner demand is for dark pink-bracted *C. kousa*-type cultivars, since none exist and all the available red-bracted *C. florida* are susceptible to powdery mildew. Breeding objectives at RU and UT reflect this desire, and a concerted effort to develop this type of plant has been going on for almost five decades with recent success. Rutgers filed a US patent application in August 2015 for its newest release, a dark pink-bracted *C. kousa* named ‘Rutpink’ Scarlet Fire™. This is the first *C. kousa* cultivar to be released from Rutgers and to this author’s knowledge is the first Kousa dogwood in the horticultural trade with floral bracts that remain dark pink even in the hot spring temperatures of the eastern US. Other pink or “red” kousa dogwoods like ‘Satomi’, ‘Rosea’, and ‘Beni Fuji’, while sometimes expressing dark pink colors in the Pacific Northwest, tend to be light pink to almost white in many years in the eastern US, which has been attributed largely to the high air temperatures during bloom period (late May in central New Jersey).

### **Molecular Tools**

The development of molecular breeding tools, such as molecular markers, for ornamental plant species lags behind agronomic crops. The first molecular markers developed for a plant species were iso- and allozymes. Eventually, molecular markers shifted toward DNA with the advent of restriction fragment length polymorphisms (RFLPs) and better understanding of the structure and function of DNA. RFLPs, random amplified

polymorphic DNA (RAPDs) and amplified fragment length polymorphisms (AFLPs) gave way to simple sequence repeats (SSRs) and eventually SSRs gave way to single nucleotide polymorphisms (SNPs; Sclötterer, 2004). With the rapid decline in price for genome sequencing, marker systems based on SNPs have become more and more commonplace; however, their development and use for ornamental crops is only in the early stages of development. SNPs have been discovered and characterized in a few tree species such as plum blossom (*Prunus mume*), and sycamore (*Platanus occidentalis*; Lee et al., 2012; Sun et al., 2014). There are no SNP markers developed for BB-dogwoods. In 1998, DNA amplification fingerprinting and arbitrary signatures from amplification profiles (ASAP) were used to genotype the *C. florida* cultivars ‘Barton’ and ‘Cloud 9.’ Along with phenotypic data, the authors concluded that these two cultivars were actually the same genotype (Windham and Trigiano, 1998). In contrast, the first genetic diversity analysis of *C. florida*, completed in 1999, showed that these two cultivars are separate, distinct genotypes (Caetano-Anolles et al., 1999). Using arbitrary DNA sequence primers, this study genotyped a collection of *C. florida* cultivars and breeding lines that included white and pink bracted accessions, anthracnose resistant cultivars and a pseudo-testcross population. Their approach using a pseudo-testcross population and DNA amplification fingerprinting (DAF) allowed this group to generate the first suitable molecular markers for dogwood. Another study using DAF and ASAP along with phenotypic characteristics failed to distinguish between three red-bracted *C. kousa* cultivars: ‘Rosabella’, ‘Satomi’ (synonymous with ‘Miss Satomi’) and ‘Heart Throb’ suggesting that these three cultivars were actually the same genotype (Trigiano et al., 2004).

Manual, controlled dogwood crosses are labor intensive and generally ineffective. Most available dogwood cultivars, besides those developed at Rutgers, are selections made from seedling populations grown in nursery rows or unique seedling trees discovered in wild populations or landscape planting (not from controlled breeding efforts). Being self-incompatible, these seedlings (cultivars) are derived from open-pollinations, which equates to incomplete pedigree records, in the best-case scenario. Many selections are of unknown origin, being ultimately selected from seed lots that may not have contained much provenance information (Capiello and Shadow, 2005; Dirr, 2009; Hillier, 2002). Genotyping was shown to be useful in identifying male pollen donors in dogwood (Ament et al., 2000). It was also shown that physically isolating dogwoods with overlapping flowering times is a good way to control pollen-flow; ‘semi-controlled’ crosses can be made by planting the two desired parent trees away from other dogwoods. In Rhoades et al (2011), 87% of all seedlings from a tree came from pollen donated from the nearest trees 3 m away. A recent paper using SSR markers to track pollen flow found that the range for successful pollination extends beyond 11 m. This longer distance was partly attributed to the identification of adrenid and halictid bees pollinating the trees, which have longer ranges than cerambycid beetles previously thought to be the only pollinators of *C. florida* (Orton, personal communication; Rhoades, et al., 2011). This study also suggests that the timing of stigma receptivity and pollen-incompatibility are other important factors in pollen-flow. Taking both of these factors into consideration, the authors suggest that ‘open-pollinated controlled crosses’ can still be accomplished and the use of SSR markers to identify seedlings from ‘off-type’ male pollen is an easy and efficient way to avoid labor-intensive controlled crosses (Rhoades et al., 2011).

It was shown that a molecular marker based dichotomous key could be used to accurately identify cultivars and breeding lines with a high-level of accuracy (Smith et al., 2007). Using AFLPS, they distinguished between six out of seven unlabeled dogwood samples tested.

Microsatellite molecular markers were first developed for *C. florida* in 2001 (Cabe and Spencer-Liles, 2001). The alleles per loci were highly variable, containing a mean of 9.25 allele/loci and mean heterozygosity of 0.84. Later, 825 SSR markers for *C. florida* and 86 SSR markers for *C. kousa* were developed by Wang et al. (2008) and Wadl et al. (2008b), greatly improving access to molecular tools for dogwoods. Of the 825 *C. florida* markers, 218 showed polymorphisms between ‘Appalachian Spring’ and ‘Cherokee Brave’ and were thus considered informative. After eight *C. kousa* markers were optimized, they provided informative polymorphic genotype data for 22 *C. kousa* cultivars. These same microsatellite markers, developed at the University of Tennessee, were also used to develop a key to identify cultivars and breeding lines (Wadl et al., 2008a). Four *C. florida* loci (CF213, CF581, CF585 and CF597) were used in the development of the identification key that successfully identified 18 of 24 unlabeled dogwood samples. Six *C. kousa* loci were used to create an identification key that successfully identified all 22 unlabeled cultivars.

The same microsatellite markers were used to develop the first genetic linkage map of *C. florida* (Wang et al., 2009). Using a pseudo-F<sub>2</sub> mapping strategy, the highly heterozygous and out-crossing nature of flowering dogwood was overcome to develop a suitable

population for genetic mapping. The pseudo-F<sub>2</sub> mapping population has advantages over typical F<sub>2</sub> mapping populations in that one parent does not need to be heterozygous and the other homozygous. It also does not require prior knowledge of segregation phases. Drawbacks to this system are that more molecular markers are needed. Also some useful loci will be lost because the F<sub>1</sub> full-sibs may not share the same loci (Wang et al., 2009). From the 825 loci, only 271 were available for map construction. A total of 255 (94.1%) of these markers were found to be located on the 11 linkage groups (LG). The total genetic distance of all the LG was 1,175 cM with an average distance of 4.6 cM between loci. These LGs covered 93.6% of the estimated 1255.9 cM genome of flowering dogwood (Wang et al., 2009; Chakravarti et al., 1991). Some clustering of loci appeared in the genetic map, which is unusual for SSR markers, but was likely due to a small mapping population size. This genetic map set the groundwork for further saturation of the genetic map with more markers and should allow for easier identification of genes of interest in the genome.

A cross-species analysis involving 36 SSRs isolated from both *C. florida* and *C. kousa* were tested on 18 *Cornus* species to elucidate the cross-species transferability (Wadl et al., 2010a). For the *C. florida* SSRs, 10 out of 17 amplified in 60% or more of the species, and 11 out of the 19 for the *C. kousa* SSRs (Wadl et al., 2010a). The resulting phylogenetic tree agreed with previous phylogenetic study of *Cornus* taxa based on ITS and matK sequences providing support for the utility of the SSR markers. Sequencing of the SSR primer sites also showed that more closely related species had conserved sequences at these locations (Xiang et al., 2006; Wadl et al., 2010a).

SSR markers developed for *C. florida* were used along with the amplification and sequencing of seven regions on the *C. nuttallii* chloroplast genome (cpDNA) to analyze the genetic diversity of wild populations of this species. It was found that for both microsatellite loci and cpDNA there is uniformly low genetic diversity. Past studies along with this provide strong evidence that this species has lower levels of genetic diversity than most tree species (Keir et al., 2011). Phenotypic variation among populations was also fairly low; however, within population phenotypic variation is high. Populations in Idaho and southern California are of the highest priority for genetic conservation because of extremely low diversity, high genetic differentiation and sensitivity to a changing climate (Keir et al., 2011).

Molecular markers are very useful tools for identifying regions on the genome where traits of interest may lie. One such trait for dogwoods is dark pink bracts. Because of the long generation time of BB-dogwoods and associated expense of growing out large populations, it is challenging to study the genetics of bract color. Pink colors in plants are generally due to anthocyanin accumulation and many times anthocyanin accumulation in one part of the plant is indicative of accumulation in other parts (NC). Red and pink bract color is generally associated with red pigmentation in the leaves (Orton, personal communication). Red pigmentation in the leaves is much quicker to evaluate than bract color. A QTL study was done to identify regions of the genetic map that are associated with red pigmentation in the leaves (Wadl et al., 2011). Four loci (CF309C [LG3], CF792A [LG6], CF367B [LG8] and CF367C [LG8]) were identified as significantly associated with red-foliage color.

Using 18 SSR loci the genetic diversity of *C. florida* populations in the Great Smoky Mountains National Park (GSMNP) was analyzed. It was found that even after the severe dogwood anthracnose epidemic genetic diversity is high. Within-population genetic diversity is high and there is a subtle yet significant difference between the two main populations that are divided by the main dividing ridge of GSMNP (Hadziabdic et al., 2012).

Dogwoods have also yet to be utilized in many genomic studies. Only a handful of studies have been published on the bioinformatics and genomics of dogwoods. One such paper, using primers designed to amplify the four different NBS-type motifs commonly found in R-genes, found 11 putative R-genes located in the *C. florida* genome (Shi et al., 2008).

*De novo* 454 sequencing of inflorescence transcriptomes of *C. canadensis* and *C. florida* was completed in order to build the foundation for future genome sequence work and to identify putative gene and gene differences between the two species. The ccTranscriptome of *C. canadensis* was the first reference transcriptome for this genera and can be used to identify putative genes and interspecific SNPs. The authors proposed that *C. florida* lacks the expression of the *C.canadensis*\_transcriptome\_contig3886, a homolog of the *Arabidopsis* ER (ERECTA) gene, which plays a role in inflorescence structure, resulting in the head-like inflorescence architecture found in the BB-dogwoods. They report multiple genes that are differentially expressed between *C. canadensis* and *C. florida* that are homologous to inflorescence architecture genes in *Arabidopsis* potentially



explaining the different inflorescence structures in the *Cornus* genera. Putative orthologs of 27 out of the 41 reported inflorescence architecture related genes in *Arabidopsis* were found in the *C. canadensis* and *C. florida* transcriptomes. The well-known regulators of flowering and inflorescence development, SOC1, FUL, KNAT1, KNAT6 and LFY are among the orthologous genes found suggesting that inflorescence architecture development and flowering are conserved between *Arabidopsis* and *Cornus* spp. This study reported SNPs discovered for dogwoods, a total of 65931 high quality SNPs distributed among 2542 unigenes. With this development, high-density genetic maps can be created (Zhang et al., 2013).

An exciting development was the approval of a NSF grant to sequence the genome of *C. florida* ‘Appalachian Spring’ in April, 2015

([http://www.nsf.gov/awardsearch/showAward?AWD\\_ID=1444567](http://www.nsf.gov/awardsearch/showAward?AWD_ID=1444567)). The project is expected to publish a high-quality reference assembly and annotated genome. It also expects to publish a transcriptome atlas and a high-density molecular marker database. At the completion of this project, a strong foundation will have been laid for breeding programs such as the one at Rutgers University to employ marker-assisted selection and other techniques to further improve BB-dogwoods in a more efficient manner.

## **Objectives**

- 1) Generate the first botanical descriptions and formally name the two hybrid dogwoods developed by the Rutgers University BB-dogwood breeding program to facilitate scientific and horticultural communication.

- 2) Analyze the genetic diversity of the current germplasm collection at Rutgers University in order to study relationships and clarify pedigree records where possible.

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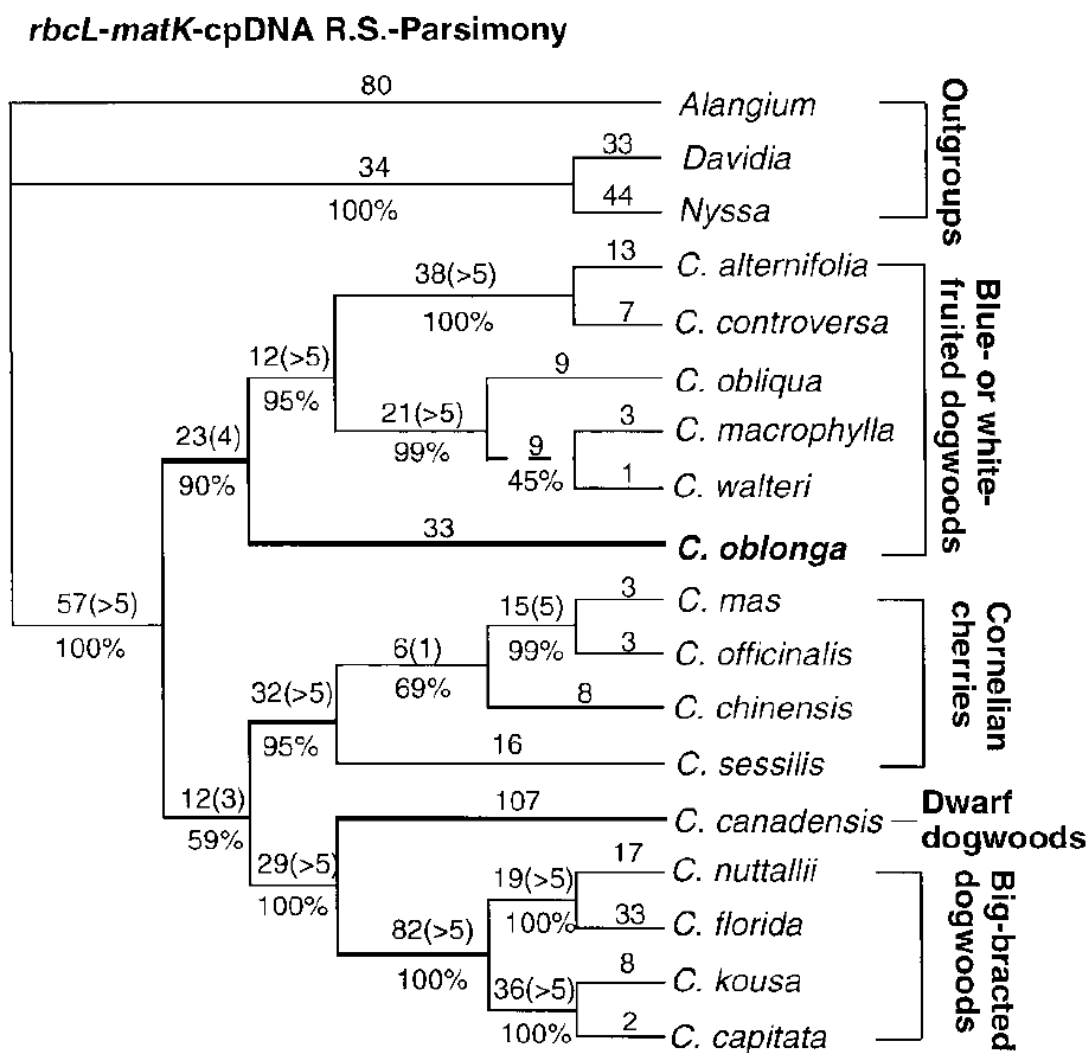
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## Figures

**Figure 1.** Dogwood Phylogeny. Parsimonious tree generated from a phylogenetic analysis of combined data of *rbcL* and *matK* sequences and cpDNA restriction site data for *Cornus* (length 5 845, consistency index 5 0.707, excluding uninformative characters, and retention index 5 0.823). Base substitutions are found above the branches; bootstrap values are below branches and decay values are found in the parentheses. (modified from Xiang et al., 2006).





**Figure 2.** Close-up of the inflorescence head of two species of dogwood. **A** *C. florida* ‘Sweetwater Red’ **B** *C. kousa* ‘K2’



**Figure 3.** *Cornus* × *rutgersensis* cultivars developed and released from Rutgers University. **A** Original ‘Rutlan’ Ruth Ellen® tree (~10m) in a field at Rutgers Gardens, **B** Close-up of the inflorescence head and bracts of ‘Rutfan’ Ruth Ellen®, **C** Close-up of inflorescence head and bracts of ‘Rutfan’ Stardust®, **D** Close-up of inflorescence head and bracts of ‘Rutgan’ Stellar Pink®. Note the pink color in the bracts.



**Figure 4.** *Cornus* × *elwinortonii* cultivars developed and released from Rutgers University. **A** Original ‘KN30-8’ Venus® tree, **B** Close-up of inflorescence head and bracts of ‘KN30-8’ Venus®, **C** Close-up of inflorescence head and bracts of ‘KN4-43’ Starlight®, **D** Close-up of inflorescence head and bracts of ‘KN144-2’ Rosy Teacups®





## Tables

**Table 1.** Rutgers Cultivar Releases. The ‘coded’ cultivar name, trademark name, patent year and number, species and pedigree record of all Rutgers University dogwood releases. Rutgers has released 10 *Cornus x rutgersensis* cultivars, 3 *Cornus x elwinortonii*, 3 *C. florida* cultivars and 1 *C. kousa* cultivar. \*Patent application process still underway. †Plant patents expired.

<b>Cultivar Name</b>	<b>Trademarked Name</b>	<b>Year Patented</b>	<b>Patent Number</b>	<b>Species</b>
<b>‘Rutgan’</b>	Stellar Pink®	1990	Plant 7,207†	<i>Cornus × rutgersensis</i>
<b>‘Rutdan’</b>	Celestial®	1990	Plant 7,204†	<i>Cornus × rutgersensis</i>
<b>‘Rutlan’</b>	Ruth Ellen®	1991	Plant 7,732†	<i>Cornus × rutgersensis</i>
<b>‘Rutcan’</b>	Constellation®	1990	Plant 7,210†	<i>Cornus × rutgersensis</i>
<b>‘Rutban’</b>	Aurora®	1990	Plant 7,205†	<i>Cornus × rutgersensis</i>
<b>‘Rutfan’</b>	Stardust®	1990	Plant 7,206†	<i>Cornus × rutgersensis</i>
<b>‘KN30-8’</b>	Venus®	2006	PP16,309 P3	<i>Cornus × elwinortonii</i>
<b>‘KN4-43’</b>	Starlight®	2006	PP16,293 P3	<i>Cornus × elwinortonii</i>
<b>‘D-376-15’</b>	Red Beauty®	1993	Plant 8,214	<i>C. florida</i>
<b>‘D-184-11’</b>	Wonderberry®	1993	Plant 8,213	<i>C. florida</i>
<b>‘Rutnut’</b>	Red Pygmy®	2004	PP15,219 P2	<i>C. florida</i>
<b>‘KF111-1’</b>	Hyperion®	2011	PP22,219 P3	<i>Cornus × rutgersensis</i>
<b>‘KF1-1’</b>	Saturn®	2007	PP17,768 P3	<i>Cornus × rutgersensis</i>
<b>‘KN144-2’</b>	Rosy Teacups®	2014	PP26211 P3	<i>Cornus × elwinortonii</i>

<b>Cultivar</b>	<b>Trademarked</b>	<b>Year</b>	<b>Patent</b>	<b>Species</b>
<b>Name</b>	<b>Name</b>	<b>Patented</b>	<b>Number</b>	
<b>'Rutpink'</b>	Scarlet Fire™	2015*	Patent Process	<i>C. kousa</i>
			Pending	

## Chapter 1

### *Cornus* × *elwinortonii* and *Cornus* × *rutgersensis* (Cornaceae), new names for two artificially produced hybrids of big-bracted dogwoods

#### Abstract:

Big-bracted dogwoods (*Cornus* sp.) are well-known plants in North America and eastern Asia where they occur as wild, generally spring-flowering understory trees. They are also popular ornamental landscape plants, and many economically important cultivars are propagated and sold across North America, Europe, and Asia. Starting in the late 1960s, Elwin Orton of Rutgers University in New Jersey (USA) utilized three geographically disjunct species of dogwoods, *C. florida* (eastern North America), *C. nuttallii* (western North America), and *C. kousa* (East Asia), in an extensive interspecific hybridization program. He was successful in developing the first-ever interspecific F<sub>1</sub> hybrids of these species, several of which have become staple items in the ornamental nursery trade due to their enhanced ornamental qualities and resistance to diseases. The original F<sub>1</sub> plants are still alive at Rutgers University. While they have been available for decades in horticultural commerce, the interspecific hybrid crosses were never formally described and their scientific hybrid names were never published. For the *C. kousa* × *C. florida* hybrids, the name *Cornus* 'rutgersensis' has been used on occasion in the horticultural trade, but without proper citation and description. Here, it is formally named *Cornus* × *rutgersensis* Mattera, T. Molnar, & Struwe, **hybr. nov.** For the *C. kousa* × *C. nuttallii* hybrids, no previous name has been used, and it is hereby named *Cornus* × *elwinortonii* Mattera, T. Molnar, & Struwe, **hybr. nov.** The need for providing scientific names for

commonly used horticultural hybrids is discussed. Holotype material for both hybrid names was collected from the original F<sub>1</sub> hybrids for full documentation, typification, and description. The comparative intermediate development of leaves, inflorescence structures, and fruit types of the hybrids and their parents is discussed and illustrated. Etymology, phenology, and cultivation aspects of these hybrids and their cultivars including backcrosses to *C. kousa* are also presented.

**Keywords:**

Cornaceae, East Asia, horticulture, hybridization, nomenclature, North America.

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## Introduction

The circumboreal genus *Cornus* L. (Cornaceae, Cornales; APG III 2009) contains about 60 species divided into ten subgenera (Fan and Xiang 2001). Species in this genus express a wide variety of morphologies, from low herbaceous ground covers, such as the boreal-temperate species *C. suecica* L., to multi-stemmed shrubs, such as *C. sericea* L. It also includes small to large trees, such as *C. kousa* Buerger ex Miq. and *C. nuttallii* Audubon ex Torr. & A.Gray, the latter of which can grow up to 24 m tall. Some taxonomists have divided the genus up into six genera, but molecular studies have shown that *Cornus* in the current circumscription is monophyletic (Xiang et al. 2006).

Several species of *Cornus* have large, showy petaloid bracts located under tight head-like, multi-flowered inflorescences. These species form the monophyletic big-bracted (BB) clade sensu (Xiang et al. 2006), and are mostly spring-flowering trees of North American and East Asian forests. The members of this clade are classified into three different subgenera: *Cynoxylon*, *Discocrania*, and *Syncarpea* (Xiang et al. 2006). The most commonly known big-bracted species in North America are *C. florida* L. and *C. nuttallii* of subgenus *Cynoxylon* and *C. kousa* of subgenus *Syncarpea*. Seed and clonally propagated big-bracted dogwoods are popular ornamental landscape trees in subtropical to temperate regions around the world. Their most conspicuous characteristics are their large, white or red petaloid floral bracts, showy red fruits, and brightly colored fall foliage (Li et al. 2009). *Cornus kousa* can be easily distinguished from the other two species by its round, fleshy multiple fused fruits formed from a whole flower head (as opposed to single, separate drupes from each flower arranged in clusters). It can also be



identified by its acute or acuminate floral bracts, whereas the others have bracts that are rounded or retuse (Harrison 2009).

Typical horticultural uses of the big-bracted dogwoods include container, specimen, or shade plantings in suburban landscapes, display gardens, and parks (Gilman and Watson 1993a, b, Mohlenrock 2006). In the eastern and southeastern USA, *Cornus florida* is a common component of native deciduous forests, gardens, and home landscapes. It is among the first trees to bloom with conspicuous flowers in the spring in North America, with a range of cultivars available that express dwarf to vigorous growth habits and white, pink or red floral bracts. *Cornus kousa* is also a common component of ornamental landscapes in the eastern USA. It blooms about a month later than *C. florida* (after the leaves have developed), has a more vase-shaped growth habit, and most have white floral bracts, although a few forms with light pink bracts exist (Cappiello and Shadow, 2005, Dirr 2009, Rhoades et al. 2011). The use of *C. nuttallii* in landscaping is much more limited than the former two species, due to limited winter hardiness in the eastern USA and it is cultivated mostly in the Pacific Northwest (USA), where it is native. Dogwood sales in the USA account for over 11% of the total deciduous flowering tree market, amounting to nearly 31 million USD in 2009 (Fulcher et al. 2012, NASS 2007).

The Rutgers University dogwood breeding program began in 1965 under the direction of horticultural plant breeder Dr. Elwin Orton. The early goals of the program were to develop novel cultivars of *Cornus florida* and *C. kousa* with improved aesthetic qualities, including pink and red floral bracts, unique growth habits, and superior disease

resistance. Several years after the program started, attention was turned toward developing interspecific hybrids between these two species as well as between *C. kousa* and *C. nuttallii*, to help reach these goals (Elwin Orton personal communication). Because of differences in flowering times between the species, which can span more than a month, Orton used two approaches to make the hybrid crosses. First, he collected, dried, and stored pollen from earlier flowering plants to apply to the stigmas of those that bloomed later in the field and greenhouse. Second, he manipulated bloom times through the careful use of cold chambers and warm greenhouses to artificially break dormancy and match flowering times of container-grown plants to those in the field (E. Orton personal communication). Orton was ultimately successful in his interspecific hybridization attempts and is credited as being one of the first to create *C. florida* × *C. kousa* and *C. kousa* × *C. nuttallii* F<sub>1</sub> hybrids (Dirr 2009). To date, eleven interspecific cultivars, comprising eight from *C. florida* × *C. kousa* crosses and three from *C. kousa* × *C. nuttallii* hybrids, have been named, released, and patented through the Rutgers University dogwood breeding program (Table 1). The two classes of interspecific hybrids display intermediate morphological and phenological characteristics between the parental species (Cappiello and Shadow 2005, Dirr 2009, E. Orton personal communication, Orton 1990a, 1990b, 1990c, 1990d, 1990e, 1991, 2014, Orton and Gant 1993a, 1993b, 2006a, 2006b, 2004, 2007, 2011). Many also show increased vigor (rates of growth) compared to their parent species, as well as improved stress tolerance.

According to the *International Code of Nomenclature for algae, fungi, and plants* (abbreviated hereafter as ICN), a hybrid between two plant species can be given two

types of scientific names to classify them within the taxonomic system of plant biodiversity (McNeill et al. 2012: Art. H1). Either the hybrid is listed with the name of the two parents separated by a multiplication ( $\times$ ) sign, such as in the oak hybrid *Quercus alba*  $\times$  *Quercus bicolor*, or they may be given a unique name with the species epithet preceded by a multiplication ( $\times$ ) sign, such as *Quercus*  $\times$  *jackiana* for the same hybrid (Haines 2011). For hybrids in horticulture and commerce, the second option is preferred since it provides a simpler name that is easier for horticulturalists and the public to learn, catalogue, use on labels, and remember. It also provides a scientific name that fits into existing databases already in use for commercial plants. For the two flowering dogwood hybrids discussed here, no formal scientific names have been proposed, although 'Cornus  $\times$  rutgersiensis' and 'Cornus  $\times$  rutgersensis' (sometimes without the multiplication sign,  $\times$ ) have been used in popular and horticultural literature for many years to indicate *Cornus florida*  $\times$  *Cornus kousa* hybrids (e.g., Gayraud 2013, Cubey et al. 2014; Shearer and Ranney 2013, Wikipedia 2014). Those names are currently invalid since, according to the ICN, all proposed scientific names, including hybrid names, require that they be formally published and described and be represented by a type specimen. A type specimen is the specimen to which the name is permanently attached and which is publicly available for consultation (McNeill et al. 2012).

We here propose the name *Cornus*  $\times$  *rutgersensis* for the hybrid *C. kousa*  $\times$  *C. florida*. We also propose a new name, *Cornus*  $\times$  *elwinortonii*, honoring our colleague Dr. Elwin Orton, for the hybrid he created between *C. kousa* and *C. nuttallii*. Full morphological descriptions, typification, illustrations, horticultural information with cultivar names,

disease response, and a discussion on the formation of intermediate morphological traits with regard to leaf size, inflorescence structure, and fruits are provided for each of these new names. In doing this, we provide both formal names and summarize information of general botanical interest of these popular garden plants for botanists and horticulturalists.

### **Taxonomic treatment**

**Cornus × elwinortonii** Mattera, T. Molnar, & Struwe, hybr. nov. (Orton's dogwood)  
Figs. 1-2.

**Diagnosis.** *Cornus* × *elwinortonii* is similar to both *C. kousa* and *C. nuttallii* but differs in its intermediate flower number per inflorescence and in its intermediate tree height. *Cornus* × *elwinortonii* has 55-80 flowers per head, whereas *C. kousa* has 20-60, and *C. nuttallii* has 70-100. *Cornus* × *elwinortonii* is also intermediate in plant height, with a maximum of 10 m height (*C. kousa* reaches 6 m height, while *Cornus nuttallii* is 12-23 m tall as a mature tree).

**Type.** USA. New Jersey: New Brunswick, Middlesex County, Ryders Lane, Horticultural Farm 1, original tree (ramet) of 'KN4-43' Starlight®, cultivated plant in open field adjacent to Rutgers Equine research farm, surrounded by hazelnut (*Corylus* spp.) trees planted in rows, GPS location (WGS84) 40.4676 N, -74.4281 E, 18 m, 17 May 2014, R. Mattera 33 (holotype: NY, isotypes: CHR, JEPS, MO, US, to be distributed).

**Description.** Tree with upright or rounded habit, 10 m in height at maturity. Bark rough, as sandpaper, with exfoliation at the base of the trunk; lenticels abundant,  $1.25\text{--}1.75 \times 0.40\text{--}0.65$  mm. Leaves opposite, simple, elliptic, ovate to obovate,  $10.3\text{--}15.3 \times 5.9\text{--}9.1$  cm; base attenuate to oblique; margin entire to slightly wavy, cuneate/crenate; apex apiculate; venation with 5 (or 6) pairs of secondary veins; midrib and abaxial surfaces with conspicuous indumentum of short, fine, downy, whitish beige trichomes with occasional dark tufts of longer brown trichomes in the axils of midvein and secondary veins, indumentum less dense on adaxial surfaces. Overwintering inflorescence buds not covered by the two outer opposing pairs of vegetative bracts, minimally covered by two inner opposing pairs of floral bracts (0-40% coverage; floral bracts more developed than in *C. kousa* during overwintering). Inflorescence capitate, globose, with 55–80 sessile flowers per head, subtended by 4 (rarely 5 or 6) simple entire, decussate pairs of bracts. Bracts petaloid at anthesis, ovate to lanceolate, sometimes wider than long, overlapping or not when fully developed, 5–8 cm long, 3.5–7.0 cm wide, usually white, or occasionally pink; base tapering to point of attachment; apex acuminate to cuspidate. Peduncle 1.5–8.0 cm long at time of flowering. Flowers actinomorphic, bisexual, 4-merous. Calyx lobes ovate; apex obtuse. Corolla lobes obovate, apex slightly acute. Stamens 4, exserted from corolla mouth, inserted in corolla lobe sinuses; filaments 1.5–2.5 mm long, 0.2–0.5 mm wide; anthers ovoid, base sagittate, longitudinally dehiscent,  $1.0\text{--}1.1 \times c. 0.25$  mm; pollen less prevalent on hybrids compared to parent species, white or yellow-brown. Gynoecium epigynous, with nectar disc; ovary syncarpous; style 1, 1.5–2.5 mm long, exserted from corolla; stigma indistinct, ca. 0.4 mm long. Fruit either many

drupes tightly compressed together, or a multiple fruit formed from 1-seeded drupelets forming a mounded raspberry-like fruit, often parthenocarpic.

**Parent source material.** The parents of the F<sub>1</sub> hybrid ('KN4-43' Starlight®) are *Cornus kousa* 'Simpson No. 1' (female), an unpatented cultivar received from Tennessee Valley Nursery (Winchester, TN, USA) and planted at Rutgers Gardens (New Brunswick, NJ) on 16 April 1970, and *C. nuttallii* 'Goldspot' (male), received from Alfred Teufel Nursery (Portland, OR, USA) and planted in 1972.

**Ecology and Phenology.** In New Jersey, *Cornus* × *elwinortonii* flowers during May and June, and the fruit matures from September to October. Various beetles and bees visit the flowers at anthesis, with an abundance of goldenrod soldier beetles (*Chauliognathus pensylvanicus*) frequently observed by the authors. The mostly sterile fruit with little pulp generally senesces and falls from the trees by October. The few fruits with a developing seed are swollen and have more pulp. We suspect they are eaten by insects and birds.

**Etymology.** The epithet, *elwinortonii*, honors the prominent dogwood breeder Dr. Elwin Orton (b. 1930), Professor Emeritus in the Department of Plant Biology and Pathology at Rutgers University. He was the first to successfully develop and release a hybrid between *Cornus kousa* and *C. nuttallii*. We propose the common name, Orton's dogwood, for this hybrid.

**Distribution.** *Cornus* × *elwinortonii* is known only from cultivation, although at times it produces viable seeds. The natural range of the staminate parent, *C. nuttallii*, is in

western North America from the lowlands of British Columbia (Canada) to southern California (USA), with a small isolated population in northern Idaho (USA, Keir et al., 2011, Klinka et al., 2000). The other parent, *C. kousa*, is native to mesic forests of Japan, Korea and China (Flint, 1997, Xiang and Boufford 2005). *Cornus nuttallii* cannot withstand sustained periods of frost, thus limiting its natural and cultivated range. In contrast, *C. kousa* can be cultivated throughout much of the USA; Europe, and Asia in U.S. Department of Agriculture cold hardiness zones 6a-9a (Daly et al. 2012, Flint 1997). The hybrid *C. × elwinortonii* can survive sustained frosts and has a similar climate range as *C. kousa*. However, for some cultivars of *C. × elwinortonii* the floral buds are less cold hardy than in the parent *C. kousa*. In colder climates, including in New Brunswick, NJ, where the hybrid originated, flower buds can be damaged by cold winter temperatures, leading to a reduced floral bract display in the spring (E. Orton personal communication).

**Horticulture.** Plants of *Cornus × elwinortonii* are grown as landscape ornamentals and can be cultivated wherever *C. kousa*, *C. nuttallii*, and *C. florida* may be grown. This hybrid is cultivated for its all-year round appeal: floral bracts, attractive foliage, autumn color and appealing bark (Eberts 2007). *Cornus × elwinortonii* is typically propagated asexually through budding and grafting on seedling rootstocks of *C. kousa* or *C. florida*. Patented and trademarked cultivars that belong to this hybrid include 'KN4-43' Starlight® (F<sub>1</sub>), 'KN 30-8' Venus® (first backcross to *C. kousa*), and 'KN144-2' Rosy Teacups® (third serial backcross to *C. kousa*; Table 1). We know of no other commercially available cultivars of *Cornus × elwinortonii*.

**Disease Response.** While dogwood anthracnose caused by the fungus *Discula destructiva* Redlin is known to infect and kill *C. nuttallii*, it has not been reported to be a significant problem on either *C. kousa* or *C. × elwinortonii* (Daughtrey and Hibben, 1994; Fulcher et al., 2012; Hagan et al., 1998).

**Additional material provided.** Additional collections from the same individual as the holotype specimen, but on different dates (*R. Mattera 27*, *R. Mattera 29*, *R. Mattera 31*, and *R. Mattera 35*) will all be deposited at CHRB, NY, and MO).

**Cornus × rutgersensis**, Mattera, T. Molnar & Struwe, hybr. nov. (Rutgers' dogwood)  
Figs. 3-5.

**Diagnosis.** *Cornus × rutgersensis* is similar to *C. kousa* and *C. florida*, but differs in its intermediate leaf size and fruit aggregation and size. *Cornus × rutgersensis* has leaves 9.0–16.8 × 4.2–9.1 cm, whereas the leaves of *C. kousa* are 5.1–10.2 × 2.0–5.0 cm and for *C. florida* 7.6–15.2 × 2.0–7.0 cm). *Cornus × rutgersensis* forms many single-seeded parthenocarpic drupes 0.5 × 0.3 mm wide, but does not form a multiple fruit as in *C. kousa*. *Cornus florida* has larger, fertile drupes 13.0–18.0 × 6.0–9.0 mm.

**Type.** USA: New Jersey: New Brunswick, Middlesex County, Ryders Lane, Rutgers Gardens, original tree (ramet) of 'Rutgan' Stellar Pink®, cultivated plant in open grass field behind Rutgers Ornamental Horticultural Field lab, adjacent to a pine tree windscreen, GPS (WSG84) 40.4732 N, -74.4238 E, 22 m, 25 May 2014, *R. Mattera 34*,



holotype (NY), isotypes (CHRB, JEPS, MO, US, to be distributed).

**Description.** Trees with upright or rounded habit,  $F_1$  hybrids cultivated at Rutgers range from 3–10 m in height at maturity. Bark smooth when young, light gray to brown older bark exfoliating; lenticels on young bark abundant,  $0.5\text{--}0.7 \times 0.3\text{--}0.4$  mm. Leaves opposite, simple, ovate to elliptic,  $9.0\text{--}16.8 \times 4.2\text{--}9.1$  cm; base attenuate, cuneate-crenate to oblique; margin entire to moderately wavy; apex apiculate or acuminate; with 5 pairs of secondary veins; abaxial surface smooth; indumentum of many white trichomes on both surfaces, abaxial margin with many white trichomes, with dark tufts of trichomes along midrib and veins. Overwintering inflorescence buds intermediate in size and developmental structure between the parents. Outermost vegetative bracts barely covering the inflorescence; inner two pairs of floral bracts enclosing flower head; unlike in either parent, floral bracts covering only 10–45% of the flower head. Occasionally full coverage of the flowers can be seen. Inflorescence capitate, globose, with 30–50 flowers per head, surrounded by 4 floral bracts; floral bracts sessile, entire, in decussate pairs, petaloid at anthesis, ovate to lanceolate, sometimes wider than long, overlapping or not;  $4.0\text{--}6.5 \times 3.0\text{--}6.0$  cm, white or pink; base tapering to point of attachment, apex acuminate to cuspidate. Peduncle 3.5–7.5 cm long at time of flowering. Flowers actinomorphic, bisexual; 4-merous. Calyx lobes ovate, acute. Corolla lobes obovate, slightly acute. Stamens 4, exserted, inserted in corolla lobe sinuses; filaments 2.7–4.5 mm long, 0.2–0.3 mm wide; anthers longitudinally dehiscent,  $0.4\text{--}2.0 \times 0.5\text{--}0.8$  mm; pollen yellowish brown. Gynoecium epigynous, with nectar disc; ovary syncarpous; style 1, inserted to exserted from corolla mouth,  $1.5\text{--}1.9 \times 0.3\text{--}0.5$  mm; stigma slightly capitate, c. 0.25 mm

long. Fruit single drupes, rarely fused into a multiple fruit; fruits often formed without proper seed development (i.e., sterile fruits), if fertile, then 1-seeded.

**Parent source materials.** The parents of the described type F<sub>1</sub> hybrid ('Rutgan' Stellar Pink®) are *Cornus kousa* K2 (female) grown at Rutgers Gardens from a seedling received from Ben C. Blackburn, Willowwood Arboretum (Gladstone, NJ) in May of 1949, and *C. florida* 'Sweetwater Red' (male), received from Boyd Nursery (McMinnville, TN) and planted at Rutgers Gardens.

**Ecology and Phenology.** *Cornus × rutgersensis* flowers in New Jersey (USA) in May; the fruits mature from September to October. Adrenid and halictid bees and cerambycid beetles pollinate the flowers of *C. kousa* while only adrenid and halictid bees pollinate *C. florida* (Rhoades et al. 2011). It is believed that the same insects visit the flowers of the hybrid. All cultivars released to the public, except 'KF111-1' Hyperion® (first backcross to *C. kousa*), are sterile. Sterile specimens produce very little pulp in the fruit and no fully formed seeds. It is unlikely that these aborted fruits serve as a significant food source for insects or birds. Hyperion® produces fruits that are more similar to *C. kousa* and likely serve as a food source for wild animals, although there are no studies to substantiate this assumption.

**Etymology.** The epithet *rutgersensis* is based on Rutgers University, The State University of New Jersey, the academic home of Dr. Elwin Orton's dogwood breeding program, which is now continued by co-author Thomas Molnar. Rutgers University was founded in 1766 in New Brunswick, NJ, and was named in 1825 after Colonel Henry

Rutgers, a US Revolutionary War veteran (Rutgers University 2014). We suggest the common name Rutgers' dogwood for this hybrid.

**Distribution.** *Cornus* × *rutgersensis* is known only from cultivation. One of the parent species, *C. florida*, an understory tree in mesic forests (Fulcher et al. 2012, Hillier Nurseries 2002, Porter 1903, Schwartz 1994, Wennerberg 2006), ranges from southern Maine to Florida, and as far west as Texas in the USA (Mohlenrock 2006, Schwartz 1994, Wennerberg 2006). *Cornus kousa* occurs in mesic forests in Japan, Korea, and China (Flint 1997, Xiang and Boufford 2005). No formal studies have been done to determine climate range for *C. × rutgersensis*; however, it is generally believed that its range is similar and intermediate between the two parent species *C. florida* and *C. kousa*.

**Horticulture.** *Cornus* × *rutgersensis* is grown as a landscape ornamental and, in general, can be cultivated wherever *C. florida* or *C. kousa* can be grown. *Cornus* × *rutgersensis* is typically propagated asexually through budding and grafting on seedling rootstocks of *C. kousa* or *C. florida*. The cultivars 'KF1-1' Saturn®, 'Rutban' Aurora®, 'Rutcan' Constellation®, 'Rutdan' Celestial®, 'Rutfan' Stardust®, 'Rutgan' Stellar Pink®, and 'Rutlan' Ruth Ellen® are all direct F<sub>1</sub> hybrids of *C. florida* and *C. kousa*, and all produce sterile fruit. 'KF111-1' Hyperion® is a first backcross to *C. kousa* and produces some fertile fruit. We know of no other commercially available plants of *C. × rutgersensis*.

**Disease Response.** *Cornus* × *rutgersensis* shows resistance to dogwood anthracnose and resistance or high levels of tolerance to powdery mildew (*Erysiphe pulchra* and *Phyllactinia guttata*; Li et al. 2009, Ranney et al. 1995, Trigiano et al. 2005).

**Additional material examined.** Additional collections from the same individual from which the holotype was collected, but at other dates: *R. Mattera* 26, *R. Mattera* 28, *R. Mattera* 30, *R. Mattera* 32, will all be deposited at CHRB, NY, and MO).

## Discussion

**Morphological intermediacy in hybrids.** Interspecific hybrids are commonly intermediate in their morphology between their parents (e.g., Tovar-Sanchez and Oyama 2004). However, in hybrids between the big-bracted dogwoods, there is the added complication of the parental species having either a multiple, berry-like fruit or single-seeded drupes, and remarkably different inflorescence buds, bract morphology and phenological development. Despite such large differences, the hybrids clearly express intermediate phenotypes and provide good examples of 'halfway' morphologies created through hybridization. Intermediate traits include leaf size, inflorescence structure, and fruit type, which are three important ornamental characteristics of big-bracted dogwoods. The shape of the bract shape is also intermediate in these hybrids, leading to increased variation in bract shape. Also, the intermediate flowering times allow for a lengthening of the display of the ornamental bracts across the big-bracted clade. Both hybrids discussed in this paper also display novel characteristics not seen in previous dogwood cultivars. For example, 'KN30-4' Venus® displays larger floral bracts than in other hybrid cultivars or in the species of *Cornus* known to us.

Generally, *C. × rutgersensis* and its parents display similar tree shape and form, but the hybrid displays increased vigor and growth (Fig. 4). In *C. × elwinortonii*, tree shape and growth habit appear similar to the parents, *C. kousa* and *C. nuttallii*, but the hybrid is significantly more vigorous than *C. kousa* and shows increased growth in younger trees. *Cornus × elwinortonii* can be significantly larger in stature (to 8 m; Fig. 2) than most trees of *C. kousa* (to 6 m; Gilman and Watson 1993b), but hybrid tends to be significantly shorter than *C. nuttallii* (to 12 m, occasionally to 22.9 m; Gucker 2005).

The leaves of *C. × rutgersensis* are intermediate between the two parents, being longer and wider than *C. kousa* and shorter and narrower than *C. florida*. A similar phenomenon was recorded in the *Quercus crassifolia* Bonpl. × *Q. crassipes* Bonpl. hybrid complex (Fagaceae; Tovar-Sanchez and Oyama 2004) and in crosses between the herbs *Brassica oleracea* L. and *Sinapis alba* L. (Brassicaceae; Hansen and Earle 1996). The leaves of *C. nuttallii* and *C. kousa* are narrower (5-7 cm) than their offspring, *C. × elwinortonii* (5-8 cm), and the leaves of the hybrid can also have a crinkled appearance, which is not characteristic of either parent. Such novel hybrid characteristics are not unusual and have also been reported in the *Quercus crassifolia* × *Q. crassipes* complex (Tovar-Sanchez and Oyama 2004) and in *Carica papaya* L. × *Vasconcellea cauliflora* (Jacq.) A.DC. (reported as *C. cauliflora* Jacq.; Caricaceae; Magdalita et al. 1996).

Inflorescence bud morphology and development shows dramatic differences between the parents of *C. × rutgersensis* and is also correlated with large differences in floral bract

display (and anthesis). The floral bracts of *Cornus florida* are displayed before vegetative bud-break in early spring, whereas in *C. kousa* the floral bracts are displayed after the foliage is fully developed. In *C. florida*, the inflorescence bud consists of two pairs of floral bracts (inner and outer) tightly clinging to a well-developed inflorescence head. Underdeveloped vegetative bracts are present but do not cover the inflorescence. *Cornus kousa* has two pairs of floral bracts that tightly cling to the underdeveloped inflorescence. In addition, they are tightly covered by two pairs of vegetative bracts. The hybrid displays an intermediate flower bud in which floral bracts cling to the inflorescence and vegetative bracts cling loosely to the flower head (Fig. 3c and 5). As expected, intermediate inflorescence bud development leads to intermediate floral bract display and flowering time. The flowering period of *Cornus*  $\times$  *rutgersensis* ranges from the end of flowering in *C. florida* to the beginning of flowering in *C. kousa*. Correlation of morphological variation in floral bud shape to intermediate flowering time has also been reported in hybrids between *Fraxinus excelsior* L. and *F. angustifolia* Vahl (Oleaceae; Gerard et al. 2006). Notably, in *C.*  $\times$  *rutgersensis*, the floral bracts tend to only weakly cover the inflorescence during overwintering, resulting in 10-45% of the flowers being naked (exposed).

Differences in the inflorescence buds also exist for *C.*  $\times$  *elwinortonii* and its parents, *C. nuttallii* and *C. kousa*. The underdeveloped inflorescence head in *C. kousa* is tightly covered by two pairs of floral and vegetative bracts. *Cornus nuttallii* has a completely exposed inflorescence head, where the small floral and vegetative bracts do not cover the developing flower buds. *Cornus nuttallii*, native to the Pacific Northwest (USA), is

exposed to milder winter temperatures than *C. kousa* from eastern Asia. *Cornus* × *elwinortonii* displays an intermediate bud ranging from completely exposed to completely covered. In *Cornus* × *rutgersensis*, there is strong variation in the degree of coverage by the bracts, with 10-45% naked to nearly completely covered floral buds.

Distinct differences between inflorescence architectures can also be observed between parents and their hybrids. In *Cornus kousa*, all flowers in the inflorescence are fused, creating a densely merged ball of flowers, while in *C. florida* the flowers are not fused, creating a more open structure. The flowers in their hybrid, *C. × rutgersensis*, are densely packed and at first appear to be fused together; however, they are separate even if closely positioned (Fig. 3 and Fig. 4A). The number of flowers in each inflorescence varies greatly within big-bracted dogwoods, from a few dozen to over one hundred. The hybrids also show intermediacy in the number of flowers: *C. × rutgersensis* (30-50 flowers/head) from parents *C. florida* (20-30) and *C. kousa* (20-50), and *C. × elwinortonii* (55-80) from parents *C. kousa* (20-60) and *C. nuttallii* (70-100).

In *C. florida*, the individual flowers develop into single-seeded drupes, while in *C. kousa* the fused flowers develop into single-seeded drupelets that are fused into a multiple, berry-like fruit (Fig. 5). The nearly always sterile hybrid *C. × rutgersensis* may produce parthenocarpic fruit displaying intermediate characteristics (Fig. 5). Fruits containing seeds swell and develop into individual drupes or drupelets. This is the only example we know of where a hybrid has been created between parents with single and multiple fruit types. The hybrid between *Jatropha curcas* L. and *J. integerrima* Jacq., formed from the

crossing of plants with large drupaceous fruits (*J. curcas*) and small deeply lobed capsules, displayed an intermediate fruit shape between two different fruit types as well (Rupert et al. 1970; Sujatha and Prabakaran 2002).

**Success of Hybrids.** Ornamental plants play an important role in society, providing aesthetic value, shade, wildlife habitat and food, and soil stabilization. As popular ornamental trees in temperate and sub-tropical regions worldwide, improved cultivars of big-bracted dogwoods are desired. Demand for novel, vigorous, and disease-resistant plant material is high; however, limited genetic variability can exist for some traits. For example, there are only a few cultivars of *C. florida* that express resistance to powdery mildew (Windham et al. 2003, Windham and Witte 1998) and the floral bracts of *C. kousa* and *C. nuttallii* lack the dark red of the most successful *C. florida* cultivars (Cappiello and Shadow 2005, Dirr 2009). Orton's use of interspecific hybridization to develop the novel plants described here (*Cornus* × *rutgersensis* and *Cornus* × *elwinortonii*) resulted in the successful development of cultivars with enhanced aesthetic qualities and improved disease resistance.

Upon its introduction to the US from Asia, dogwood anthracnose devastated natural stands of *C. florida*, a plant species highly susceptible to this fungal disease. For example, mortality rates as high as 86% occurred in a ten year period in Connecticut (Holzmueller et al. 2006). *Cornus nuttallii* is also highly susceptible to dogwood anthracnose. The Asian dogwood *C. kousa* occurs sympatrically with the causal agent of dogwood anthracnose *Discula destructiva* in Asia, and most cultivars of *C. kousa* have a high level



of tolerance or resistance to this disease (Hibben 1990, Ranney et al. 1995). Because of results from field evaluations and the *C. kousa* parentage, all of Orton's hybrids were believed to be highly resistant to this disease at the time of their commercial release. The Stellar® Series and Jersey Star® releases came at a time when disease incidence was high in the United States. However, Ranney et al. (1995) showed that not all of the Rutgers hybrids maintained resistance over the years, although some still displayed tolerance.

Powdery mildew, believed to be introduced from Asia, is less devastating to natural stands of *C. florida*. Instead, this disease has strongly impacted the nursery industry, raising production costs and reducing aesthetic appeal. Cultivars of *C. florida* display little resistance to this fungal disease. Of more than 100 available cultivars of *C. florida* (Santamour and McArdle 1985), only five ('Jean's Appalachian Snow', 'Karen's Appalachian Blush', 'Kay's Appalachian Mist', 'Appalachian Joy' and 'Cherokee Brave') display high levels of tolerance or resistance to powdery mildew (Li et al., 2009, Ranney et al., 1995). Again, cultivars of *C. kousa* generally show high levels of tolerance (Li et al. 2009, Ranney et al. 1995). Due to Orton's selection of parents, several cultivars of *C. × rutgersensis* (e.g., Stellar Pink®, Aurora®, Stardust®, Celestial®, and Constellation®) are resistant to powdery mildew (Li et al. 2009).

**Scientific naming of horticultural plants.** Crucial to communication in all parts of our lives is the naming of objects and phenomena. We need words to tell other people what we are talking about, and the words need to have uniform and clear meanings. For

botany, our scientific names form such a uniform language that is universal and used in fields including biodiversity inventories, phytochemistry, horticulture, crop plants, and other scientific and/or economic endeavors. Many scientific plant names are listed in the International Plant Names Index ([www.ipni.org](http://www.ipni.org)) and in other resources such as floras, dictionaries, The Plant List (<http://www.theplantlist.org/>) , RHS Plant Finder ([www.rhs.org.uk/plants/](http://www.rhs.org.uk/plants/)) , Encyclopedia for Life ([eol.org](http://eol.org)), Wikipedia ([Wikipedia.com](http://Wikipedia.com).. Unfortunately, many misspelled, outdated, unpublished, illegitimate, and invalid names are still in use worldwide in popular literature, websites, and non-taxonomic publications, especially for commonly cultivated and medicinal plants (Bennett and Balick 2014, for examples, see Struwe 2014).

It can be argued that we do not need formal scientific names for all artificially created hybrid plants, since cultivar and trademark names exist and names of cultivated plants follow *The International Code of Nomenclature for Cultivated Plants* (ICNCP, Brickell et al. 2009). However, names of hybrids following the *International Code for algae, fungi, and plants* may be useful when cataloging species diversity, natural or human-made, and linking hybrids with their parental species. *Cornus* × *rutgersensis* is a name already in use on a global scale, but was never proposed formally according to the rules of the ICN. Validating this name is the simplest way to provide an acceptable and useful name to the horticultural community. Since the second hybrid, *C.* × *elwinortonii*, is also a commonly grown and well-known hybrid in gardens, to propose it formally is also useful. Even if self-propagating seedlings from these hybrids are not known, we do know

that viable seeds are sometimes produced; making it is possible that spontaneous progeny will arise in the future

### **Summary**

The hybrids *Cornus* × *rutgersensis* (*C. florida* × *C. kousa*) and *Cornus* × *elwinortonii* (*C. kousa* × *C. nuttallii*) were developed at Rutgers University by Dr. Elwin Orton, and are good examples of controlled hybrid crosses showcasing intermediate morphological and phenological characteristics for leaf size, inflorescence bud structure, flowering time, and fruit structure. The horticultural success of big-bracted dogwood hybrids in the nursery and landscape industry can largely be attributed to their inherent disease resistance and enhanced aesthetic qualities that represent novel intermediate phenotypes between their parent species.

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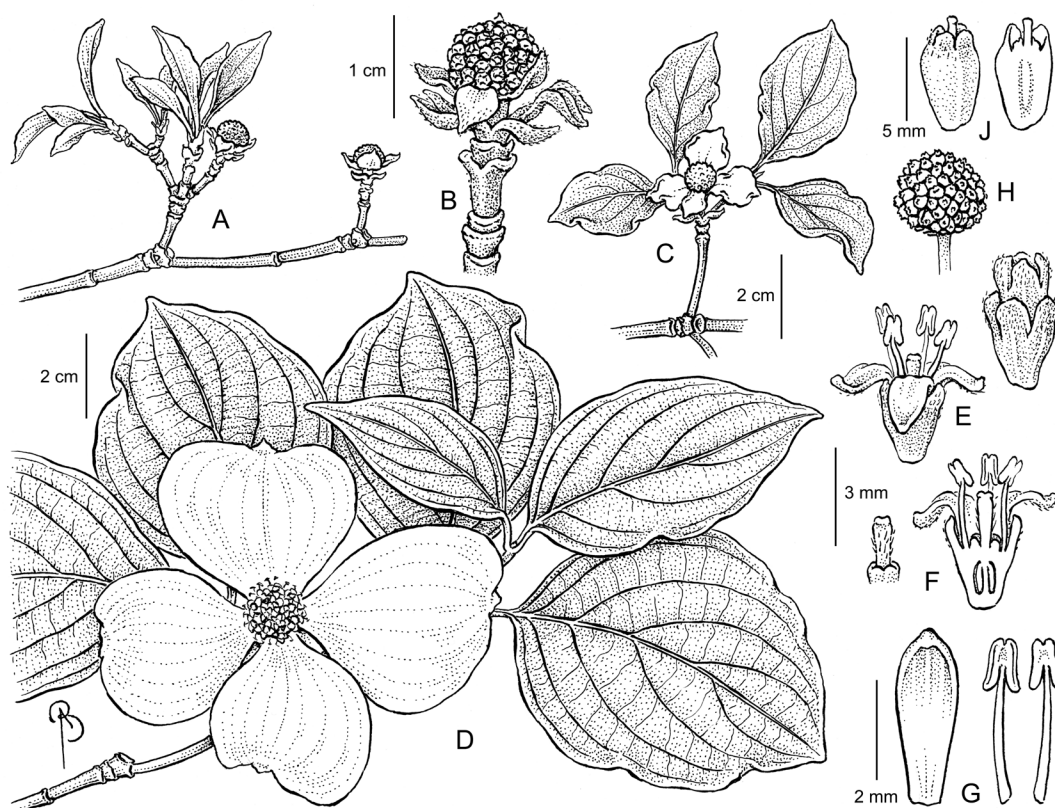
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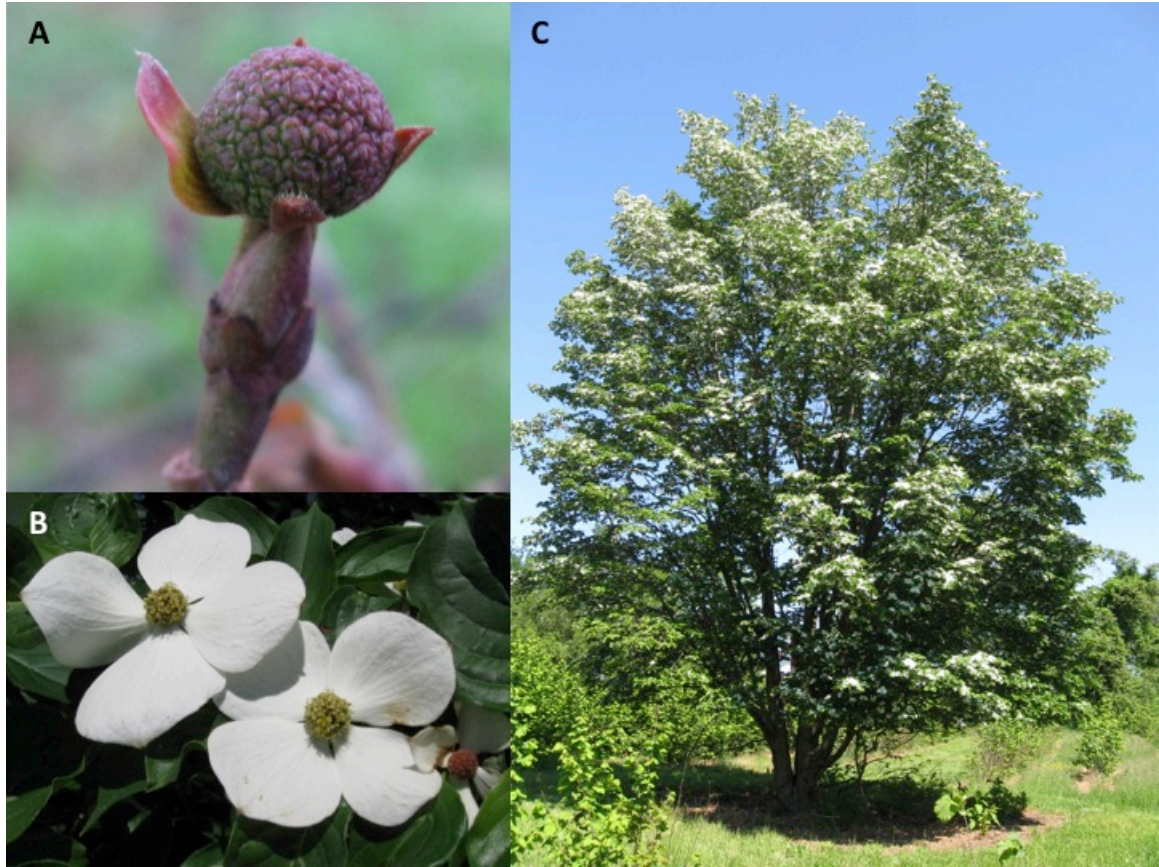
## FIGURES

**Figure 1.** Illustration of *Cornus* × *elwinortonii* ‘KN4-43’, PP 16293, Starlight®. **A** Branch, showing expanding leaf and floral bract tissues in the spring. **B** Close up of inflorescent bud prior to complete bract and leaf expansion. **C** Node, showing fully expanded leaves and partially expanded floral bracts. **D** Branch, showing inflorescence with flowers in full bloom; floral bracts fully expanded. **E** Close up of flower at dehiscence, note synsepalous calyx and apopetalous corolla. **F** Dissected flower, showing single gynoecium. **G** Close up of petal and stamens, note dehiscence occurs longitudinally. **H** Single inflorescence, showing many tightly compressed parthenocarpic drupes. **J** Single drupe, showing compressed form and protruding style. Drawings by Bobbi Angell from the holotype.



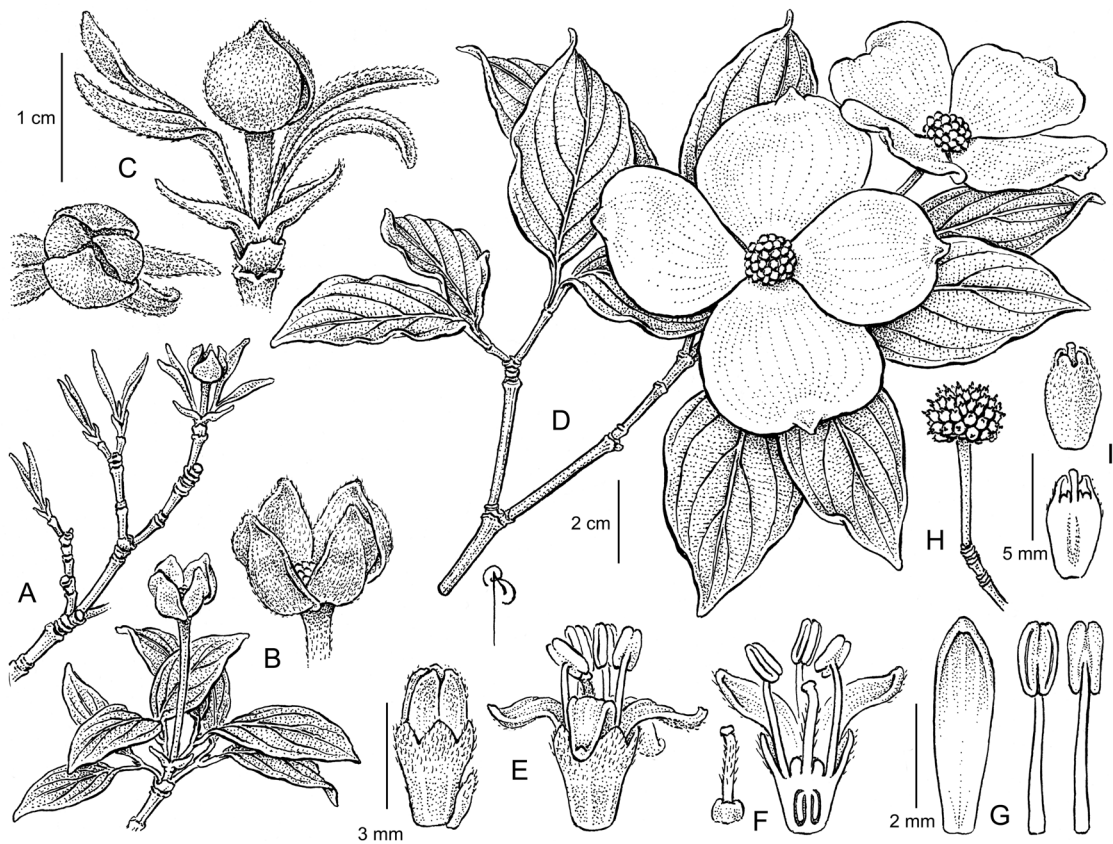


**Figure 2.** Photos of *Cornus*  $\times$  *elwinortonii*. **A** Close up of dormant inflorescent bud; note the exposed flower buds and partially developed floral bracts. **B** Flowers and floral bract display after dehiscence; note frost damaged inflorescence on the far right. **C** Habit of mature plant. Photos by Thomas Molnar.



**Figure 3.** Illustration of *Cornus*  $\times$  *rutgersensis* Cornus ‘Rutgan’, PP7207, Stellar Pink®. **A-B** Branch, showing expanding leaf and opening of floral bract tissues in the spring. **B** Close up of inflorescent bud prior to complete bract and leaf expansion. **C** Close up of single inflorescence post bud-break, showing pair of unexpanded floral bracts clinging to flower head; note pair vegetative bracts still attached at base of inflorescence. **D** Branch, showing inflorescence with flower buds still closed; floral bracts fully expanded. **E** Close

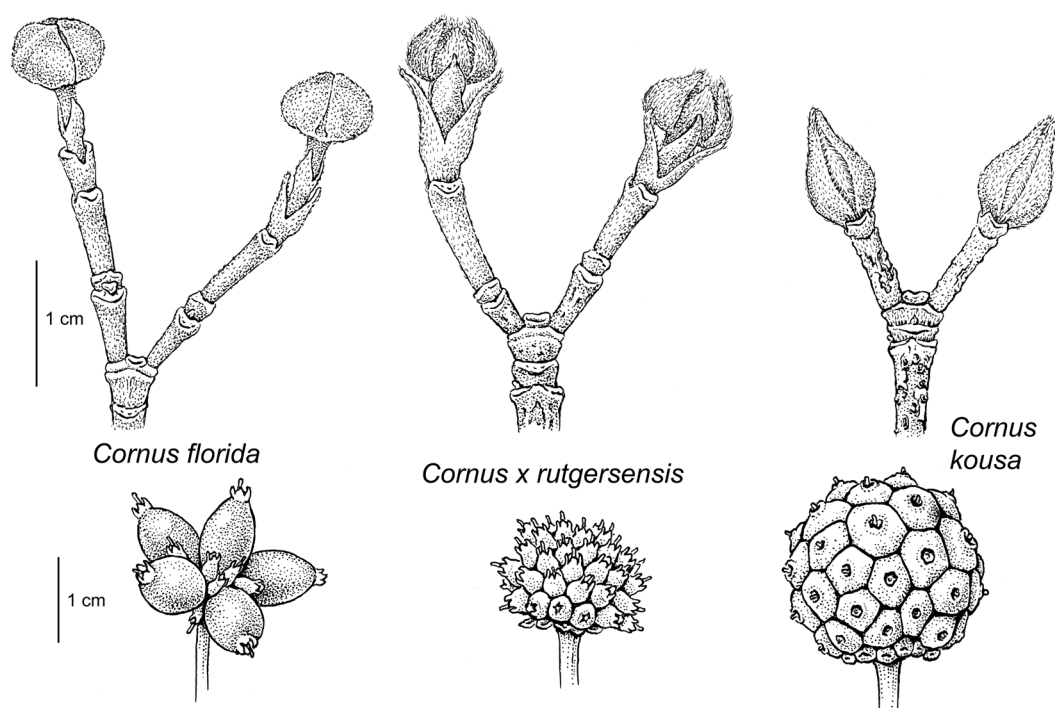
up of flower, showing both before and after anthesis; note synsepalous calyx, apopetalous corolla and exerted stamens. **F** Dissected flower, showing single gynoeceium and exerted style. **G** Close up of petal and stamens, note dehiscence occurs longitudinally. **H** Single inflorescence, showing many tightly compressed parthenocarpic drupes. **I** Single drupe, showing compressed form and protruding style. Drawings by Bobbi Angell from the holotype.



**Figure 4.** Photos of *Cornus × rutgersensis*. **A** Close up of inflorescence, showing varying stages of flowering. **B** Inflorescence with full floral bract display and flowers before anthesis. **C** Habit of mature plant. Photos A and C by Thomas Molnar; photo B by Robert Mattera.



**Figure 5.** Comparison of flowering bud and fruit development in *Cornus florida*, *Cornus* × *rutgersensis*, and *Cornus kousa*. Drawing by Bobbi Angell.



**Table 1.** Parentage of the eleven interspecific hybrids released from the Rutgers University dogwood breeding program. PP refers to plant patent number. OP indicates open pollination. Brackets ([ ]) contain pedigree information of an interspecific hybrid parent

Scientific name	Cultivar, Patent number, Trademark	Female Parent	Male Parent
<b>Cornus × elwinortonii</b>	‘KN30-8’, PP 16309, Venus® (Jersey Star® Series)	[ <i>C. kousa</i> ‘Chinensis’ × <i>C. nuttallii</i> ‘Goldspot’]	<i>C. kousa</i> ‘Rosea’
<b>Cornus × elwinortonii</b>	‘KN4-43’, PP 16293, Starlight® (Jersey Star® Series)	<i>C. kousa</i> ‘Simpson No. 1’	<i>C. nuttallii</i> ‘Goldspot’
<b>Cornus × elwinortonii</b>	‘KN144-2’, PP application number 2014-0283242, Rosy Teacups®	[ <i>C. kousa</i> ‘Chinensis’ × <i>C. nuttallii</i> ‘Goldspot’] × OP	<i>C. kousa</i> ‘Rosabella’
<b>Cornus × rutgersensis</b>	‘KF111-1’, PP 22219, Hyperion®	<i>C. kousa</i> K2 × <i>C. florida</i> ‘Sweetwater Red’	Unknown
<b>Cornus × rutgersensis</b>	‘KF1-1’, PP 17768, Saturn®	<i>C. kousa</i> K2	<i>C. florida</i> D1
<b>Cornus × rutgersensis</b>	Cornus ‘Rutlan’, PP 7732, Ruth Ellen® (Stellar® Series)	<i>C. kousa</i> K2	<i>C. florida</i> ‘Meyer White’
<b>Cornus ×</b>	Cornus ‘Rutfan’, PP 7206,	<i>C. kousa</i> K2	<i>C. florida</i>

Scientific name	Cultivar, Patent number, Trademark	Female Parent	Male Parent
<b>rutgersensis</b>	Stardust® (Stellar® Series)		‘Cherokee Princess’
<b>Cornus × rutgersensis</b>	Cornus ‘Rutcan’, PP 7210, Constellation® (Stellar® Series)	<i>C. kousa</i> K2	<i>C. florida</i> ‘Cherokee Princess’
<b>Cornus × rutgersensis</b>	Cornus ‘Rutdan’, PP 7204, Celestial® (Stellar® Series)	<i>C. kousa</i> K2	<i>C. florida</i> D1
<b>Cornus × rutgersensis</b>	Cornus ‘Rutban’, PP7205, Aurora® (Stellar® Series)	<i>C. kousa</i> K2	<i>C. florida</i> ‘Springtime’
<b>Cornus × rutgersensis</b>	Cornus ‘Rutgan’, PP7207, Stellar Pink® (Stellar® Series)	<i>C. kousa</i> K2	<i>C. florida</i> ‘Sweetwater Red’

## Chapter 2

### **Genetic diversity analysis of the big-bracted dogwoods *Cornus florida*, *C. kousa*, *C. nuttallii* and their inter-specific hybrids**

#### **Abstract**

Big-bracted dogwoods (*Cornus* spp.) are popular landscape trees in the United States prized for their ornamental traits and four-season appeal (petaloid bracts, foliage, berries and bark). The Rutgers University woody ornamentals breeding program, started in the 1960s, holds one of the largest big-bracted dogwood germplasm collections in the world containing over 50 cultivars and 1000s of advanced generation hybrid seedlings. From this collection, eleven inter-specific and four intra-specific hybrid cultivars have been released with several now widely grown by the nursery and landscape trade with breeding efforts continuing. While pedigree records exist for most of the releases, a number have incomplete records largely due to one or more ancestors being derived from open-pollination events. Also, many of the advanced generation hybrids, which make up a majority of the current program, originated from only a few original fertile inter-specific hybrids, presenting the potential for a genetic bottleneck in existing breeding lines. Thus, examining the genetic diversity and relationships of the germplasm collection could help clarify breeding records and provide a means to assess genetic diversity in support of future improvement efforts. In this study, 11 simple sequence repeat (SSR) markers were used to fingerprint 337 accessions, which included 276 from Rutgers University, 59 from the University of Tennessee and two outgroups. Of the total, 93

were named cultivars, 180 breeding selections and 61 have unknown identities. SSR marker loci were amplified via PCR, products run on a capillary electrophoresis genetic analyzer (ABI 3500xl; Applied Biosystems) and scored using GeneMapper v5 software was used to score peak data. Using this data, a UPGMA dendrogram was generated from cluster analysis using POWERMARKER v3.25 and visualized in Mega v6.0. Further, a Bayesian model-based clustering analysis was done using the program STRUCTURE v2.3.4. Based on allele number and frequency, results showed that the collection as a whole was genetically diverse ( $H_o=.53$ ). The UPGMA and STRUCTURE analysis were in strong agreement and resolved five statistically distinct clades ( $K=5$ ) that were closely aligned with pedigree records and known breeding histories of most accessions. Each of the clades were represented by a predominant species, species hybrid or known parental line. Within population variance was low for two groups predominantly comprised of inter-specific hybrids suggesting a genetic bottleneck due to sterility issues. From these analyses, relationships and genetic groups were elucidated, a number of unknown accessions were identified, and the first consensus groups were developed for big-bracted dogwood. The results of this study increase the understanding of the current pool of big-bracted dogwood genetic resources.

**Keywords:** Cornaceae, flowering dogwood, Kousa dogwood, Pacific dogwood, tree breeding, genotyping, microsatellites



## Introduction

The monophyletic genus *Cornus* L. contains ten subgenera consisting of 58 species (Fan, 2001; Xiang et al., 2006). *Cornus* is a diverse genus containing herbs, shrubs and small to large trees. The big-bracted (BB) clade sensu is made up of tree species that display showy petaloid bracts beneath multi-flowered inflorescences (head-like; Xiang et al., 2006). These spring-flowering trees are native to the mesic forests of North America and Eastern Asia and are placed into three different subgenera: *Cynoxylon*, *Discocrania* and *Syncarpea* (Xiang et al., 2006). *Cornus florida* L. and *C. nuttallii* Audobon of subgenus *Cynoxylon* and *C. kousa* Hance of subgenus *Syncarpea* are popular landscape trees in the United States (US). The most popular, *C. florida*, or flowering dogwood, is native to the eastern and southern US (Gilman and Watson, 1993a; Hillier Nurseries, 2002; Mohlenrock, 2006; Porter, 1903; Schwartz, 1994; Wennerberg, 2006), while *Cornus nuttallii*, or the Pacific dogwood, is not as widespread, and is confined to a small area primarily in the Pacific Northwest (Gucker, 2005; Habziabdic et al., 2012). Native to eastern Asian mesic forests, *C. kousa*, is becoming popular in the US due to its versatility, disease resistance and similar planting range and growth habit as the flowering dogwood (Gilman and Watson, 1993b; Xiang and Boufford, 2005). These trees and their inter-specific hybrids are prized for their four season appeal: petaloid bracts (spring), attractive foliage (summer), ornamental berries (fall) and appealing bark (winter; Gilman and Watson, 1993a; Gilman and Watson, 1993b; Li et al., 2009; Molhenrock, 2006). Demonstrating their popularity, annual sales of dogwoods totaled nearly 31 million USD in 2009 accounting for over 11% of the total deciduous flowering market (Fulcher et al., 2012; NASS, 2014).

Horticultural uses of BB-dogwoods include container, specimen and shade plantings. They are commonly found in suburban landscapes, gardens and parks (Gilman and Watson, 1993a-b; Mohlenrock, 2006). *Cornus florida* flowers in the early spring (March–May) after magnolias, crabapples and pears. Over 100 commercially available *C. florida* cultivars exist (Santamour and McArdle, 1985). *Cornus kousa* blooms about a month later (April–June) after the leaves have emerged and has a vase-like growth habit when young (Gilmore and Watson, 1993b). There are at least 30 commercially available cultivars of *C. kousa* (Santamour and McArdle, 1985). Being frost sensitive, *C. nuttallii* is less widely adapted than *C. florida* and *C. kousa* and is cultivated primarily in the Pacific Northwest. There are at least seven commercially available cultivars of *C. nuttallii* (Santamour and McArdle, 1985).

Big-bracted dogwoods are generally diploid with a base chromosome number of 11 ( $2n = 2x = 22$ ; Dermen, 1932; Goldblatt, 1978; Shearer and Ranney, 2013; Xiang et al., 2006). They are self-incompatible based on a gametophytic incompatibility system (Reed, 2004). Using flow cytometry, it was found that the hybrid cultivar ‘KN30-8’ Venus® is a triploid. It is the only known polyploid dogwood. BB-dogwoods are propagated either by seed, or more commonly, by grafting and budding of clonal cultivars onto seedling rootstocks.

The Rutgers University dogwood-breeding program began in 1965 under the direction of Dr. Elwin Orton with the goal of creating novel *C. florida*, *C. kousa* and *C. nuttallii*

cultivars with improved ornamental qualities (Molnar and Capik, 2013; Orton, personal communication). The initial focus of the breeding program was on intra-specific hybrids; however, inter-specific hybrids between these three species were later developed that displayed unique ornamental qualities, increased vigor and improved stress and disease tolerance (Molnar and Capik, 2013). Dr. Orton was the first to make interspecific crosses among these three species (*C. florida* × *C. kousa* and *C. kousa* × *C. nuttallii*; Cappiello and Shadow, 2005; Dirr, 2009). In total, four intra- and twelve inter-specific hybrid cultivars were selected, patented and released as new cultivars from this program (Orton, 1990a-e; Orton, 1991; Orton, 2014; Orton and Gant, 1993a-b; Orton and Gant, 2004; Orton and Gant, 2006a-b; Orton and Gant, 2007; Orton and Gant, 2011). *Cornus* × *elwinortonii* Mattera, T. Molnar, & Struwe, *hybr. nov.*, hybrids (*C. kousa* × *C. nuttallii*) were named in honor of Dr. Orton and comprise the Jersey Star® Series (Table 1) while *Cornus* × *rutgersensis* Mattera, T. Molnar, & Struwe, *hybr. nov. hybrids* (*C. kousa* × *C. florida*) were named in honor of Rutgers University and comprise the popular ornamental group Stellar® Series. Both hybrids display many intermediate characteristics between the two respective parent species such as inflorescence shape, flowering time, fruit type and leaf size (Mattera et al., 2015). While detailed pedigree records were kept for many of the plants, much is unknown about the relationships and genetic diversity of the current germplasm in the program. Inherently unknown origins of many of the first accessions used in breeding (poorly documented selections from the wild, seedlings selections from nurseries, or plants introduced from Asia many decades ago) and the use of open-pollinated (OP) seeds as the basis for most selection efforts make it difficult to discern existing relationships. Additionally, all but a few of the first F<sub>1</sub> inter-specific

hybrids were sterile, resulting in a limited pool of parents used to form the basis for advanced inter-specific breeding lines. Thus, the potential exists for a substantial genetic bottleneck in the breeding program. Further, many of the more recent advanced generation hybrids were again the result of open-pollination (OP) events, although from limited and better-documented breeding blocks, which further dilutes the understanding of genetic relationships between and among the trees. Thus, it is essential to clarify these relationships to help maintain high genetic diversity in breeding lines and future cultivar selections.

Fortunately, molecular tools exist to analyze and discern genetic relationships from BB-dogwood germplasm. Amplified fragment length polymorphism (AFLP) markers, randomly amplified polymorphic DNA (RAPD) markers, arbitrary signals from amplification profile (ASAP) markers and simple sequence repeat (SSR) markers have all been developed from either *C. florida* or *C. kousa*. These markers have been successfully used for genetic diversity analysis, DNA fingerprinting or cultivar identification (Cabe and Liles, 2002; Caetano-Anollés, 1998; Hadziabdic et al., 2013; Rhoades et al., 2011; Smith et al., 2007; Trigiano et al., 2004; Wadl et al., 2008; Wadl et al., 2010; Wadl et al., 2013; Wang et al., 2008). Both SSRs and EST-SSRs have been developed from *C. florida* and *C. kousa*, and have been shown to be valuable in assessing genetic diversity and analyzing relationships both within and across BB-dogwood species (Hadziabdic et al., 2013; Wadl et al., 2008; Wadl et al., 2010; Wadl et al., 2013; Wang et al., 2008). These markers were used to develop a linkage map in *C. florida* and identify quantitative trait loci for red-leaf color in young leaves (Wadl et al., 2011; Wang et al. 2009). Red-leaf

color is associated with red or pink-bract color (Orton, personal communication; Wadl et al., 2011) a highly desirable ornamental characteristic. DNA fingerprinting with molecular markers has also been used to confirm male pollen parents in open-pollinated seedlings of flowering dogwood (Ament et al., 2000). Simple sequence repeat markers have also been used to analyze the genetic diversity of wild *C. florida* populations in the Great Smoky Mountain Nation Park finding that wild populations still display high levels of genetic diversity (Hadziabdic et al., 2013). No previous study has examined a large pool of cultivated BB-dogwood germplasm including particularly, a complex collection that includes *C. florida*, *C. kousa*, *C. nuttallii* and inter-specific hybrid species. Thus, there is a general lack of understanding of genetic diversity and relationships in the available plant material utilized in the landscape and in breeding in the United States. In this study, 11 SSR markers were used to examine the genetic diversity, relationships and population structure of a total of 337 accessions of BB-dogwoods comprised of commercial cultivars, unreleased breeding selections, and F<sub>1</sub> and advanced generation hybrids held in the Rutgers University and University of Tennessee (UT) germplasm collections. The objective of the current study was to broaden the understanding of BB-dogwood genetic resources and relationships in support of future breeding efforts where the maintenance of high genetic diversity is considered a priority.

## **Materials and Methods**

### *Plant material*

A total of 337 unique accessions were genotyped (Table 2) including 59 UT accessions and 276 RU accessions and 2 outgroups. The UT accessions included 25 unique cultivars,

13 accessions acquired from Texas and 21 unreleased breeding selections. The 276 Rutgers accessions consist of 68 cultivars, 134 advanced generation breeding selections, 12 F<sub>1</sub> breeding selections, 2 replicates of *C. kousa* ‘K2’ (a *C. kousa* from Willowwood Arboretum? of unknown background that is an important breeding parent in inter-specific Rutgers hybrids), 61 accessions whose identity was lost or is unknown. Many of the unknown plants are either in a Stellar Series® stock block or planted on the grounds of the Rutgers Gardens, New Brunswick, NJ, where the original breeding program was located and where many field plans have since been lost when the grounds were turned over to the Display Gardens. Fortunately, the unlabeled trees exhibit hybrid phenotypes limiting the potential cultivars they may be. The advanced generation selections consisted of 40 *C. kousa* hybrids, 4 *C. kousa* var. *angustata* Chun × OP, 46 *Cornus* × *rutgersensis* hybrids, 4 hybrids with *C. kousa*, *C. florida* and *C. nuttallii* background (KFN), 37 *Cornus* × *elwinortonii* hybrids and 3 accessions with unknown backgrounds (part of the total 59 unknown accessions above). The F<sub>1</sub> breeding selections consisted of 9 *C. kousa* hybrids, 1 *C. florida* hybrid, 1 *Cornus* × *elwinortonii* hybrid and 1 *Cornus* × *rutgersensis* hybrid. Many F<sub>1</sub> hybrids are infertile and represent genetic dead ends in the breeding program. In total, 70 unique commercially available cultivars (93 total accessions) were included in this collection and consist of 26 inter-specific hybrids, 1 *C. kousa* var. *angustata* (syn. *C. angustata*, *C. capitata* var. *angustata* or *C. elliptica*), 31 *C. kousa*, 28 *C. florida* and 3 *C. nuttallii* (two cultivars are uncertain as to species: ‘Headquarters’ and ‘Pink Girard’s’).

#### *Genomic DNA extraction*

Young leaf (spring growth) or dormant inflorescent bud material was collected from all accessions growing at Rutgers University and University of Tennessee in 2013 and 2014 and stored at -80 °C. Plant material was ground in liquid nitrogen, and genomic DNA was isolated using a QIAGEN DNeasy kit following a modified protocol developed at the University of Tennessee. The modifications were as follows: 20-minute incubation at 65°C (instead of 10-minutes) and a 30-minute incubation on ice (instead of 5-minutes). Quantification of extracted DNA was done using a NanoDrop ND-1000 (Thermo Scientific, Waltham, MA) spectrophotometer. DNA was diluted to 5 ng mL<sup>-1</sup> before PCR reactions were carried out.

#### *Nuclear SSR markers*

Eleven SSR markers developed at the University of Tennessee (Wadl et al., 2008; Wadl et al., 2012; Wang et al., 2008) were used to genotype all accessions (Table 3). These primers were chosen from a subset of 25 SSR and EST-SSR markers screened based on their level of polymorphism in the dataset, quality of amplification, reproducibility and ability to amplify PCR products in all species. All forward primers included the M13 (-21) 18-bp sequence (5'-TGTAACGACGGCCAGT-3') added to the 5' end to facilitate economical fluorescent labeling of PCR fragments (Shuelke, 2000), while all reverse primers included the "PIG-tailing" sequence (GTTTCTT) added to the 5' end which results in the adenylation of the 3' end of the forward strand of the PCR product. The "PIG-tailing" sequence reduces the problem of scoring "true" vs. "plus-A" alleles (Brownstein et al., 1996). Integrated DNA Technologies (IDT - Coralville, IA) synthesized all PCR primers.

### *SSR genotyping*

Genotyping PCR reactions were done in 96-well plates in 13- $\mu$ L reaction volumes. Reactions consisted of 5.0 ng genomic DNA, 2x Ramp-Taq PCR buffer (Denville Scientific, Metuchen, NJ), 2.0 mM MgCl<sub>2</sub>, 0.25 mM each dNTP (Denville Scientific), 0.5 U Ramp-Taq DNA polymerase (Denville Scientific), 0.5 pmol forward primer with M13(-21) addition, 1 pmol reverse primer with “PIG-tailing” addition, and 1 pmol forward M13(-21) primer with FAM, NED, PET, or VIC fluorescent labels (Brownstein et al, 1996; Shuelke, 2000). PCR reactions were carried out in GeneAmp 9700 thermocyclers (Applied Biosystems, Foster City, CA). The conditions were as follows: Initial denaturation at 94 °C for 5 minutes (min) followed by 30 cycles of 94 °C for 30 seconds (s), 55 °C for 45 s, 72 °C for 45 s; followed by 20 cycles of 94 °C for 30 s, 53 °C for 45 s, 72 °C for 45 s; followed by a final extension of 72 °C for 10 min.

### *SSR data analysis*

A capillary electrophoresis genetic analyzer (ABI 3500xl; Applied Biosystems) was used to analyze PCR products using a LIZ600 size standard (Applied Biosystems). Four controls were included on each 96-well plate: *C. kousa* ‘Radiant Rose’ a light pink-bracted cultivar; *C. florida* Red Beauty® a red-bracted cultivar; *Cornus*  $\times$  *rutgersensis* Stellar Pink® a popular *C. florida*  $\times$  *C. kousa* light pink-bracted cultivar; and the GeneScan Installation Standard DS- 33 (Applied Biosystems). The genotyping data was then scored and analyzed using Genemapper v5.0 (Applied Biosystems).



### *UPGMA dendrogram and STRUCTURE*

The data obtained were inputted into the cluster analysis program PowerMarker v3.0 and a distance matrix based on allele frequencies was obtained. A UPGMA dendrogram was constructed from this distance-matrix and visualized in Mega v6.0. PowerMarker v3.0 was also used to calculate the numbers of alleles for each locus, allele frequencies, observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ) and polymorphism information content (PIC; Liu and Muse, 2005).

STRUCTURE, a Bayesian model-based clustering analysis program (Pritchard et al, 2000), was used to elucidate the most likely number of groups ( $K$ ). Software parameters included the admixture ancestry model and assumed that all loci were unlinked and in linkage equilibrium. Fifty replicates of each value of ( $K$ ) for ( $K$ )=2 to 47 were run (20,000 burn ins; 50,000 Markov chain Monte-Carlo [MCMC]), to determine the appropriate group number (Evanno et al. 2005; Pritchard et al, 2000). The STRUCTURE results were uploaded into STRUCTURE harvester v0.6.94, a web-based program used to determine the most parsimonious value of ( $K$ ) (Earl and vonHoldt, 2012). Based on the average estimated log probability  $\Pr(X|K)$  and the Evanno ad hoc (DeltaK) statistic a value for ( $K$ ) was chosen.

Consensus group data was subjected to analysis of molecular variance (AMOVA) using GenAlEx v6.5 (Peakall and Smouse, 2012). This analysis was used to analyze within and among population variance between the consensus populations.

## Results and Discussion

### *SSR Markers*

The 11 microsatellite markers amplified 170 alleles across the accessions. As a diploid species, all accessions but one displayed separate multiallelic inheritance in a codominant fashion. *Cornus* × *elwinortoni* ‘KN30-8’ Venus®, a known triploid, displayed polyploidy inheritance in the SSR data (CF701), and was treated as a diploid (Shearer and Ranney, 2013). Microsatellites that displayed polyploidy were treated as missing data as was the case with the locus CF701 for Venus®. Allele number per marker ranged from 8 to 24 with an average of 16 alleles per locus. The mean expected heterozygosity ( $H_e$ ), observed heterozygosity ( $H_o$ ), polymorphic information content (PIC) and inbreeding coefficient ( $f$ ) were 0.75, 0.53, 0.72 and 0.288, respectively (Table 4). Expected heterozygosity levels are within the range of previous studies for BB-dogwoods; however, the mean  $H_o$  value of 0.53 is higher than previously reported (Hadziabdic et al., 2011; Keir et al., 2011; Wadl et al., 2013; Wadl et al., 2008). The ( $f$ ) of 0.288 was also lower than a previous study (Habziabdic et al., 2011) where an ( $f$ ) of 0.54 was reported for a natural population of *C. florida* in the Great Smoky Mountains. This finding suggests that the germplasm evaluated, as a whole, has a high level of genetic diversity despite potential bottlenecks due to infertile hybrids and heavy breeding selections.

### *UPGMA Clustering*

The UPGMA dendrogram can be broken into five major clades. These clades, in general, were divided up among different species and species hybrids, thus, were named accordingly. From most basal to most interior, the five groups are the: *C. florida* group

(Group 1), *Cornus* × *rutgersensis* group (Group 2), *Cornus* × *elwinortonii* group (Group 3), *C. kousa* inter-specific hybrid group (Group 4) and Pink-bracted *C. kousa* group (Group 5; Figure 1)

**Group 1: *C. florida* group**

The most basal clade on the dendrogram (Figure 1) holds 97 accessions of which 77 are *C. florida*, 15 are interspecific hybrids with *C. florida*, and 5, which appear to be of hybrid origin, are lacking records on their species identities and/or cultivar names (Figure 2). Fourteen of the *C. florida* accessions are also lacking identity information but are largely from the collection held at the Rutgers Gardens. Thirty-three known cultivars are included in this group, all being *C. florida* except for ‘Eddie’s White Wonder’, a *C. florida* × *C. nuttallii* hybrid (Figure 2).

The most basal accession in the *C. florida* Clade is TX1 (Figure 1), a *C. florida* from Texas (Table 2; Hadziabdic et al., 2010). Interior to this single accession are two adjacent, large subgroups. Subgroup 1 (n=51; Figure 2) is broken into three clades and one small basal subgroup. The basal subgroup containing *C. florida* accessions from UT clustered into Subgroup 1 which was surprising because breeding history suggests it shares more genetic background with Subgroup 2, discussed subsequently, which holds the remainder of the UT *C. florida* accessions (Figure 2). The most interior clade in subgroup 1 (n=15; Figure 2), named the KF95-1 clade, contains 12 open-pollinated (OP) seedlings of the interspecific hybrid KF95-1, *C. florida* ‘Cherokee Brave’ and two unknown *C. florida* that appear to be closely related or the same clone. The KF95-1

seedlings all have distinct *C. florida* phenotypes, and it is assumed they are the crosses of KF95-1 with one or more unknown *C. florida* accessions. KF95-1 was derived from an open-pollination event of KF45-29, which is a cross of *C. kousa* ‘K2’ × *C. florida* ‘Sweetwater Red’ (a full sibling of *C. × rutgersensis* ‘Rutgan’ Stellar Pink®). It should be noted that KF45-29 is one of the few fertile F<sub>1</sub> hybrids used in the Rutgers breeding program. *C. florida* ‘Sweetwater Red’ is a dark pink-bracted cultivar which links the KF95-1 seedlings to ‘Cherokee Brave’, which is also dark-pink, as well as the placement of this clade adjacent to the and Pink-bracted clade in Subgroup 1, discussed immediately below.

The Pink-bracted Clade (n=21, Figure 2) contains both pink-bracted *C. florida* cultivars, seedlings, and several advanced generation hybrids. Two unknown *C. florida* accessions D224 and D248 are grouped together with biological replicates of ‘Sweetwater Red’ suggesting that these two accessions are also clones of ‘Sweetwater Red’ or its offspring (Figure 2). D224 and the accession Sweetwater 182 shared 91% of their alleles; however, if you eliminate missing SSR data (CF1045) these two accessions share 100% of their alleles suggesting these two are the same genotype (data not shown). D248 and ‘Sweetwater Red’ share 73% of their alleles suggesting it may be the progeny of ‘Sweetwater Red’ or a close relative. Also in this clade, *C. florida* ‘Red Beauty’ was placed in a cluster with three of its offspring (H4AR17P05, H4AR17P48 and H4AR17P50 [parentage ‘Red Beauty’ × *C. florida* ‘Forma rubra’], Figure 2).

The cultivars ‘Karen’s Appalachian Blush’ (*C. florida* 95-12 Blush), ‘Pink Girards’ and ‘Spring Song’ are all pink-bracted varieties. *C. florida* ‘D-184-11’ Wonderberry® is the

only cultivar in this clade with white-bracts; however the bracts display a red tip. The breeding history shows that this cultivar is the direct offspring of a red-bracted *C. florida* supporting its placement in this clade (Cappiello and Shadow, 2005; Orton and Gant, 1993a). The most basal cluster of this clade is the *C. florida* × *C. nuttallii* hybrid ‘Eddie’s White Wonder’ (n=2) cluster (Figure 2). The *C. florida* parent is reported to be *C. florida* ‘Rubra’ (E. Orton, personal communication), which links it to the larger clade. The final plant, KFN1-1, is a cross of ‘Eddie’s White Wonder’ × *C. kousa* K23-2 ‘Chinensis’.

Subgroup 2 (n=50; Figure 3) contains many accessions with uncertain backgrounds making it somewhat more difficult to explain the genetic relationships of this group. For example, the Texas accessions, acquired from UT, originated from seed collections of wild trees found at the GPS coordinates 30.55944 -96.62972, and therefore have no specific pedigree backgrounds (Hadziabdic et al., 2010). Accessions like *C. florida* 95-17 also have unclear pedigree and geographic information because seed from which they were derived originated from bulked mixtures of seeds collected from trees growing in abandoned dogwood nurseries in Tennessee, Georgia and Alabama after a powdery mildew (PM) epidemic forced many nurseries to close (Windham et al., 2003).

Regardless, two clades were identified in subgroup 2, labeled as Clade A (n=20) and Clade B (n=26), which help to clarify relationships among the accessions. Subgroup 2 also contains four accessions in basal positions to Clade A and Clade B. Clade A consists of 15 breeding selections from UT including nine from Texas (Hadziabdic et al., 2010), three identified for powdery mildew resistance (95-10, *C. florida* 94-25 and *C. florida* 95-25; Windham et al., 2003) and the two cultivars ‘Cherokee Daybreak’ and ‘Double

White' (Figure 3). 'Cherokee Daybreak' clusters together with *C. florida* 95-11 Mist, *C. florida* 94-25 and *C. florida* 95-25. All four of these accessions are known to be powdery mildew resistant.

The most interior group consists of four accessions from Texas (TX13, TX9 TX3 and TX5, Figure 3). From the remaining five accessions, three are cultivars ('Little Princess', 'Dwarf' and 'Mystery'), one RU advanced generation selection (H4AR15P30, KF95-1 × OP) and one unidentified *C. florida* (D229, Figure 3).

Clade B holds 16 UT accessions, five cultivars from RU and five unidentified RU accessions. Ten of the UT accessions are PM resistant selections (Windham et al., 2003) and only one is from Texas (Figure 3; Habziabdic et al., 2010). The remaining five UT accessions are cultivars held in their collection (Jean's Appalachian Snow, Appalachian Joy, Rainbow, Langdon Y, Snow Princess; Figure 3). An interior cluster holds the red-bracted cultivars 'Prosser Red' and 'Forma rubra'. Another interior cluster consists of replicates of the cultivar 'First Lady'. An unidentified *C. florida* accession D227 clustered only with *C. florida* 'Cherokee Princess' likely indicating that this accession is a clone or full-sibling of 'Cherokee Princess'. When eliminating missing data (CF273, CF597 and CF1020) these two accessions share 94% of their alleles suggesting it to be a clone. D226, another accession with missing identity information clustered together with the *C. florida* cultivar 'Rainbow'. These two accessions share 100% of their alleles, supporting the identification of D226 as the cultivar 'Rainbow'.

Interior to the *C. florida* Clade, the accessions were divided up into four major clades as well as individual accessions placed in a more basal position. The most basal position is held by *Cornus angustata* 'Elsbry' Empress of China, and placed interior are the three *C. nuttallii* cultivars ('Barrick', Corigo Giant' and Goldspot'), and the outgroup accessions *Cornus mas* (C\_mas\_198; STRUCTURE ID 345) and Hydrangea spp. (Hydrangea; STRUCTURE ID 246).

### **Group 2: *Cornus* × *rutgersensis* group**

This group (n=47; Figure 4) is located in the most basal position interior to the outgroup accessions. It contains all the accessions from the Stellar Series® that were included in this study, which are F<sub>1</sub> hybrids of *C. kousa* and *C. florida* (*Cornus* × *rutgersensis*). Ruth Ellen®, Stellar Pink®, Variegated Stellar Pink®, Constellation®, Aurora® and Stardust® all appear in their own clades in this group. Another RU cultivar, Hyperion®, which is not part of the Stellar Series®, can be found in its own clade in this group as well. A total of 19 Stellar Series® accessions are included in this clade. Biological replicates of 'Rutlan' Ruth Ellen® (n=3), 'Rutgan' Stellar Pink® (n=4 for Stellar Pink®; n=3 for variegated Stellar Pink®), 'Rutcan' Constellation® (n=2), 'Rutban' Aurora® (n=4) and 'KF111-1' Hyperion® (n=3) all clustered tightly with their respective replicates. All accessions in this group share *C. kousa* 'K2' as a common ancestor. *C. kousa* 'K2' is the female parent to all Stellar Series® cultivars and is the grandmother of Hyperion. Thirty five accessions in this group share *C. kousa* 'K2' in their lineage; 25 are direct offspring and twelve are direct or indirect offspring of KF45-29, which is an offspring of 'K2' × *C. florida* Sweetwater Red'.

The most basal cluster in this group is the Ruth Ellen® clade ( $K2 \times C. florida$  ‘Springtime’) and the accession K196-76 (a *C. kousa* offspring of ‘Beni fuji’). Stellar Pink® is the next clade followed by its sister clade Hyperion®. As would be expected, KF45-29 biological replicates clustered together and KF137 half-sibs clustered together with their female parent KF83-1. KF83-1 is on OP seedling of KF45-29. KF137 and KF45-29 accessions clustered in the Hyperion® clade along with two seedlings H3DR08P74 and H3DR08P73, which are OP seedlings of Hyperion®. All of these accessions share a common ancestor in K2 and/or *C. florida* ‘Sweetwater Red’.

The Hyperion® and Stellar Pink® clades were placed adjacent to one another, which was expected since KF45-29, Hyperion®’s mother, and Stellar Pink® are full siblings. The Constellation® clade is sister clades with the clade that includes both Aurora® and Stardust®. Constellation® and Stardust® are full siblings ( $K2 \times C. florida$  ‘Cherokee Princess’)

It is possible to place the likely identities of nine out of the fourteen unidentified accessions in this group based where they are placed in the dendrogram and the fact that they are from a limited pool of possible genotypes being clearly hybrid dogwoods, which are sterile (with the exception of Hyperion®) and of which a very limited number have been released commercially (only the Stellar Series® plants). All unidentified accessions except D039 and DB02 belong to a stock block or plantings throughout the Rutgers Gardens that contains only Stellar Series® plants. Unfortunately the field maps were lost when the land was turned over to the display gardens decades ago and the trees cannot be



identified. Our data helped elucidate the identity of these accessions. Accessions DB02 and D220 both clustered within the Ruth Ellen® clade suggesting that these two accessions are Ruth Ellen® clones. The other accessions RGC-209 in the Stellar Pink® clade, D233 and D039 in the Hyperion® clade, RGC-200 in the Constellation® clade, RGC-199 in the Aurora® clade and lastly D242 and RGC-210 in the Stardust® clade are all likely clones of the Stellar® Series cultivar clade they clustered into (Table 5). Shared allele data strongly support these identity placements (data not shown). The Constellation® clade contains three more unknown varieties but they cluster with K196-48, an offspring of *C. kousa* ‘Benifuji’ × *C. kousa* ‘Rosabella’ making it difficult to place their potential identity. Allele data is inconclusive. All of these unidentified accessions were part of a field of Stellar® Series clones limiting the possible genotypes to the six cultivars in the Stellar® Series.

### **Group 3: *Cornus* × *elwinortonii* group**

The *Cornus* × *elwinortonii* group is a small group (n=19; Figure 5) that contains *Cornus* × *elwinortonii* accessions and cultivars from the RU breeding program. It is found interior to a group of four *C. kousa* accessions (‘Galzam’ Galilean™, two Polly Hill seedlings from UT, and an unknown cultivars held in the Rutgers collection) and the Stellar Series® clade. The two cultivars from the *Cornus* × *elwinortonii*® series, Venus® ([*C. kousa* ‘Chinensis’ × *C. nuttallii* ‘Goldspot’] × *C. kousa* ‘Rosea’) and Starlight® (*C. kousa* ‘Simpson No. 1’ × *C. nuttallii* ‘Goldspot’), are held in this group as well as *C. kousa* ‘K2’. All accessions in the group share at least one of the following accessions in their breeding histories: *C. nuttallii* ‘Goldspot’ or KN3G-3 (*C. kousa* ‘Chinensis’ × *C. nuttallii*

‘Goldspot’) the offspring of ‘Goldspot’. While the pedigree record is lost, it is known the accession D178 is an F<sub>1</sub> of *C. kousa* × *C. nuttallii* (Orton, personal communication) supporting placement in this clade. Similarly, it can be assumed that the unidentified accessions DB09 and D074 also share these common ancestors.

**Group 4:** *C. kousa* inter-specific hybrid group

The *C. kousa* hybrid group (n=57; Figure 6) contains many advanced generation hybrids (n=25) with diverse pedigree records and was broken into three clades by the UPGMA analysis: the Cultivar clade, Hybrid clade 1 and Hybrid clade 2. The cultivar clade (n=12) is the most interior clade and contains 10 cultivars or OP seedlings from cultivars (Polly Hill PHK201 and Polly Hill PHK3; Table 2) and two accessions where identities have been lost (note D245 is a variegated *C. kousa*) and cannot be confirmed with our data.

Accessions in both hybrid clade 1 and hybrid clade 2 share many common ancestors to Group 1, 2 and 3 supporting this clades more interior position to the dendrogram. Common hybrids to this group, while sharing similar ancestors to Groups 2 and 3, KN144, KN71 and KN123, appear to be unique to this group because they share ancestry with additional germplasm accessions (Figures 1 and 6). All hybrid accessions of these types share KN30-1 (*[C. kousa* ‘Chinensis’ × *C. nuttallii* ‘Goldspot’] × *C. kousa* ‘Rosea’) in their breeding histories. KF45-29, a hybrid of *C. kousa* ‘K2’ × *C. florida* ‘Sweetwater Red’ is also another common ancestor in both Hybrid clade 1 & 2.

Based on breeding history, these two clades appear to be more closely related to each other than the cultivar clade; however, the dendrogram places the cultivar clade and hybrid clade 1 as sister clades and hybrid clade 2 as the most basal group. This makes the hybrid clade group paraphyletic. This clade includes many accessions with the codes H4A and H3D. Many of these accessions arose from open pollination events from a similar pool of parent trees (Rutgers breeding block located in Millstone, NJ); thus, potentially sharing unknown pollen parents. Most of these trees share phenotypic characteristics to *C. kousa* including flowering in late May in New Jersey and producing aggregate fruit. These trees, while being hybrids with *C. florida* and/or *C. nuttallii* ancestry, likely represent multi-generation backcrosses to *C. kousa* and *C. kousa* hybrids.

#### **Group 5:** Pink-bracted *C. kousa* group

The largest group (n=104; Figure 7 and 8) in the UPGMA dendrogram is the pink-bracted *C. kousa* group, which contains 15 accessions that are cultivars, of which nine are distinct. The majority of this group is made up of advanced generation breeding selections and nine accessions that are lacking identity information. This group is divided into five smaller clusters.

The most basal cluster holds the four *C. kousa* ssp. *angustata* ‘Elsbry’ Empress of China progeny that are the results of a cross of ‘Elsbry’ with a mixture of pollen collected from *C. kousa* ‘Satomi’ and ‘Rosea’ (Figure 7). Immediately interior to these are a cluster of four *C. kousa* accessions largely with uncertain origins. The remainder of the plants in this group were divided into four major clusters. The Kousa-Nuttallii hybrid clade, holds

two unidentified hybrid accessions, two known *Cornus* × *elwinortonii* hybrids and *C. kousa* ‘Simpson No. 1’ (K26-2; Figure 7). The lack of clear breeding histories makes the relationships in this clade difficult to discern, although ‘Simpson No. 1’ has been used in the Rutgers breeding program (parent of KN4-43' Starlight®).

The *C. kousa* hybrid Clade 1 (n=16) is immediately below the Kousa-Nuttallii hybrid group and has the accession H4AR05P63 placed in a basal position. This accession is an open pollinated seedling of the hybrid K194-7. K197 hybrids are from a *C. kousa* ‘Rosabella’ × ‘Rosea’ or ‘Satomi’ cross. This clade contains 12 OP seedlings from the following inter- and intra-specific hybrids: KF99-540, KF137-47, KN161-119, K202-14, K206-239 and K185-20. *C. kousa* ‘K2’ and the KN30 hybrids are common in this clade. KF137-47 is the offspring of KF83-1 × *C. kousa* ‘K2’. The mother tree, KF83-1 is an OP seedling of KF45-29. KF45-29 is the offspring of *C. kousa* ‘K2’ × *C. florida* ‘Sweetwater Red’. KN161-119 is the OP offspring of KN30-1. K202-14 is the female parent to one of the seedlings in this clade (H3DR06P70) and is a cross between *C. kousa* ‘K2’ and one of three trees: KF95-1, KN30-8, KN30-1. K206-239 is the female parent to one seedling in this clade (H4AR13P11) and is a cross between *C. kousa* ‘Doubloon’ × *C. kousa* ‘K2’. KF99-540 is the parent to one seedling (H4AR11P04) and is a cross between *C. kousa* ‘Red’ × *C. florida* ‘Spring Song’.

The kousa hybrid clade 1 is placed adjacent to the largest clade in the group (n=62), named the pink-bracted Kousa clade because it holds 41 *C. kousa* accessions, most of which have pink floral bracts (Figure 8). Eighteen inter-specific hybrids and three

unidentified accessions are also included in this clade. The most basal group in this clade consists of *C. kousa* inter-specific hybrids all of which have pink-bracted ancestors. Less basal groups in this clade contain intra- or inter-specific hybrids or OPOP seedlings of the following pink-bracted *C. kousa* cultivars: ‘Rosabella’, ‘Rosea’, ‘Heart Throb’, ‘Miss Satomi’ (syn. ‘Satomi’, syn. ‘Red Satomi’), ‘Radiant Rose’, ‘Benifuji’ and ‘Akatsuki’ (a variegated sport of ‘Satomi’). This dendrogram supports previous reports that describe cultivar synonymy in pink-bracted *C. kousa* cultivars (Trigiano et al., 2004). OP seedlings, cultivars and intra-specific hybrids of all the above pink-bracted *C. kousa* cultivars are dispersed throughout this clade and do not necessarily cluster by the maternal parent cultivar, which may be due the contribution of their unknown and potentially diverse male parents. These accessions cluster together because they are derived from only a few parental sources. There are a few possible explanations for this close relationship of available cultivars of pink-bracted *C. kousa*. One hypothesis is that while these accessions are supposed to be different cultivars they are actually highly related, if not genotypically identical, which was shown to be the case for the cultivars ‘Heart Throb’, ‘Rosabella’ and ‘Miss Satomi’ (Trigiano et al., 2004). A second hypothesis could be mislabeling of similar pink-bracted cultivars at the nursery level resulting in distinct genotypes being sold and marketed as the same cultivar.

The final clade in this group (n= 12; Figure 7), called Kousa hybrid clade 2, contains nine inter-specific hybrids, one unidentified accession and two intra-specific *C. kousa* hybrids. KN148 hybrids are unique to this clade and are offspring of *C. kousa* ‘K2’ and one of the following pollen parents: *C. kousa* ‘Satomi’, *C. kousa* ‘Rosea’, *C. kousa* ‘Rosabella’, KN30-1 or KN30-8. Two selections (H3DR06P80 and H4AR12P02) are OP offspring of

K202-14. As stated earlier, K202-14 is the offspring from *C. kousa* ‘K2’ and either KF95-1, KN30-8 or KN30-1. KN161-119  $\times$  OP and KF137  $\times$  OP selections are also included in this clade. All accessions in this clade are again connected through *C. kousa* ‘K2’ and/or accessions of KN30. The small sub-clade (n=3) consisting of KF137 hybrids, while some having light pink-bracts, does not have any pink-bracted *C. kousa* in its background. The only pink-bracted ancestor in these hybrids’ breeding history is the pink-bracted *C. florida* ‘Sweetwater Red’.

### *Structure analysis*

Bayesian clustering analysis results from the program STRUCTURE are shown in Figure 9. Accessions were inputted into the STRUCTURE analysis in the order they appeared in the UPGMA dendrogram. The top-most accession (TX1 107) is represented by number 1 in Figure 9 and this continues as you move down the dendrogram. The (*K*) value for the most parsimonious number of populations was chosen based on the maximum value for the first plateau of the graphical representation of the average estimated log probability  $\Pr(X|K)$  curve as well as the Delta*K*, both of which agreed. The (*K*) was chosen to be 5 based on these criteria. The value of (*K*)=5 also matched the number of groups in UPGMA dendrogram and nicely matched the breeding histories.

The STRUCTURE results closely match the UPGMA dendrogram and breeding histories with a few exceptions. Using the UPGMA output, the STRUCTURE analysis and known breeding histories the accessions were placed into final consensus groups. A small number of accessions were placed into different final consensus groups from the

UPGMA placement based on support from STRUCTURE and known breeding histories. A level of admixture greater than 50% was considered strong support from the STRUCTURE analysis. According to STRUCTURE, if admixture was high and not a single (K) group was above 50%, accessions were moved based on breeding history. Thirteen accessions were moved into the *Cornus* × *elwinortonii* consensus group even though they did not place in the corresponding clade in the UPGMA dendrogram. The *Cornus* × *rutgersensis* group in STRUCTURE strongly coincided with the UPGMA dendrogram grouping except for a lone accession found in the Pink-bracted *C. kousa* group (K2; 258) which was moved to the final *Cornus* × *rutgersensis* consensus group. Seven accessions were moved into the Pink-bracted *C. kousa* group even though they placed outside the *C. kousa* hybrid group (n=4) and internal to the *C. kousa* hybrid group (n=3) in the UPGMA dendrogram. The hybrid *C. kousa* group contains a high level of admixture, but predominantly consists of accessions that coincide with the UPGMA group. Three accessions (215, 222 and 223) which STRUCTURE places into the Pink-bracted *C. kousa* group (Figure 9) and six accessions (228-233) which STRUCTURE places into the *Cornus* × *elwinortonii* group (Figure 9) were moved to better fit the final consensus groupings. The STRUCTURE Pink-bracted *C. kousa* group strongly agreed with the UPGMA except six accessions that were moved into the group and seven accessions that were moved out of the group.

#### **Group 1: *C. florida* group**

The corresponding *C. florida* STRUCTURE grouping coincides strongly with the UPGMA *C. florida* grouping and consists of 99 accessions forming the *C. florida*

consensus group. Accession with the STRUCTURE ID 8 (KFN1-1 048), a hybrid containing *C. kousa*, *C. nuttallii* and *C. florida* in its breeding history, showed admixture from three groups (Figure 9) (*C. florida* group, *Cornus* × *rutgersensis* and *Cornus* × *elwinortonii*). As such, the STRUCTURE placement of this accession accurately represents its known breeding history. This accession was moved to the *Cornus* × *elwinortonii* consensus group because the color bar representing this group is largest and it agrees with the breeding history.

### **Group 2: *Cornus* × *rutgersensis* group**

This STRUCTURE grouping placed all accessions included in the UPGMA *Cornus* × *rutgersensis* group except for one accession (105, K196-76 089) (Figure 9).

STRUCTURE did not resolve the grouping of this accession because of high levels of admixture. Only 1 accession (258; K2) that belongs in this grouping is placed outside of the grouping in the UPGMA dendrogram. This accession *C. kousa* ‘K2’ is the parent to all the *Cornus* × *rutgersensis* trees and is in the breeding history of many *Cornus* × *rutgersensis* hybrids so its placement into the *Cornus* × *rutgersensis* consensus group agrees with the breeding history.

### **Group 3: *Cornus* × *elwinortonii* group**

The *Cornus* × *elwinortonii* consensus group includes more accessions than the corresponding group in the UPGMA dendrogram. Accessions with STRUCTURE IDs 102, 103 and 104 (Barrick 116, Corigo Giant 115 and Gold Spot 114) were all included in this group while the UPGMA dendrogram placed these accessions as an outgroup to



the large clade that includes the *Cornus* × *rutgersensis*, *Cornus* × *elwinortonii*, *C. kousa* hybrid and Pink-bracted *C. kousa* groups. These three accessions are cultivars of *C. nuttallii*, one of the parent species of *Cornus* × *elwinortonii* hybrids agreeing with the placement into the *Cornus* × *elwinortonii* consensus group. The unknown accession with STRUCTURE ID 177 (D071; Figure 9) is included in this group as well, while it is placed as an outgroup to the clade two *C. kousa* groups in the UPGMA dendrogram (Figure 1). This accession is unidentified so the validity of either grouping is impossible to confirm. Another six accessions (STRUCTURE IDs 228-233; K26-2 236, Chinensis 186, K26-2 237, DB07, D118 and RGC-201), which fall in the interior of the UPGMA dendrogram *C. kousa* inter-specific hybrid group (Group 4, Figure 6) are placed in the *Cornus* × *elwinortonii* group by STRUCTURE (Figure 9). This small clade (Figure 4) consists of three unidentified accessions and three *C. kousa* cultivars. *C. kousa* ‘Chinensis’ can be found in the breeding history of KN30 *Cornus* × *elwinortonii* hybrids such as Venus® supporting the STRUCTURE placement of these accessions into this group. K26 accessions are distinct trees of the *C. kousa* ‘Simpson’s No. 1’ cultivar. This cultivar can be found in the background of Starlight® confirming the placement of K26-2 in this group.

Three more accessions with STRUCTURE IDs 246, 249 and 250 (KN161-204 009, DB04 and KFN88-17 004) were placed into this group (Figure 9) even though the UPGMA analysis placed them in a small clade in the Pink-bracted *C. kousa* group along with accessions 247 and 248 (K26-2 235 and DB04; Figure 7-8). Accession 246, 249 and 250 were moved into this consensus group because the breeding history of the two

identified accessions match with the *Cornus* × *elwinortonii* group containing KN30 hybrid parents. STRUCTURE ID 273 (D244) is another accession that was placed in the *Cornus* × *elwinortonii* group based on STRUCTURE analysis (Figure 9) and in the Pink-bracted *C. kousa* group based on the UPGMA dendrogram (Figure 8). It was moved to the *Cornus* × *elwinortonii* consensus group; however it is impossible to confirm this grouping because it is unidentified. STRUCTURE ID 158, which is included in the *Cornus* × *elwinortonii* group in the UPGMA dendrogram, has an unclear grouping in STRUCTURE but will be kept in the *Cornus* × *elwinortonii* consensus group because it is a KN161 hybrid with a breeding history that agrees with this placement.

#### **Group 4: *C. kousa* hybrid group**

This STRUCTURE group, which consists of 62 accessions, is partly congruent with the respective UPGMA group (Figure 6-9). As discussed previously, a few accessions that were placed in the UPGMA dendrogram group do not belong based on the STRUCTURE analysis. Accessions 215 (H3DR03P10-KN144-2 × OP) and 222 (H3DR03P75-KF-137-47 × OP) were removed from this group (Figure 6) placed in the Pink-bracted *C. kousa* consensus group based on STRUCTURE and that both of these accessions have pink-bracted *kousa* dogwoods in their breeding history. H3DR03P10 is an offspring of KN144-2, whose mother tree was an offspring of *C. kousa* ‘Benifuji’ × ‘Rosabella’. Both of these accessions were moved out of this group and to their appropriate consensus group suggested by the STRUCTURE analysis, as well as supported with known breeding histories.

As stated previously, a small group of accessions (228-233) were placed in this group based on the UPGMA dendrogram (Figure 6) but breeding history and STRUCTURE suggest a more appropriate placement as the *Cornus* × *elwinortonii* consensus group. One major difference is the UPGMA dendrogram includes accessions 238-241 (H3DR01P77-Empress of China × OP, H3DR07P22-Empress of China × OP, H3DR04P17-Empress of China × OP and H3DR07P17-Empress of China × OP) in the Pink-bracted *C. kousa* group (Figure 7-8). STRUCTURE places these four accessions in the *C. kousa inter-specific* hybrid group (Figure 9), which agrees more with the breeding history than the UPGMA grouping. All four accessions are *C. kousa* var. *angustata* × *C. kousa* hybrids. *C. kousa* var. *angustata* is a white-bracted subspecies of *C. kousa* that is evergreen and flowers several weeks later. Breeding history (male pollen parent of *C. kousa* ‘Rosea’ or ‘Satomi’) supports the placement of these accessions here. Three accessions (261, 262 and 263; D491, Sun Splash 483 and H3DR04P03-KF137-47 × OP) also clustered into this STRUCTURE group (Figure 9) but were placed on the interior of the UPGMA Pink-bracted *C. kousa* group (Figure 8). Accession 262 is a variegated *C. kousa* cultivar and accession 263 is a *Cornus* × *rutgersensis* hybrid. Neither of these accessions are pink-bracted, agreeing with the STRUCTURE placement of these accessions now placed into the *C. kousa* hybrid consensus group.

Accessions 152-155 (Galilean 006, Polly Hill C10-08-57 74, Polly Hill PHK2 73 and K-6 222) are also included in this consensus group even though the UPGMA analysis places them in basal groups to the *Cornus* × *elwinortonii* group. These four accessions are *C. kousa* cultivars and breeding selections. Their breeding histories coincide more closely with the *C. kousa* hybrid group and therefore were moved into this consensus group.

Three more accessions (101, 178 and 272; Empress of China Elsby, KN09 061 and KF83-1 083; Figure 9) were moved into this consensus group as well. *C. kousa* ‘Empress of China Elsby’ is a cultivar of *C. kousa* ssp. *angustata*; therefore, it should be clustering in this group that also contains other *C. kousa* ssp. *angustata*. In the UPGMA dendrogram, this accession clustered as part of a basal grouping to the large clade that includes the *Cornus* × *rutgersensis*, *Cornus* × *elwinortonii*, *C. kousa* hybrid and Pink-bracted groups (Figure 1). KF83 1 083 is *Cornus* × *rutgersensis* hybrid with a breeding history that agrees with the STRUCTURE placement.

Accession 236 has a high level of admixture making its placement here unclear; therefore, it was kept in this group. Accession 342 (Champions Gold 051) is a *C. kousa* cultivar making its placement as one of the most basal groups in the UPGMA dendrogram skeptical (Figure 1). STRUCTURE places this accession in the *C. kousa* hybrid consensus group a more accurate placement (Figure 9)

#### **Group 5: Pink-bracted *C. kousa* group**

This group consists of 92 accessions and is generally in agreement with the respective UPGMA group. As previously stated, accessions 249 and 250 (DB04 and KFN88-17 004; Figure 9) were placed into the *Cornus* × *elwinortonii* consensus group. Accession 250 has a breeding history that agrees with the placement of it into the *Cornus* × *elwinortonii* group. Accessions 261, 262, 263, 264 272 (D491, Sun Splash 483, H3DR04P03-KF137 × OP, H3DR10P02-KF137 × OP and KF83-1) were placed into the *C. kousa* inter-specific hybrid group (Group 4). As discussed earlier these accessions fit

better in the *C. kousa* hybrid group than this one. STRUCTURE places accession 343 (Lemon Ripple 488) into this group as well. Accessions 175, 176, 179 and 180 (Lustgarten Weeping 196, RGC-197, KN112-50 133 and H4AR04P02-K196-29  $\times$  OP) were also placed into this group. One of these accessions is unidentified but H4AR04P02-K196-29  $\times$  OP and KN112-50 have breeding histories that agree with the placement of these accessions into the Pink-bracted *C. kousa* consensus group.

### AMOVA

Accessions were placed into consensus groups based on the UPGMA dendrogram, the STRUCTURE analysis and known breeding histories. In general, the UPGMA dendrogram and STRUCTURE analysis agreed. All of the accessions in this study were assigned to one of the five consensus groups for the AMOVA.

The AMOVA showed 78% of the genetic variation was due to within-population variance, compared to 22% being due to among-population variance (Figure 10). The within-population variance was partitioned out into the five consensus groups. The percentage each consensus group contributed to the within-population variance was calculated showing a range from 10% to 36% (Figure 10). The highest percentage of within-population variation was found in the *C. florida* (Group 1) consensus group. This consensus group consisted of many wild selections from diverse origins potentially explaining the high percentage. The two lowest percentages of within-population variation were found in the *Cornus*  $\times$  *elwinortonii* (Group 3) consensus group and the *Cornus*  $\times$  *rutgersensis* (Group 2) with 10% and 14%, respectively (Figure 10). These

groups, which comprise mostly inter-specific hybrids, show low within-population variance, which is likely due to bottlenecks caused by the use of similar breeding parents and sterility in the  $F_1$  hybrid generation.

Pairwise  $F_{ST}$  values generated from the AMOVA analysis indicate that there exists a large genetic differentiation between consensus groups (Table 6). The AMOVA results also indicate that each consensus group is statistically different from the rest ( $P < 0.01$ ; Table 6).

## Conclusions

The results of this study help clarify some pedigree records, narrow the possible identities of 11 accessions (Table 5) and also create a clearer picture of the genetic diversity and relationships found in a large collection of BB *Cornus* germplasm. Similar to previous studies, SSR data shows an  $H_o$  of 0.5314, a PIC of 0.7177 and a (f) of 0.288, supporting that the combined Rutgers and UT germplasm collection is genetically diverse. The UPGMA dendrogram and the STRUCTURE analysis agree on the group placement of most of the accessions, and both are in agreement, in most cases, with known breeding histories and origins of the plant material. The UPGMA analysis placed the *C. florida* accessions basal to the remainder of the germplasm. The Stellar Series® clade, hybrids between *C. florida* and *C. kousa* (*Cornus* × *rutgersensis*) are interior to the *C. florida* clade. The *Cornus* × *elwinortonii* clade, hybrids of *C. kousa* and *C. nuttallii*, is interior to the Stellar Series® clade. The two most interior clades are the sister clades *C. kousa* hybrid clade and the Pink-bracted *C. kousa* clade. Both of these clades consist mostly of

*C. kousa* accessions. With this data, the potential identities of 13 unidentified accessions could be elucidated and five consensus groups (*C. florida* clade, *Cornus* × *rutgersensis* clade, *Cornus* × *elwinortonii* clade, *C. kousa* hybrid clade and *Pink-bracted C. kousa* clade) were identified in the collection. Six accessions could not be clearly placed into a consensus group (STRUCTURE IDs: 105, 236, 270, 335, 339 and 345) based on UPGMA and STRUCTURE analysis; known breeding histories were used to place these accessions. The population structure, high  $H_o$  and low ( $f$ ) show that the genetic diversity in the RU germplasm remains high even after multiple generations of selection and the repeated use of the same parents, such as *C. kousa* ‘K2’ and its offspring the interspecific hybrid KF45-29. However results of the AMOVA show that there were bottlenecks (likely due to few fertile hybrids) in two groups (Group 2 and 3) in the germplasm collection. Group 2 consists of largely half-sibs and some full-sibs which can also explain the low genetic variance in this group. It is essential for breeding programs to maintain high levels of genetic diversity, especially when the species is highly susceptible to inbreeding depression like BB-dogwoods. These findings are not entirely unexpected being that this germplasm collection consists of highly heterozygous breeding selections and because BB-dogwoods are highly self-incompatible, outcrossing species. These five consensus groups can help breeders place their germplasm collections and can be used to help select unrelated, diverse germplasm for use as parents in crosses to maintain and bolster genetic diversity in future releases.

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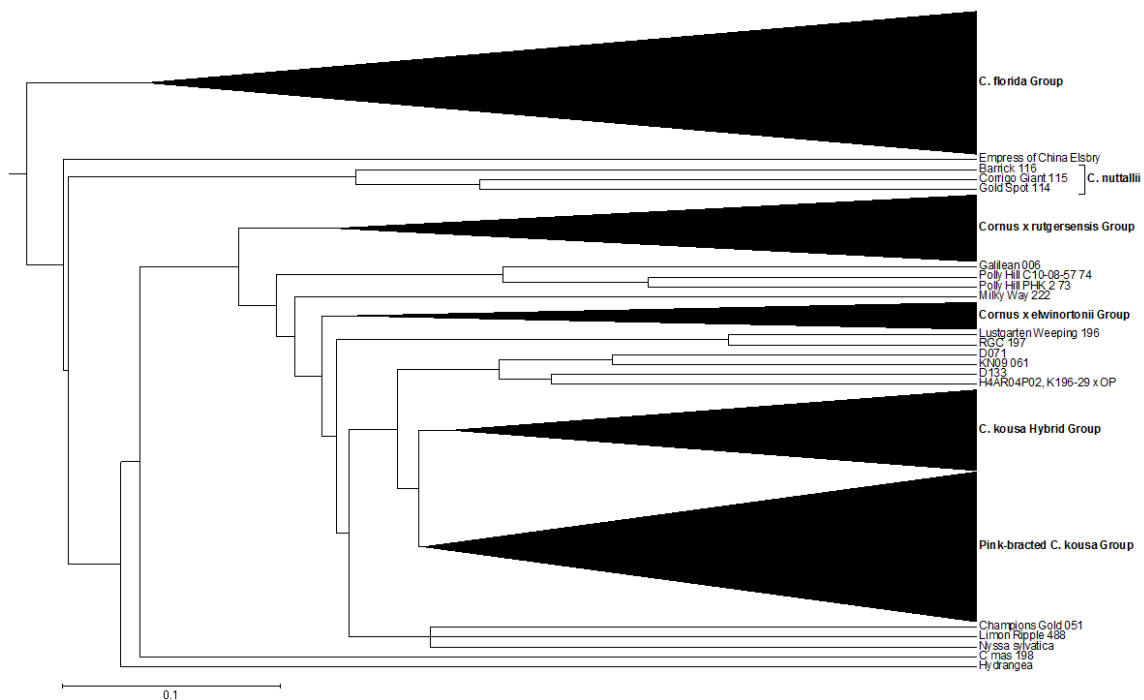
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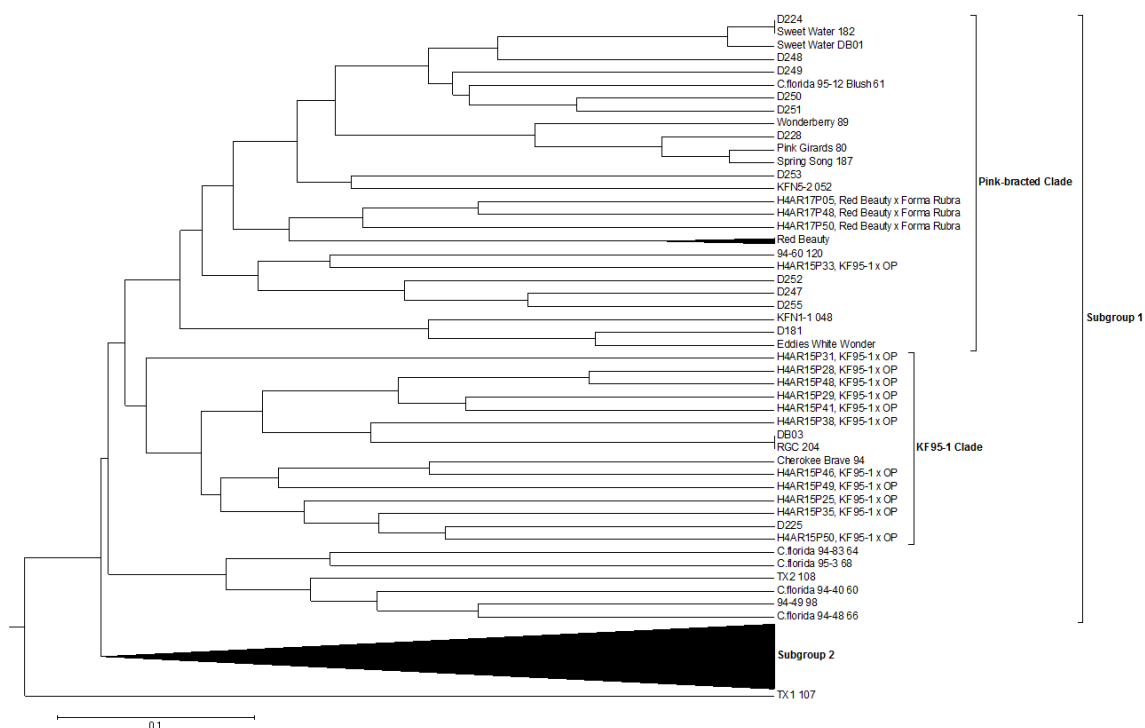
## Figures

**Figure 1.** Collapsed unweighted pair group method using arithmetic averages (UPGMA) dendrogram showing five groups. Each clade is condensed so the entire UPGMA dendrogram can be visualized. Accessions that are not condensed are outgroups and do not fit into other groups.



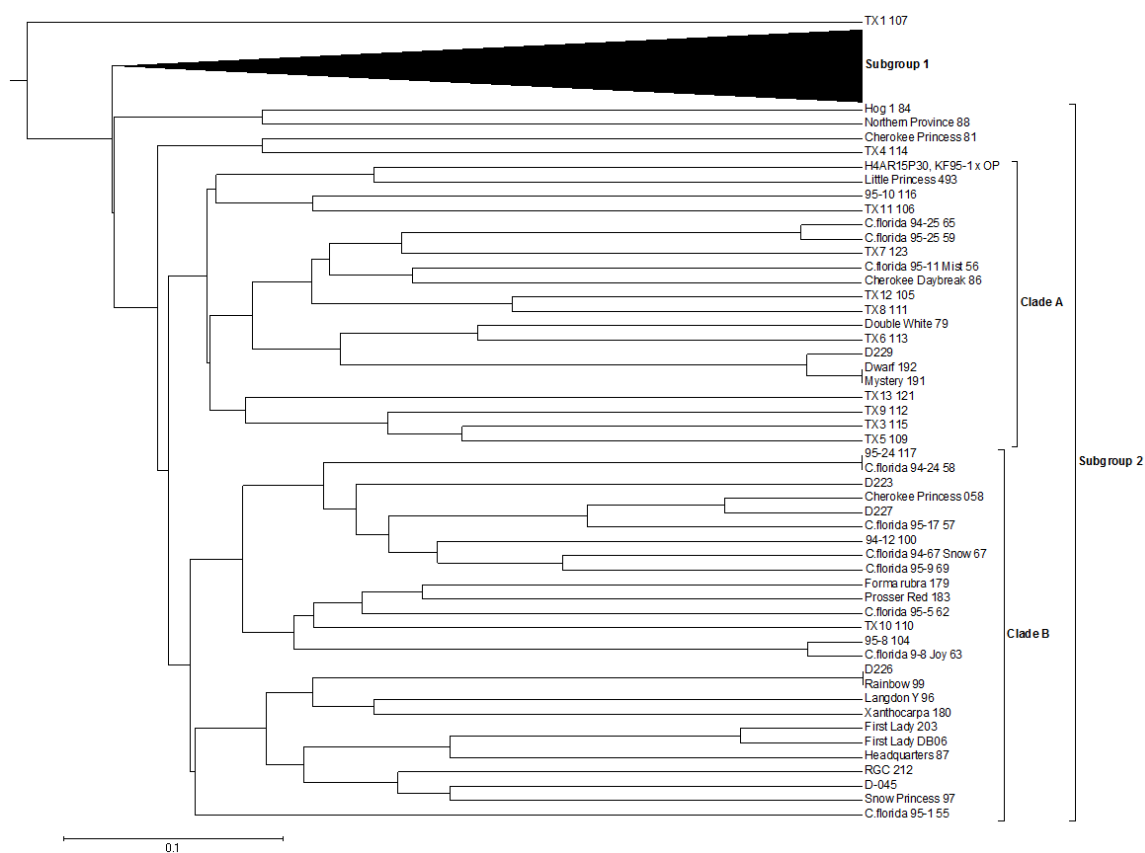
**Figure 2.** An unweighted pair group method using arithmetic averages (UPGMA)

dendrogram showing the *C. florida* group (Group 1) node. This node is shown with subgroup 2 collapsed for clarity. Subgroup 1 consists of three clades: KF95-1 clade, pink-bracted clade and Florida-Nuttallii hybrid clade.

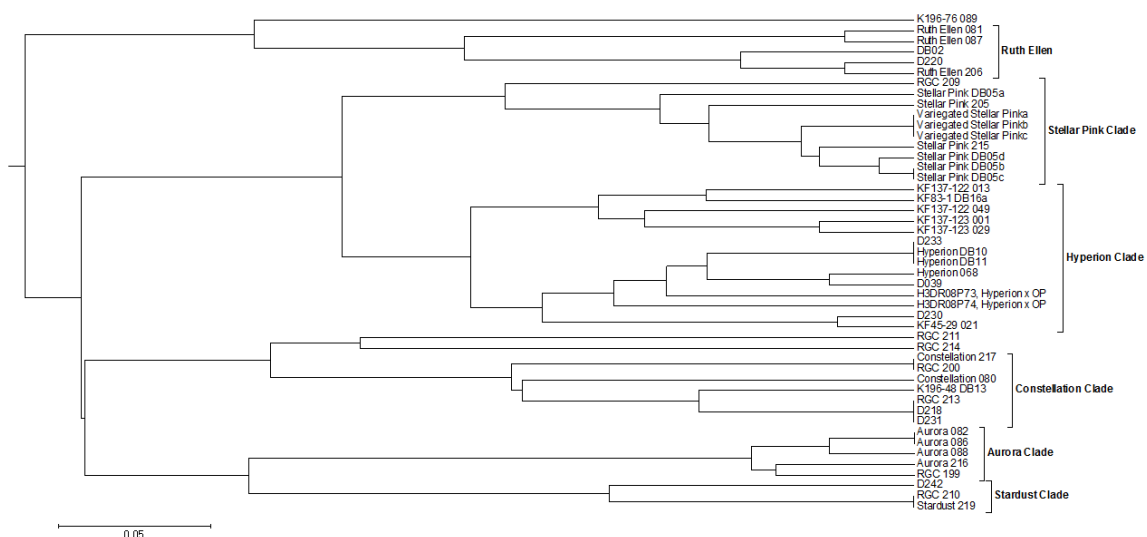


**Figure 3.** An unweighted pair group method using arithmetic averages (UPGMA)

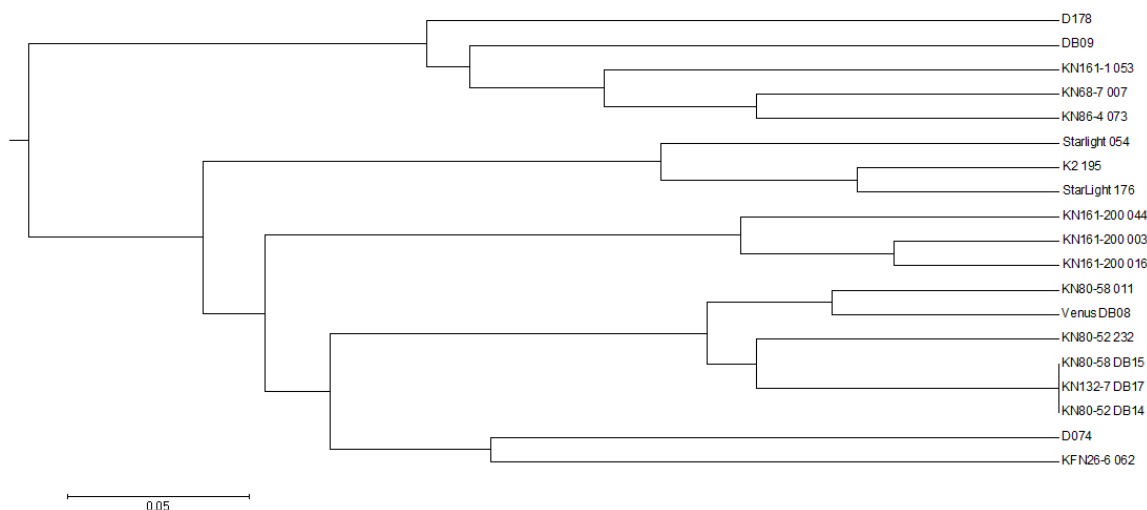
dendrogram showing the *C. florida* group (Group 1) node. This node is shown with subgroup 1 collapsed for clarity. Subgroup 2 contains three clades as well: University of Tennessee clade, red-bracted clade and cultivar clade.



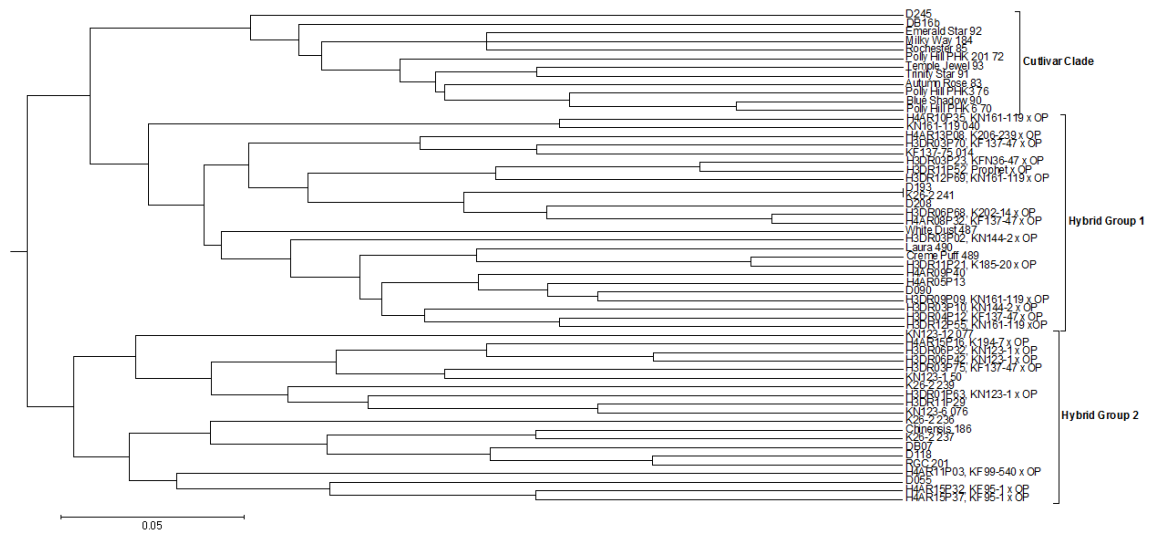
**Figure 4.** An uncollapsed unweighted pair group method using arithmetic averages (UPGMA) dendrogram showing the Stellar Series® (Group 2) node. This group contains six distinct clades all representing distinct cultivars.



**Figure 5.** An uncollapsed unweighted pair group method using arithmetic averages (UPGMA) dendrogram showing *Cornus × elwinortonii* (Group 3) node. This group is small and does not contain smaller distinct clades.

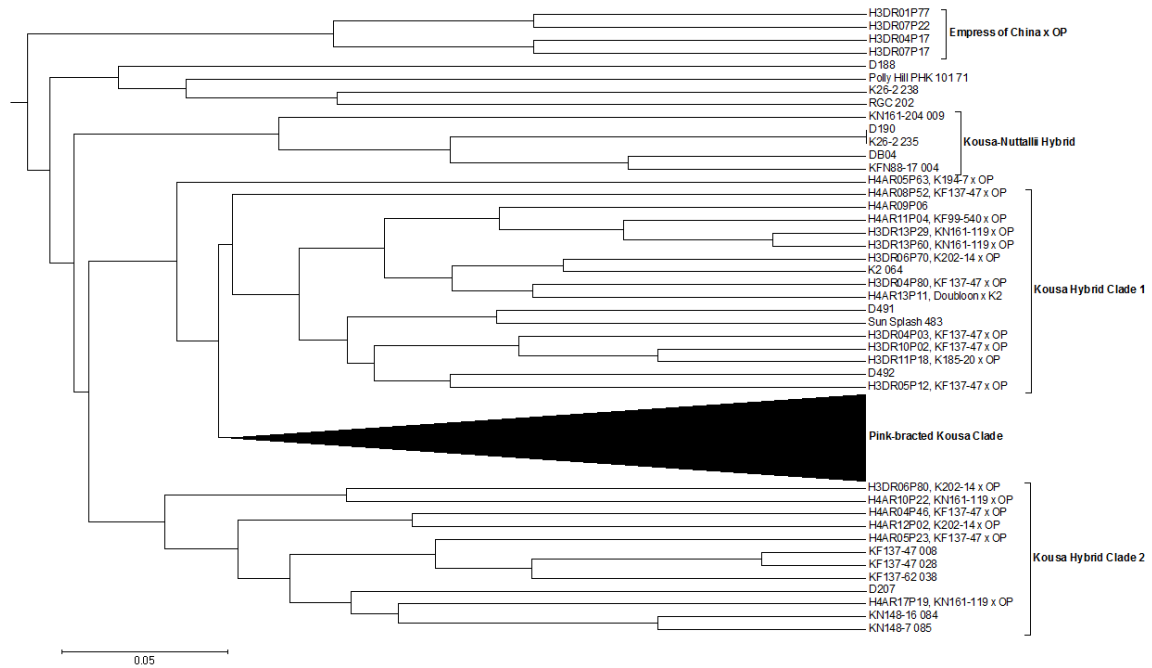


**Figure 6.** An uncollapsed unweighted pair group method using arithmetic averages (UPGMA) dendrogram showing *C. kousa* hybrid group (Group 4) node. This group contains three distinct clades: Cultivar clade, Hybrid group 1 and hybrid group 2.



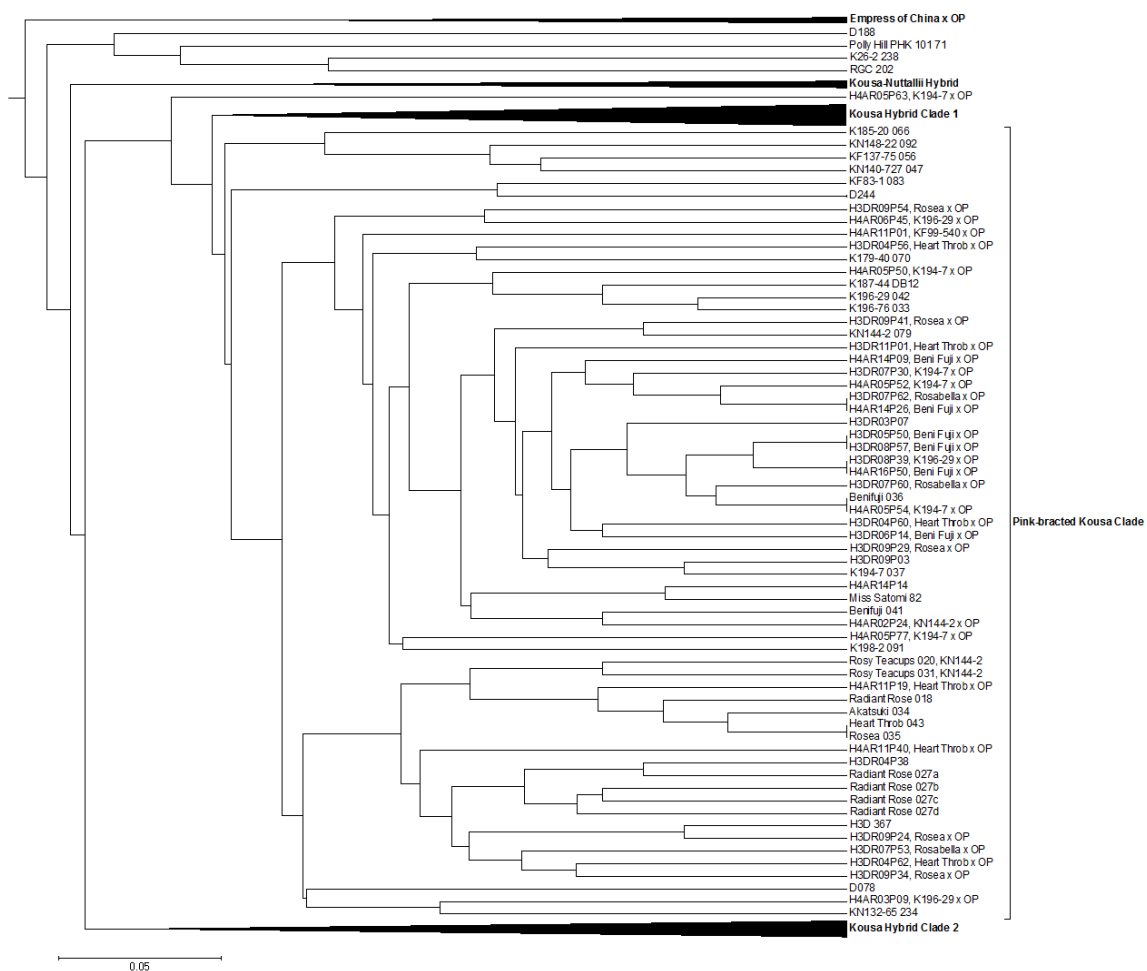


**Figure 7.** An unweighted pair group method using arithmetic averages (UPGMA) dendrogram showing the Pink-bracted *C. kousa* group (Group 5) node. This node is shown with a collapsed pink-bracted clade for clarity. There are five total clades in the group: Empress of China x OP, Kousa-Nuttallii hybrids, Kousa hybrid 1, pink-bracted Kousa and Kousa hybrid 2.

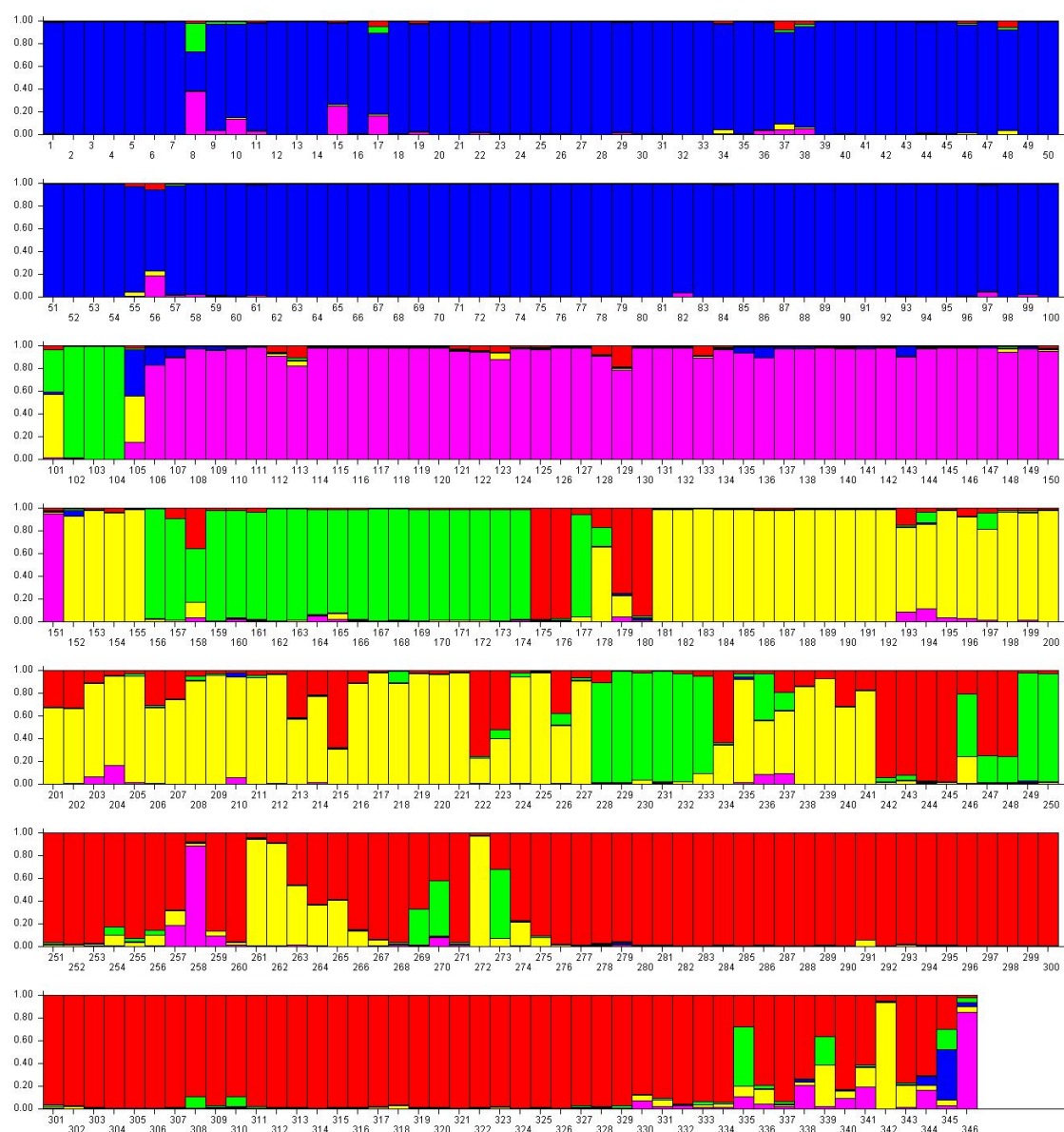


**Figure 8.** An unweighted pair group method using arithmetic averages (UPGMA)

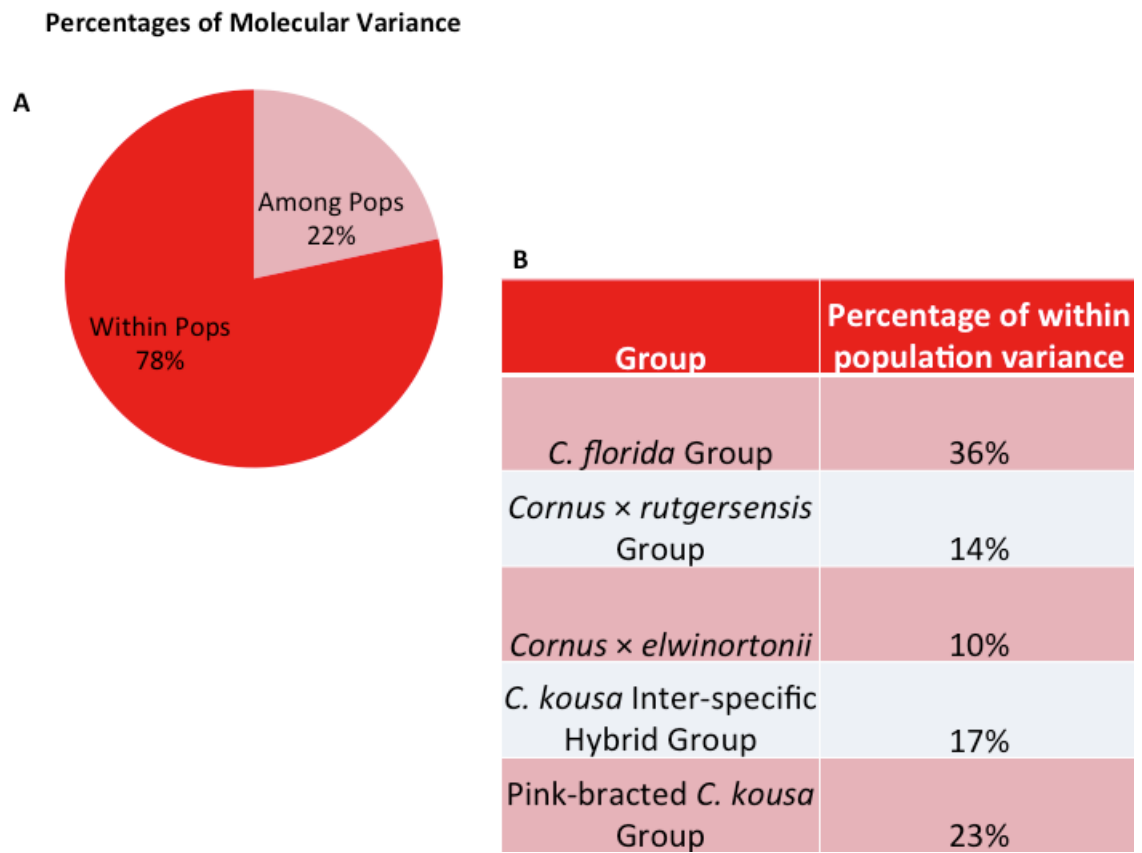
dendrogram showing the Pink-bracted *C. kousa* group (Group 5) node. This node is shown with all groups collapsed except the pink-bracted clade for clarity. There are five total clades in the group: Empress of China x OP, Kousa-Nuttallii hybrids, Kousa hybrid 1, Pink-bracted Kousa and Kousa hybrid 2.



**Figure 9.** STRUCTURE analysis resulting in the most parsimonious number of populations ( $K=5$ ). The accessions in the output are labeled with respect to their placement in the unweighted pair group method using arithmetic average (UPGMA) dendrogram (Figure 1-8), with the top most accession in the UPGMA dendrogram assigned Accession 1.



**Figure 10.** AMOVA Results **A** AMOVA generated pie-chart indicating the within-population and among-population variance. **B** A table indicating the breakdown of the within-population variance by consensus group.



## Tables

**Table 1.** Rutgers University cultivar releases including trademark name, parentage, year of plant patent (PP) and patent number. OP indicates open-pollination and brackets ([ ]) indicate the parentage of a hybrid parent.

<b>'Patent Name' Trademark Name</b>	<b>Species</b>	<b>Year – Plant Patent (PP) Number</b>	<b>Female Parent</b>	<b>Male Parent</b>
<b>'Rutdan' Celestial®</b>	<i>Cornus</i> × <i>rutgersensis</i>	1990 – PP7,204	<i>C. kousa</i> 'K2'	<i>C. florida</i> 'D1'
<b>'Rutban' Aurora®</b>	<i>Cornus</i> × <i>rutgersensis</i>	1990 – PP7,205	<i>C. kousa</i> 'K2'	<i>C. florida</i> 'Springtime'
<b>'Rutfan' Stardust®</b>	<i>Cornus</i> × <i>rutgersensis</i>	1990 – PP7,206	<i>C. kousa</i> 'K2'	<i>C. florida</i> 'Cherokee Princess'
<b>'Rutgan' Stellar Pink®</b>	<i>Cornus</i> × <i>rutgersensis</i>	1990 – PP7,207	<i>C. kousa</i> 'K2'	<i>C. florida</i> 'Sweetwater Red'
<b>'Rutcan' Constellation®</b>	<i>Cornus</i> × <i>rutgersensis</i>	1990 – PP7,210	<i>C. kousa</i> 'K2'	<i>C. florida</i> 'Cherokee Princess'
<b>'Rutlan' Ruth Ellen®</b>	<i>Cornus</i> × <i>rutgersensis</i>	1991 – PP7,732	<i>C. kousa</i> 'K2'	× <i>C. florida</i> 'Meyer White'

<b>‘Patent Name’ Trademark Name</b>	<b>Species</b>	<b>Year – Plant Patent (PP) Number</b>	<b>Female Parent</b>	<b>Male Parent</b>
<b>‘Rutman’ (Syn. ‘D-184-11’) Wonderberry®</b>	<i>C. florida</i>	1993 – PP8,213	<i>C. kousa</i> (unnamed)	<i>C. florida</i> ‘Forma rubra’
<b>‘Rutnam’ (Syn. ‘D376-18’) Red Beauty®</b>	<i>C. florida</i>	1993 – PP8,214	[ <i>C. florida</i> ‘Rubra’ × <i>C. florida</i> ‘Pygmy’]	[ <i>C. florida</i> ‘Royal Red’ × <i>C. florida</i> ‘Pygmy’]
<b>‘Rutnut’ Red Pygmy®</b>	<i>C. florida</i>	2004 – PP15,219	<i>C. florida</i> ‘Rutnam’ Red Beauty®	<i>C. florida</i> ‘Forma rubra’
<b>‘KN4-43’ Starlight®</b>	<i>Cornus</i> × <i>elwinortonii</i>	2006 – PP16,293	<i>C. kousa</i> ‘Simpson No. 1’	<i>C. nuttallii</i> ‘Goldspot’
<b>‘KN30-8’ Venus®</b>	<i>Cornus</i> × <i>elwinortonii</i>	2006 – PP16,309	[ <i>C. kousa</i> ‘Chinensis’ × <i>C. nuttallii</i> ‘Goldspot’]	<i>C. kousa</i> ‘Rosea’
<b>‘KF1-1’ Saturn®</b>	<i>Cornus</i> × <i>rutgersensis</i>	2007 – PP17,768	<i>C. kousa</i> ‘K2’	<i>C. florida</i> ‘D1’
<b>‘KF111-1’ Hyperion®</b>	<i>Cornus</i> × <i>rutgersensis</i>	2011 – PP22,219	KF45-29 [ <i>C. kousa</i> ‘K2’ × <i>C. florida</i> ]	Unknown

'Patent Name' Trademark Name	Species	Year – Plant Patent (PP) Number	Female Parent	Male Parent
'Sweetwater Red']				
'KN144-2' Rosy Teacups®	<i>Cornus</i> × <i>elwinortonii</i>	2014 – PP26,211	[KN30-4 × OP]	<i>C. kousa</i> 'Rosabella'

**Table 2.** Accession name, species, field location, pedigree record, unweighted par group method using arithmetic average (UPGMA) group, STRUCTURE (Pritchard et al, 2000) ID no. and consensus group. Species and pedigree information is displayed in shorthand code with the following key: 'F' indicates *C. florida* origins, 'K' indicates *C. kousa* origins, 'N' indicates *C. nuttallii* origins, 'OP' indicates open-pollination and 'OG' indicates the accession is an outgroup.

Accession	Species	Field Location	Pedigree Record	UPGMA Group	STRUCTURE ID No.	Consensus Group
KF137-123 001	KF	HF1 GH	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	2	124	2
Empress of China	A	HF1 GH	<i>C. kousa</i> var. <i>angustata</i> Chun 'Elsbry' Discovered by John Elsley in 1993	/	101	4

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Elsbry						
KN161- 200 003	KN	HF1 GH	KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'	3	165	3
KFN88-17 004	KFN	HF1 GH	KN30-1 × FN73-84 + OP; FN73 ⇒ FN63-15 × D1001 ( <i>C. florida</i> 'Red Cloud'); FN63 ⇒ FN10- 271 × OP; FN10 ⇒ <i>C. nuttallii</i> 'Goldspot' × D75-2 ( <i>C. florida</i> 'Welches Jr. Miss')	5	250	3
Galilean 006	K	/	<i>C. kousa</i> 'Galzam' of the Biblical Series™ from Lake County Nursery, Ohio (Cappiello and Shadow, 2005)	/	152	4
KN68-7 007	KN	HF1 GH	KN68 ⇒ KN6-18 × K144-7; K144 ⇒ K2 × K41; KN6 ⇒ K32 ( <i>C. kousa</i> 'Summer Stars') × <i>C. nuttallii</i>	3	159	3



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
'Goldspot'						
KF137-47 008	KF	HF1 GH	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	5	336	5
KN161- 204 009	KN	HF1 GH	KN30-1 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'	5	246	3
KN80-58 011	KN	HF1 GH	KN3G-3 × K58 ( <i>C. kousa</i> 'Red'); KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'	3	167	3
KF137-122 013	KF	HF1 GH	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	2	121	2
KF137-75 014	KF	HF1 GH	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	4	197	4
KN161-	KN	HF1 GH	KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i>	3	166	3

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
200 016			'Rosea'; KN3 $\Rightarrow$ <i>C. kousa</i> 'Chinensis' $\times$ <i>C. nuttallii</i>  'Goldspot'			
Radiant Rose 018	K	HF1 GH	<i>C. kousa</i> 'Hanros' Radiant Rose™ selected by Gary Handy of Handy Nursery in Boring, Oregon (Cappiello and Shadow, 2005)	5	313	5
Rosy  Teacups  020	KN	HF1 GH	KN144-2; KN144 $\Rightarrow$ KN109-92 $\times$ <i>C. kousa</i>  'Rosabella'; KN109 $\Rightarrow$ KN30-4 $\times$ OP; KN30 $\Rightarrow$ KN3G-3 $\times$ <i>C. kousa</i> 'Rosea'; KN3 $\Rightarrow$ <i>C. kousa</i>  'Chinensis' $\times$ <i>C. nuttallii</i> 'Goldspot'	5	310	5
KF45-29  021	KF	HF1 GH	KF45 $\Rightarrow$ <i>C. kousa</i> $\times$ <i>C. florida</i> 'Sweet Water'	2	127	2
Radiant  Rose 027	K	Millstone	<i>C. kousa</i> 'Hanros' Radiant Rose™ selected by Gary Handy of Handy Nursery in Boring, Oregon	5	318, 319, 320, 321	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
(Cappiello and Shadow, 2005)						
KF137-47 028	KF	Millstone	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	5	337	5
KF137-123 029	KF	Millstone	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	2	125	2
Rosy Teacups 031	KN	Millstone	KN144-2; KN144 ⇒ KN109-92 × <i>C. kousa</i> 'Rosabella'; KN109 ⇒ KN30-4 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'	5	311	5
K196-76 033	K	Millstone	<i>C. kousa</i> 'Beni Fuji' × <i>C. kousa</i> 'Rosea' + <i>C. kousa</i> 'Red Satomi'	5	282	5
Akatsuki 034	K	Millstone	Variegated sport of <i>C. kousa</i> 'Miss Satomi' found in Japan	5	314	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Rosea 035	K	Millstone	N/A	5	316	5
Benifuji 036	K	Millstone	Selected by Nobuo Yamashita, Hisao Ishikawa and Toshihiro Hagiwara in 1970 from Mt. Fuji in 1970 (Cappiello and Shadow, 2005)	5	297	5
K194-7 037	K	Millstone	<i>C. kousa</i> 'Beni Fuji' × <i>C. kousa</i> 'Rosabella'	5	303	5
KF137-62 038	KF	Millstone	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	5	335	5
D039	F	Millstone	N/A	2	134	2
KN161- 119 040	KN	Millstone	KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'	4	194	4
Benifuji	K	Millstone	Selected by Nobuo Yamashita, Hisao Ishikawa	5	306	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
041			and Toshihiro Hagiwara in 1970 from Mt. Fuji in 1970 (Cappiello and Shadow, 2005)			
K196-29	K	Millstone	<i>C. kousa</i> 'Beni Fuji' × <i>C. kousa</i> 'Rosea' + <i>C. kousa</i>	5	281	5
042			'Red Satomi'			
Heart	K	Millstone	<i>C. kousa</i> 'Schmred' Heart Throb™ Introduced by	5	315	5
Throb 043			Jim Schmidt of Don Schmidt Nursery in Boring, Oregon (Cappiello and Shadow, 2005)			
KN161-	KN	Millstone	KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i>	3	164	3
200 044			'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
D-045	F	Millstone	N/A	1	99	1
KN140-	KN	Millstone	KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i>	5	271	5
727 047			'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i>			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
'Goldspot'						
KFN1-1	KFN	Millstone	D40-6 ( <i>C. nuttallii</i> 'Eddies White Wonder') ×	1	8	1
048			K23-2 ( <i>C. kousa</i> 'Chinensis')			
KF137-122	KF	Millstone	KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP;	2	123	2
049			KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'			
KN123-1	KN	Millstone	KN71 × OP; KN71 ⇒ KN30-1 × OP; KN30 ⇒	4	223	5
50			KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i>			
			'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
Champion	K	Millstone	N/A	/	342	4
s Gold 051						
KFN5 2	KFN	Millstone	Eddies White Wonder' × <i>C. kousa</i> 'Summer Star'	/	17	1
052						
KN161-1	KN	Millstone	KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i>	3	158	3

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
053			'Rosea'; KN3 $\Rightarrow$ <i>C. kousa</i> 'Chinensis' $\times$ <i>C. nuttallii</i> 'Goldspot'			
Starlight	KN	Millstone	Starlight®, KN4-43 $\Rightarrow$ <i>C. kousa</i> 'Simpson No. 1' $\times$	3	161	3
054			<i>C. nuttallii</i> 'Goldspot'			
D055	F	Millstone	N/A	4	235	4
KF137-75	KF	Millstone	KF83 $\times$ <i>C. kousa</i> 'K2'; KF83 $\Rightarrow$ KF45-29 $\times$ OP;	5	270	5
056			KF45 $\Rightarrow$ <i>C. kousa</i> $\times$ <i>C. florida</i> 'Sweet Water'			
Cherokee	F	Millstone	Discovered by W.C. Higden (Cappiello and	1	53	1
Princess			Shadow, 2005)			
058						
KN09 061	KN	Millstone	KN09 $\Rightarrow$ <i>C. kousa</i> 'K41' $\times$ <i>C. nuttallii</i> 'D82'	/	178	4
KFN26-6	KFN	Millstone	KFN26 $\Rightarrow$ KN3G-3 $\times$ OP; KN3 $\Rightarrow$ <i>C. kousa</i>	3	174	3
062			'Chinensis' $\times$ <i>C. nuttallii</i> 'Goldspot'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
K2 064	K	Millstone	Acquired from Ben C. Blackburn from  Willowood Nursery on May 23rd 1949	5	258	2
K185-20 066	K	Adelphia	<i>C. kousa</i> 'Red Satomi' × <i>C. kousa</i> 'Rosea'	5	268	5
Hyperion 068	KF	Adelphia	Hyperion, KF111-1 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'	2	133	2
K179-40 070	K	Adelphia	<i>C. kousa</i> 'Rosea' × <i>C. kousa</i> 'Beni Fuji'	5	278	5
D071	unknown	Adelphia	N/A	/	177	3
KN86-4 073	KN	Adelphia	KN86 ⇒ KN6-18 × K59; KN6 ⇒ <i>C. kousa</i> 'Simpson No. 2' × <i>C. nuttallii</i> 'Goldspot'	3	160	3
D074	unknown	Adelphia	N/A	3	173	3
KN123-6	KN	Adelphia	KN71 × OP; KN71 ⇒ KN30-1 × OP; KN30 ⇒	4	227	4



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
076			KN3G-3 × Rosea; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
KN123-12	KN	Adelphia	KN71 × OP; KN71 ⇒ KN30-1 × OP; KN30 ⇒	4	218	4
077			KN3G-3 × Rosea; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
D078	unknown	Adelphia	N/A	5	327	5
KN144-2	KN	Adelphia	KN144-2 ⇒ KN109-92 × <i>C. kousa</i> 'Rosabella';	5	284	5
079			KN109 ⇒ KN30-4 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
Constellati on 080	KF	Adelphia	KF23-1; KF23 ⇒ <i>C. kousa</i> 'K2' × <i>C. florida</i> 'Cherokee Princess'	2	137	2
Ruth Ellen	KF	Adelphia	KF24-1; KF24-1 ⇒ <i>C. kousa</i> K2 × <i>C. florida</i>	2	106	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
081			'Meyer White' also known as Hillen Meyer White			
Aurora	KF	Adelphia	KF25-7; KF25 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	145	2
082			'Springtime'			
KF83-1	KF	Adelphia	KF83 $\Rightarrow$ KF45-29 $\times$ OP; KF45 $\Rightarrow$ <i>C. kousa</i> $\times$ <i>C.</i>	5	272	4
083			<i>florida</i> 'Sweet Water'			
KN148-16	KN	Adelphia	<i>C. kousa</i> 'K2' $\times$ ( <i>C. kousa</i> 'Satomi', <i>C. kousa</i>	5	340	5
084			'Rosea', <i>C. kousa</i> 'Rosabella', KN30-1, KN30-8)			
KN148-7	KN	Adelphia	<i>C. kousa</i> 'K2' $\times$ ( <i>C. kousa</i> 'Satomi', <i>C. kousa</i>	5	341	5
085			'Rosea', <i>C. kousa</i> 'Rosabella', KN30-1, KN30-8)			
Aurora	KF	Adelphia	KF25-7; KF25 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	146	2
086			'Springtime'			
Ruth Ellen	KF	Adelphia	KF24-1; KF24-1 $\Rightarrow$ <i>C. kousa</i> K2 $\times$ <i>C. florida</i>	2	107	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
087			'Meyer White' also known as Hillen Meyer White			
Aurora	KF	Adelphia	KF25-7; KF25 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	144	2
088			'Springtime'			
K196-76	K	Adelphia	<i>C. kousa</i> 'Beni Fuji' $\times$ <i>C. kousa</i> 'Rosea' + <i>C. kousa</i>	2	105	4
089			'Red Satomi'			
D090	unknown	Adelphia	N/A	4	213	4
K198-2	K	Adelphia	<i>C. kousa</i> 'Beni Fuji' $\times$ <i>C. kousa</i> 'Red Satomi'	5	309	5
091						
KN148-22	KN	Adelphia	<i>C. kousa</i> 'K2' $\times$ ( <i>C. kousa</i> 'Satomi', <i>C. kousa</i>	5	269	5
092			'Rosea', <i>C. kousa</i> 'Rosabella', KN30-1, KN30-8)			
H4AR05P6	K x OP	Hort	K194-7 $\times$ OP; K194 $\Rightarrow$ <i>C. kousa</i> 'Beni Fuji' $\times$ C.	5	251	5
3		Farm 4	<i>kousa</i> 'Rosabella'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H4AR05P7	K x OP	Hort	K194-7 × OP; K194 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	308	5
7		Farm 4	<i>kousa</i> 'Rosabella'			
H4AR05P5	K x OP	Hort	K194-7 × OP; K194 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	279	5
0		Farm 4	<i>kousa</i> 'Rosabella'			
H4AR05P2	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	5	334	5
3		Farm 4	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i> <i>florida</i> 'Sweet Water'			
H4AR04P0	K x OP	Hort	K196-29 × OP; K196 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	/	180	5
2		Farm 4	<i>kousa</i> 'Rosea' + <i>C. kousa</i> 'Red Satomi'			
H4AR03P0	K x OP	Hort	K196-29 × OP; K196 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	328	5
9		Farm 4	<i>kousa</i> 'Rosea' + <i>C. kousa</i> 'Red Satomi'			
Gold Spot	N	HF1 GH	N/A	/	104	3
114		Grafts				

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Corrigo	N	HF1 GH	Discovered in Columbia River Gorge (Cappiello	/	103	3
Giant 115		Grafts	and Shadow, 2005)			
Barrick	N	HF1 GH	N/A	/	102	3
116		Grafts				
Eddies	N	HF1 GH	N/A	1	10	1
White		Grafts				
Wonder						
D118	unknown	HF1 Field	N/A	4	232	3
KN112-50	KN	/	KN112 $\Rightarrow$ KN30-8 $\times$ <i>C. kousa</i> 'K2'	/	179	5
133						
H4AR12P0	K $\times$ OP	Hort	K202-14 $\times$ OP; K202 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ (KF95-1,	5	333	5
2		Farm 4	KN30-8, KN30-1)			
H4AR13P1	K	Hort	<i>C. kousa</i> 'Doubloon' $\times$ <i>C. kousa</i> 'K2'	5	260	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
1		Farm 4				
H4AR14P0	K x OP	Hort	<i>C. kousa</i> 'Beni Fuji' × OP	5	286	5
9		Farm 4				
H4AR14P1	K x OP	Hort	<i>C. kousa</i> 'Beni Fuji' × OP	5	304	5
4		Farm 4				
H4AR15P2	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ <i>C.</i>	1	44	1
5		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P2	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ <i>C.</i>	1	38	1
8		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P2	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ <i>C.</i>	1	40	1
9		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P3	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ <i>C.</i>	1	37	1
1		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H4AR15P3	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	4	236	4
2		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P3	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	4	237	4
7		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P4	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	41	1
1		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P4	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	50	1
6		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P4	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	48	1
9		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P5	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	47	1
0		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
H4AR15P4	KF x OP	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	39	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
8		Farm 4	<i>kousa</i> 'K2' × <i>C. florida</i> 'Sweet Water'			
StarLight	KN	Hort	Starlight®, KN4-43 ⇒ <i>C. kousa</i> 'Simpson No. 1' ×	3	163	3
176		Farm 1	<i>C. nuttallii</i> 'Goldspot'			
Red	F	D376-15	Red Beauty®, 'D376-15'; D376 ⇒ D328-3 ×	1	30, 31, 32,	1
Beauty C1		Original	D331-13; D328 ⇒ <i>C. florida</i> 'Rubra' × <i>C. florida</i> 'Pygmy'; D331 ⇒ <i>C. florida</i> 'Royal Red' × <i>C.</i> <i>florida</i> 'Pygmy'		33	
D178	unknown	Hort	N/A	3	156	3
		Farm 4				
Forma	F	Hort	N/A	1	88	1
rubra 179		Farm 4				
Xantho	F	Rutgers	Selection with yellow fruit	1	94	1
carpa 180		Gardens				



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Eddies	FN	/	N/A	1	9	1
White						
Wonder						
181						
Sweet	F	Rutgers	Selected by Boyd Nursery, McMinnville,	1	25	1
Water 182		Gardens	Tennessee in 1954 (Cappiello and Shadow, 2005)			
Prosser	F	Rutgers	Discovered by Bruce Howell in Knoxville,	1	89	1
Red 183		Gardens	Tennessee in 1917 (Cappiello and Shadow, 2005)			
Milky Way	K	Rutgers	Originated from 15 OP seedlings of Wayside	4	185	4
184		Gardens	Gardens in Perry, Ohio (Cappiello and Shadow, 2005)			
Chinensis	K	Rutgers	<i>C. kousa</i> var. <i>chinensis</i>	4	229	3

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
186		Gardens				
Spring	F	Rutgers	From New Canaan, Connecticut (Cappiello and	1	21	1
Song 187		Gardens	Shadow, 2005)			
D188	K	Rutgers	N/A	5	242	5
		Gardens				
D190	K	Rutgers	N/A	5	247	5
		Gardens				
Mystery	F	Rutgers	Discovered by Fred Galle in Winchester,	1	61	1
191		Gardens	Tennessee in 1965 (Cappiello and Shadow, 2005)			
Dwarf 192	F	Rutgers	N/A	1	60	1
		Gardens				
D193	K	Rutgers	N/A	4	201	4
		Gardens				

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
K2 195	K	Rutgers Gardens	Acquired from Ben C. Blackburn from Willowood Nursery on May 23rd 1949	3	162	3
Lustgarten Weeping 196	K	Rutgers Gardens	K-51; Selection by Jim Cross (Cappiello and Shadow, 2005)	/	175	5
RGC 197	K	Rutgers Gardens	N/A	/	176	5
C. mas 198	C. mas	Rutgers Gardens	N/A	/	345	1
RGC 199	unknown	Rutgers Gardens	N/A	2	148	2
RGC 200	unknown	Rutgers Gardens	N/A	2	136	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
RGC 201	unknown	Rutgers Gardens	N/A	4	233	3
RGC 202	unknown	Rutgers Gardens	N/A	5	245	5
First Lady 203	F	Rutgers Gardens	Selected by Boyd Nursery, McMinnville, Tennessee in 1969 (Cappiello and Shadow, 2005)	1	96	1
RGC 204	F	Rutgers Gardens	N/A	1	43	1
Stellar Pink 205	KF	Rutgers Gardens	KF27-3; KF27 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i> 'Sweetwater Red'	2	117	2
Ruth Ellen 206	KF	Rutgers Gardens	KF24-1; KF24-1 $\Rightarrow$ <i>C. kousa</i> K2 $\times$ <i>C. florida</i> 'Meyer White' also known as Hillen Meyer	2	110	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
White						
D207	K	Rutgers Gardens	N/A	5	338	5
D208	K	Rutgers Gardens	N/A	4	203	4
RGC 209	unknown	Rutgers Gardens	N/A	2	111	2
RGC 210	unknown	Rutgers Gardens	N/A	2	150	2
RGC 211	unknown	Rutgers Gardens	N/A	2	142	2
RGC 212	F	Rutgers Gardens	N/A	1	98	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
RGC 213	unknown	Rutgers Gardens	N/A	2	139	2
RGC 214	unknown	Rutgers Gardens	N/A	2	143	2
Stellar	KF	Hort	KF27-3; KF27 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	113	2
Pink 215		Farm 1	'Sweetwater Red'			
Aurora	KF	Hort	KF25-7; KF25 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	147	2
216		Farm 1	'Springtime'			
Constellati	KF	Hort	KF23-1; KF23 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	135	2
on 218		Farm 1	'Cherokee Princess'			
D218	KF	Hort	N/A	2	140	2
		Farm 1				
Stardust	KF	Hort	KF23-1; KF23 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	151	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
219		Farm 1	'Cherokee Princess'			
D220	KF	Hort	N/A	2	109	2
		Farm 1				
Milky Way	K	Stock	K-6; Originated from 15 OP seedlings of	3	155	4
222		Block	Wayside Gardens in Perry, Ohio (Cappiello and			
		R1P1	Shadow, 2005)			
D223	F	Stock	N/A	1	77	1
		Block				
		R1P2				
D224	unknown	Stock	N/A	1	24	1
		Block				
		R2P1				
D225	unknown	Stock	N/A	1	46	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
		Block				
		R2P2				
D226	unknown	Stock	N/A	1	91	1
		Block				
		R2P3				
D227	unknown	Stock	N/A	1	80	1
		Block				
		R3P1				
D228	unknown	Stock	N/A	1	19	1
		Block				
		R3P2				
D229	unknown	Stock	N/A	1	59	1
		Block				



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
		R4P1				
D230	unknown	Stock	N/A	1	126	2
		Block				
D231	unknown	Stock	N/A	2	141	2
		Block				
KN80-52	KN	Hort	KN3G-3 × K58 ( <i>C. kousa</i> 'Red'); KN3G-3 × <i>C.</i>	3	169	3
232		Farm 3	<i>kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C.</i>			
			<i>nutallii</i> 'Goldspot'			
D233	unknown	Hort	N/A	2	131	2
		Farm 3				
KN132-65	KN	HF3 graft	KN132 ⇒ KN30-1 × ( <i>C. kousa</i> 'Rosea', <i>C. kousa</i>	5	329	5
234			'Red Satomi', <i>C. kousa</i> 'K2', OP)			
K26-2 235	K	Hort	<i>C. kousa</i> 'Simpson No. 1'	5	248	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
		Farm 1				
K26-2 236	K	Hort	<i>C. kousa</i> 'Simpson No. 1'	4	228	3
		Farm 1				
K26-2 237	K	Hort	<i>C. kousa</i> 'Simpson No. 1'	4	230	3
		Farm 1				
K26-2 238	K	Hort	<i>C. kousa</i> 'Simpson No. 1'	5	244	5
		Farm 1				
K26-2 239	K	Hort	<i>C. kousa</i> 'Simpson No. 1'	4	224	4
		Farm 1				
K26-2 241	K	Hort	<i>C. kousa</i> 'Simpson No. 1'	4	202	4
		Farm 1				
D242	unknown	Hort	N/A	2	149	2
		Farm 1				

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
D244	K	Hort	N/A	5	273	3
		Farm 1				
D245	K	Hort	N/A	4	181	4
		Farm 1				
D247	F	Hort	N/A	1	12	1
		Farm 1				
D248	F	Hort	N/A	1	22	1
		Farm 1				
D249	F	Hort	N/A	1	26	1
		Farm 1				
D250	F	Hort	N/A	1	28	1
		Farm 1				
D251	F	Hort	N/A	1	29	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
		Farm 1				
D252	F	Hort	N/A	1	11	1
		Farm 1				
D253	F	Hort	N/A	1	16	1
		Farm 1				
D255	F	Hort	N/A	1	13	1
		Farm 1				
H4AR02P2	KN x OP	Hort	KN144-2 × OP; KN144 ⇒ KN109-92 × <i>C. kousa</i>	5	307	5
4		Farm 4	'Rosabella'; KN109 ⇒ KN30-4 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
H4AR04P4	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	5	332	5
6		Farm 4	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i>			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
<i>florida</i> 'Sweet Water'						
H4AR05P5	K x OP	Hort	K194-7 × OP; K194 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	288	5
2		Farm 4	<i>kousa</i> 'Rosabella'			
H4AR05P5	K x OP	Hort	K194-7 × OP; K194 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	298	5
4		Farm 4	<i>kousa</i> 'Rosabella'			
H4AR06P4	K x OP	Hort	K196-29 × OP; K196 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	275	5
5		Farm 4	<i>kousa</i> 'Rosea' + <i>C. kousa</i> 'Red Satomi'			
H4AR08P5	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × K2; KF83 ⇒	5	252	5
2		Farm 4	KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> 'K2' × <i>C. florida</i>			
			'Sweet Water'			
H4AR10P2	KN x OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	5	331	5
2		Farm 4	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i>			
			'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H4AR10P3	KN x OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	4	193	4
5		Farm 4	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
H4AR11P0	KF x OP	Hort	KF99-540 × OP; <i>C. kousa</i> 'Red' × <i>C. florida</i>	5	276	5
1		Farm 4	'Spring Song'			
H4AR11P0	KF x OP	Hort	KF99-540 × OP; <i>C. kousa</i> 'Red' × <i>C. florida</i>	4	234	5
3		Farm 4	'Spring Song'			
H4AR11P0	KF x OP	Hort	KF99-540 × OP; <i>C. kousa</i> 'Red' × <i>C. florida</i>	5	254	5
4		Farm 4	'Spring Song'			
H4AR11P1	K x OP	Hort	<i>C. kousa</i> 'Heart Throb' × OP	5	312	5
9		Farm 4				
H4AR11P4	K x OP	Hort	<i>C. kousa</i> 'Heart Throb' × OP	5	317	5
0		Farm 4				

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H4AR13P0	K x OP	Hort	K206-239 × OP; K206 ⇒ <i>C. kousa</i> 'Doubloon' × <i>C.</i>	4	195	4
8		Farm 4	<i>kousa</i> 'K2'			
H4AR15P1	K x OP	Hort	K194-7 × OP; K194 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	4	219	4
6		Farm 4	<i>kousa</i> 'Rosabella'			
H4AR16P5	K x OP	Hort	<i>C. kousa</i> 'Beni Fuji' × OP	5	295	5
0		Farm 4				
H4AR17P0	F	Hort	Red Beauty® × Forma rubra	1	35	1
5		Farm 4				
H4AR17P1	KN x OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	5	339	5
9		Farm 4	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
H3DR01P6	KN x OP	Hort	KN123-1 × OP; KN123 ⇒ KN71 × OP; KN71 ⇒	4	225	4
3		Farm 3	KN30-1 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ <i>C.</i>			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
			kousa 'Chinensis' × C. nuttallii 'Goldspot'			
H3DR01P7	A x OP	Hort	<i>C. kousa</i> 'Elsbry' Empress of China™ × OP	5	238	4
7		Farm 3				
H3DR03P0	KN x OP	Hort	KN144-2 × OP; KN144 ⇒ KN109-92 × C. kousa	4	207	4
2		Farm 3	'Rosabella'; KN109 ⇒ KN30-4 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ C. kousa 'Chinensis' × C. nuttallii 'Goldspot'			
H3DR03P1	KN x OP	Hort	KN144-2 × OP; KN144 ⇒ KN109-92 × C. kousa	4	215	5
0		Farm 3	'Rosabella'; KN109 ⇒ KN30-4 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ C. kousa 'Chinensis' × C. nuttallii 'Goldspot'			
H3DR03P2	KFN x OP	Hort	KFN36 × OP; KFN36⇒ KN6-18 × C. florida 'Red	4	199	4
3		Farm 3	Beauty'; KN6 ⇒ C. kousa 'Summer Star' × C.			



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
nuttallii 'Goldspot'						
H3DR03P7	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	4	196	4
0		Farm 3	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i>			
<i>florida</i> 'Sweet Water'						
H3DR04P1	A x OP	Hort	<i>C. kousa</i> 'Elsbry' Empress of China™ × OP	5	240	4
7		Farm 3				
H3D 367	unknown	Hort	N/A	5	322	5
		Farm 3				
H3DR04P6	K x OP	Hort	<i>C. kousa</i> 'Heart Throb' × OP	5	325	5
2		Farm 3				
H3DR04P8	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × K2; KF83 ⇒	5	259	5
0		Farm 3	KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i>			
			'Sweet Water'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H3DR05P1	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	5	267	5
2		Farm 3	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'			
H3DR05P5	K x OP	Hort	<i>C. kousa</i> 'Beni Fuj'i' × OP	5	292	5
0		Farm 3				
H3DR06P1	K x OP	Hort	<i>C. kousa</i> 'Beni Fuj'i' × OP	5	300	5
4		Farm 3				
H3DR06P3	KN x OP	Hort	KN123-1 × OP; KN123 ⇒ KN71 × OP; KN71 ⇒	4	220	4
2		Farm 3	KN30-1 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
H3DR06P4	KN x OP	Hort	KN123-1 × OP; KN123 ⇒ KN71 × OP; KN71 ⇒	4	221	4
2		Farm 3	KN30-1 × OP; KN30 ⇒ KN3G-3 × Rosea; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H3DR06P6 8	K x OP	Hort Farm 3	K202-14 × OP; K202 ⇒ <i>C. kousa</i> 'K2' × (KF95-1, KN30-8, KN30-1)	4	204	4
H3DR06P7 0	K x OP	Hort Farm 3	K202-14 × OP; K202 ⇒ <i>C. kousa</i> 'K2' × (KF95-1, KN30-8, KN30-1)	5	257	5
H3DR06P8 0	K x OP	Hort Farm 3	K202-14 × OP; K202 ⇒ <i>C. kousa</i> 'K2' × (KF95-1, KN30-8, KN30-1)	5	330	5
H3DR07P1 7	A x OP	Hort Farm 3	<i>C. kousa</i> 'Elsbry' Empress of China™ × OP	5	241	4
H3DR07P2 2	A x OP	Hort Farm 3	<i>C. kousa</i> 'Elsbry' Empress of China™ × OP	5	239	4
H3DR07P3 0	K x OP	Hort Farm 3	K194-7 × OP; K194 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i> <i>kousa</i> 'Rosabella'	5	287	5
H3DR07P5	K x OP	Hort	<i>C. kousa</i> 'Rosabella' × OP	5	324	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
3		Farm 3				
H3DR07P6	K x OP	Hort	<i>C. kousa</i> 'Rosabella' × OP	5	296	5
0		Farm 3				
H3DR07P6	K x OP	Hort	<i>C. kousa</i> 'Rosabella' × OP	5	289	5
2		Farm 3				
H3DR08P3	K x OP	Hort	K196-29 × OP; K196 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	5	294	5
9		Farm 3	<i>kousa</i> 'Rosea' + <i>C. kousa</i> 'Red Satomi'			
H3DR08P7	KF x OP	Hort	KF111-1 × OP; Hyperion, KF111-1 ⇒ KF45-29 ×	2	129	2
3		Farm 3	OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'			
H3DR08P7	KF x OP	Hort	KF111-1 × OP; Hyperion, KF111-1 ⇒ KF45-29 ×	2	128	2
4		Farm 3	OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i> 'Sweet Water'			
H3DR09P0	KN x OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	4	214	4
9		Farm 3	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i>			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
'Chinensis' × <i>C. nuttallii</i> 'Goldspot'						
H3DR09P3	K x OP	Hort	<i>C. kousa</i> 'Rosea' × OP	5	326	5
4		Farm 3				
H3DR09P4	K x OP	Hort	<i>C. kousa</i> 'Rosea' × OP	5	283	5
1		Farm 3				
H3DR09P5	K x OP	Hort	<i>C. kousa</i> 'Rosea' × OP	5	274	5
4		Farm 3				
H3DR10P0	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	5	264	4
2		Farm 3	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i>			
<i>florida</i> 'Sweet Water'						
H3DR11P0	K x OP	Hort	<i>C. kousa</i> 'Heart Throb' × OP	5	285	5
1		Farm 3				
H3DR11P1	K	Hort	K185-20 × OP; K-185 ⇒ <i>C. kousa</i> 'Red Satomi' ×	5	265	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
8		Farm 3	<i>C. kousa</i> 'Rosea'			
H3DR11P2	K	Hort	K185-20 × OP; K-185 ⇒ <i>C. kousa</i> 'Red Satomi' ×	4	210	4
1		Farm 3	<i>C. kousa</i> 'Rosea'			
H3DR11P5	K × OP	Hort	<i>C. kousa</i> 'Propzam' Prophet™ × OP	4	200	4
2		Farm 3				
H3DR12P5	KN × OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	4	217	4
5		Farm 3	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
H3DR12P6	KN × OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	4	198	4
9		Farm 3	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
H3DR13P2	KN × OP	Hort	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30	5	255	5
9		Farm 3	⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i>			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
'Chinensis' × <i>C. nuttallii</i> 'Goldspot'						
H3DR04P0	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	5	263	4
3		Farm 3	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i>			
<i>florida</i> 'Sweet Water'						
H3DR03P0	unknown	Hort	F70R11P13 × OP	5	291	5
7		Farm 3				
H3DR03P7	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	4	222	5
5		Farm 3	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i>			
<i>florida</i> 'Sweet Water'						
H3DR04P1	KF x OP	Hort	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2';	4	216	4
2		Farm 3	KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i>			
<i>florida</i> 'Sweet Water'						
H3DR08P5	K x OP	Hort	<i>C. kousa</i> 'Beni Fuj'i × OP	5	293	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
7		Farm 3				
H3DR09P0	unknown	Hort	F70R11P13 × OP	5	302	5
3		Farm 3				
H3DR09P2	K x OP	Hort	<i>C. kousa</i> 'Rosea' × OP	5	323	5
4		Farm 3				
H3DR09P2	K x OP	Hort	<i>C. kousa</i> 'Rosea' × OP	5	301	5
9		Farm 3				
H3DR04P5	K x OP	Hort	<i>C. kousa</i> 'Heart Throb' × OP	5	277	5
6		Farm 3				
H3DR04P6	K x OP	Hort	<i>C. kousa</i> 'Heart Throb' × OP	5	299	5
0		Farm 3				
H3DR11P2	unknown	Hort	F70R4P39 × OP	4	226	4
9		Farm 3				



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
H3DR13P6 0	KN x OP	Hort Farm 3	KN161-119 × OP; KN161 ⇒ KN30-1 × OP; KN30 ⇒ KN3G-3 × <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'	5	256	5
H4AR05P1 3	unknown	Hort Farm 4	N/A	4	212	4
H4AR08P3 2	KF x OP	Hort Farm 4	KF137-47 × OP; KF137 ⇒ KF83 × <i>C. kousa</i> 'K2'; KF83 ⇒ KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C.</i> <i>florida</i> 'Sweet Water'	4	205	4
H4AR09P0 6	unknown	Hort Farm 4	NA	5	253	5
H4AR09P4 0	unknown	Hort Farm 4	N/A	4	211	4
H4AR14P2	K x OP	Hort	<i>C. kousa</i> 'Beni Fuj'i × OP	5	290	5

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
6		Farm 4				
H4AR15P3	unknown	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	55	1
0		Farm 4	<i>kousa</i> × <i>C. florida</i> 'Sweet Water'			
H4AR15P3	unknown	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	15	1
3		Farm 4	<i>kousa</i> × <i>C. florida</i> 'Sweet Water'			
H4AR15P3	unknown	Hort	KF95-1 × OP; KF95 ⇒ KF45-29 × OP; KF45 ⇒ C.	1	45	1
5		Farm 4	<i>kousa</i> × <i>C. florida</i> 'Sweet Water'			
H4AR17P4	unknown	Hort	Red Beauty® × Forma rubra	1	36	1
8		Farm 4				
H4AR17P5	unknown	Hort	Red Beauty® × Forma rubra	1	34	1
0		Farm 4				
Sun	K	Greenho	Selected by Gary Handy of Handy Nursery in	5	262	4
Splash		use	Boring, Oregon (Cappiello and Shadow, 2005)			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
483		clones				
White	K	Greenho	N/A	4	206	4
Dust 487		use				
		clones				
Lemon	K	Greenho	N/A	/	343	5
Ripple 488		use				
		clones				
Crème	K	Greenho	Selected by Bill Barnes of Lorax Farms in	4	209	4
Puff 489		use	Warrington, Pennsylvania (Cappiello and			
		clones	Shadow, 2005)			
Laura 490	K	Greenho	N/A	4	208	4
		use				
		clones				

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
D491	unknown	Greenho	N/A	5	261	4
		use				
		clones				
D492	unknown	Greenho	N/A	5	266	5
		use				
		clones				
Little	F	Greenho	Selected and introduced by Don Shadow	1	56	1
Princess		use	(Cappiello and Shadow, 2005)			
493		clones				
Sweet	F	Rutgers	Selected by Boyd Nursery, McMinnville,	1	23	1
Water		Gardens	Tennessee in 1954 (Cappiello and Shadow,			
DB01			2005)			
DB02	unknown	Rutgers	N/A	2	108	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
		Gardens				
DB03	unknown	Rutgers	N/A	2	42	1
		Gardens				
DB04	K	Rutgers	N/A	5	249	3
		Gardens				
Stellar	KF	Rutgers	KF27-3; KF27 $\Rightarrow$ <i>C. kousa</i> K2 $\times$ <i>C. florida</i>	2	112, 118,	2
Pink DB05		Gardens	'Sweetwater Red'		119, 120	
First Lady	F	Rutgers	Selected by Boyd Nursery, McMinnville,	1	97	1
DB06		Gardens	Tennessee in 1969 (Cappiello and Shadow, 2005)			
DB07	K	Rutgers	N/A	4	231	3
		Gardens				
Venus	KN	Hort	KN30-8; KN30 $\Rightarrow$ KN3-3 $\times$ <i>C. kousa</i> 'Rosea'; KN3-	3	168	3

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
DB08		Farm 4	3 ⇒ <i>C. kousa</i> Chinensis (K23-2) × <i>C. nuttallii</i> 'Goldspot' (D88)			
DB09	unknown	F70R04P	N/A	3	157	3
		36				
Hyperion	KF	F70R06P	Hyperion, KF111-1 ⇒ KF45-29 × OP; KF45 ⇒ <i>C.</i>	2	132	2
DB10		39	<i>kousa</i> × <i>C. florida</i> 'Sweet Water'			
Hyperion	KF	F70R06P	Hyperion, KF111-1 ⇒ KF45-29 × OP; KF45 ⇒ <i>C.</i>	2	130	2
DB11		41	<i>kousa</i> × <i>C. florida</i> 'Sweet Water'			
K187-44	K	F70R12P	K187 ⇒ <i>C. kousa</i> 'Red Satomi' × <i>C. kousa</i> 'Beni	5	280	5
DB12		36	fuji'			
K196-48	K	F70R08P	K196-48 × OP; K196 ⇒ <i>C. kousa</i> 'Beni Fuji' × <i>C.</i>	2	138	2
DB13		58	<i>kousa</i> 'Rosea' + <i>C. kousa</i> 'Red Satomi'			
KN80-52	KN	F70R05P	KN80 ⇒ KN3G-3 × K58 ( <i>C. kousa</i> 'Red'); KN3G-3	3	172	3

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
DB14		77	× <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
KN80-58	KN	F70R06P	KN80 ⇒ KN3G-3 × K58 ( <i>C. kousa</i> 'Red'); KN3G-3	3	170	3
DB15		75	× <i>C. kousa</i> 'Rosea'; KN3 ⇒ <i>C. kousa</i> 'Chinensis' × <i>C. nuttallii</i> 'Goldspot'			
KF83-1	KF	F70R32P	KF45-29 × OP; KF45 ⇒ <i>C. kousa</i> × <i>C. florida</i>	2	122	2
DB16a		14	'Sweet Water'			
DB16b	unknown	F70R32P	N/A	4	182	4
		14				
KN132-7	KN	F70R33P	KN132 ⇒ KN30-1 × ( <i>C. kousa</i> 'Rosea', <i>C. kousa</i>	3	171	3
DB17		25	'Red Satomi', <i>C. kousa</i> 'K2', OP)			
Variegate	KF	Milltown	KF27-3; KF27 ⇒ <i>C. kousa</i> 'K2' × <i>C. florida</i>	2	114	2
d Stellar			'Sweetwater Red'			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Pink DB18						
Variegate	KF	Milltown	KF27-3; KF27 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	115	2
d Stellar			'Sweetwater Red'			
Pink DB19						
Variegate	KF	Milltown	KF27-3; KF27 $\Rightarrow$ <i>C. kousa</i> 'K2' $\times$ <i>C. florida</i>	2	116	2
d Stellar			'Sweetwater Red'			
Pink DB20						
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	90	1
95-1			resistance to powdery mildew after screening			
			~20,000 seedlings			
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	66	1
95-11			resistance to powdery mildew after screening			
Mist			~20,000 seedlings			



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
C. florida 95-17	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening ~20,000 seedlings	1	78	1
C. florida 94-24	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening ~20,000 seedlings	1	76	1
C. florida 95-25	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening ~20,000 seedlings	1	70	1
C. florida 94-40	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening ~20,000 seedlings	1	5	1
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	27	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
95-12			resistance to powdery mildew after screening			
Blush			~20,000 seedlings			
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	87	1
95-5			resistance to powdery mildew after screening			
			~20,000 seedlings			
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	85	1
9-8 Joy			resistance to powdery mildew after screening			
			~20,000 seedlings			
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	2	1
94-83			resistance to powdery mildew after screening			
			~20,000 seedlings			
C. florida	F	U of Tenn	Identified from Windham et al., 2003 for	1	69	1
94-25			resistance to powdery mildew after screening			



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Polly Hill	K	U of Tenn	Wadl et al., 2014 'Pam's Mountain Bouquet'	4	190	4
PHK 6						
Polly Hill	K	U of Tenn	Wadl et al., 2014 'Empire'	5	243	5
PHK 101						
Polly Hill	K	U of Tenn	OP Selection - Paternal parents of the trees	4	186	4
PHK 201			were 'Julian',  'Steeple', 'Big Apple' and an unnamed tree.  Maternal parents included 'Steeple', 'Big Apple', 'Snowbird' and the unnamed tree. Auge et al., 2002.			
Polly Hill	K	U of Tenn	OP Selection - Auge et al., 2002.	/	154	4
PHK 2						
Polly Hill	K	U of Tenn	PHK-8 × 'Galilean'	/	153	4

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
C10-08-57						
Polly Hill	K	U of Tenn	OP Selection	4	192	4
PHK3						
Double	F	U of Tenn	<i>C. florida</i> 'Eternal' Discovered by Pierre W.	1	62	1
White			Simmen in Davidson, North Carolina in the			
			1990s (Cappiello and Shadow, 2005)			
Pink	unknown	U of Tenn	N/A	1	20	1
Girards						
Cherokee	F	U of Tenn	Discovered by W.C. Higden (Cappiello and	1	79	1
Princess			Shadow, 2005)			
Miss	K	U of Tenn	Discovered by Mr. Gilardelli of Milan, Italy	5	305	5
Satomi			(Cappiello and Shadow, 2005)			
Autumn	K	U of Tenn	Discovered by Glenda Schmoyer of Handy	4	189	4

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Rose			Nursery in Boring, Oregon (Cappiello and Shadow, 2005)			
Hog 1	F	U of Tenn	N/A	1	51	1
Rochester	K	U of Tenn	Selected by Hoogendorn Nursery of Newport, Rhode Island (Cappiello and Shadow, 2005)	4	183	4
Cherokee Daybreak	F	U of Tenn	<i>C. florida</i> 'Daybreak' Discovered and released by Commercial Nursery Company in Decherd, Tennessee (Cappiello and Shadow, 2005)	1	67	1
Headquarters	unknown	U of Tenn	N/A	1	95	1
Northern Province	F	U of Tenn	N/A	1	52	1
Wonderbe	F	U of Tenn	<i>C. florida</i> 'Rutman' Wonderberry® D-184-11 C.	1	18	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
rry			<i>florida</i> × <i>C. florida</i> var. <i>rubra</i>			
Blue	K	U of Tenn	Selected by Polly Hill and named after Don	4	191	4
Shadow			Shadow (Cappiello and Shadow, 2005)			
Trinity	K	U of Tenn	Selected by Gary Handy of Handy Nursery in	4	188	4
Star			Boring, Oregon (Cappiello and Shadow, 2005)			
Emerald	K	U of Tenn	N/A	4	184	4
Star						
Temple	K	U of Tenn	Selected by Brotzman's Nursery of Madison,	4	187	4
Jewel			Ohio in the 1970s (Cappiello and Shadow, 2005)			
Cherokee	F	U of Tenn	Selection from 'Cherokee Chief' at Commercial	1	49	1
Brave			Nursery, Decherd, TN. Actual cultivar name is Comco#9. This has a PP.			

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
Langdon Y	F	U of Tenn	N/A	1	93	1
Snow	F	U of Tenn	N/A	1	100	1
Princess						
94-49	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening ~20,000 seedlings	1	6	1
Rainbow	F	U of Tenn	Discovered by A. Mizzilli of Canton, Ohio (Cappiello and Shadow, 2005)	1	92	1
94-12	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening ~20,000 seedlings	1	81	1
95-8	F	U of Tenn	Identified from Windham et al., 2003 for resistance to powdery mildew after screening	1	84	1



Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
~20,000 seedlings						
TX12	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	64	1
TX11	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	58	1
TX1	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	1	1
TX2	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	4	1
TX5	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	74	1
TX10	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	86	1
TX8	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	65	1
TX9	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	72	1
TX6	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	63	1
TX4	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	54	1
TX3	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	73	1
95-10	F	U of Tenn	Identified from Windham et al., 2003 for	1	57	1

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
resistance to powdery mildew after screening ~20,000 seedlings						
95-24	F	U of Tenn	Identified from Windham et al., 2003 for	1	75	1
resistance to powdery mildew after screening ~20,000 seedlings						
94-60	F	U of Tenn	Identified from Windham et al., 2003 for	1	14	1
resistance to powdery mildew after screening ~20,000 seedlings						
TX13	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	71	1
TX7	F	U of Tenn	All TX samples are from Hadziabdic et al., 2010.	1	68	1
Nyssa	OG	Rutgers	Specimen located in Rutgers Gardens	/	344	5
sylvatica		Gardens				
Hydrangre	OG	Foran	Specimen located in garden outside Foran Hall,	/	346	2

Accession	Species	Field	Pedigree Record	UPGMA	STRUCTURE	Consensus
		Location		Group	ID No.	Group
a spp.		Hall	Rutgers University			

**Table 3.** Characteristics of the 11 simple sequence repeat primers used to analyze the genetic diversity of 337 accessions.

Primer	Source	LG	Direction	Primer Sequence	Motif	Size Range (bp)
<b>CF020</b>	Wang et al., 2008	2	F	TATGGCTTGCTTTGGCTAATTGTT	(TC) <sub>22</sub>	110-164
			R	CCAACTTATGCACACAGTGACACA		
<b>CF048</b>	Wang et al., 2008		F	GCTTTGACATCCTCTTTGCTTCTC	(GT) <sub>9</sub>	141-154
			R	AAGAGGCTTCACAAGACAATCAGC		
<b>CF055</b>	Wang et al., 2008		F	TGGAGTAGGGCAAAAGATCAAGAG	(GT) <sub>7</sub> T(TG) <sub>10</sub>	146-187
			R	TCCAGGGAATGTTCGGTAGATTAG		
<b>CF150</b>	Wadl et al., 2008	7	F	TGCAATATCTACATAGTCGATACACACA	(AC) <sub>9</sub>	132-148
			R	TTAGGGATGTTTGTGCCTTGTTAG		
<b>CF273</b>	Wadl et	8	F	TCATATTTATGCTTTCCTTGCCGT	(AC) <sub>14</sub>	122-144

al.,2008						
			R	GTGATCCTCTCCTAACGACTTCCA		
<b>CF597</b>	Wang et al., 2008	11	F	AAGTCAGATCATTTCAGATTAACA	(AC) <sub>13</sub>	90-122
			R	CGAATTGACGATAAATACAAAATA		
<b>CF646</b>	Wang et al., 2008	10	F	ACTCATTCTTCCCAGTTTACAT	(AG) <sub>24</sub>	109-125
			R	TCCACTGACTGAGAAAGTAAATAA		
<b>CF701</b>	Wang et al., 2008	1	F	GTACCAACCTCTCTAACAGAAAAT	(CT) <sub>19</sub>	115-132
			R	TTTCTGAGAGATCTTGATTCTTG		
<b>CF1001</b>	Wadl et al., 2012		F	GGTCAGCAAAATCTGAAAAACC	(CGC) <sub>5</sub> cgt(C GC) <sub>3</sub>	126-151
			R	GGTGGAGAGTCCGTACGAGTTA		
<b>CF1020</b>	Wadl et al., 2012		F	GTCTAGGGTTTCGGGATTGG	(TTG) <sub>8</sub>	168-194

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		R	TTGTAGTGATCCAACATCTCATAGC		
<b>CF1045</b>	Wadl et al., 2012	F	ACGTCTGTGTCGTACTGGTTCC	(TC) <sub>6</sub> ta(TG) <sub>7</sub>	145-171
		R	GCCTTGAAGGAAAAGAAAAGC		

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**Table 4.** Summary population statistics including observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ), polymorphism information content (PIC) and inbreeding coefficient (f) for 337 accessions analyzed with 11 simple sequence repeat markers.

Marker	Major Allele Frequency	Genotype No	No. of obs.	Allele No	Gene Diversity ( $H_e$ )	Heterozygosity ( $H_o$ )	PIC
CF20	0.1890	79.0	328.0	24.0	0.8844	0.6311	0.8740
CF048	0.5015	21.0	326.0	9.0	0.6770	0.2883	0.6378
CF055	0.6121	16.0	330.0	8.0	0.5736	0.3848	0.5337
CF150	0.3775	45.0	298.0	17.0	0.7727	0.6443	0.7446
CF273	0.3047	66.0	297.0	21.0	0.8534	0.6869	0.8413
CF597	0.1751	80.0	317.0	21.0	0.8956	0.6372	0.8867
CF646	0.3948	46.0	328.0	15.0	0.7598	0.6250	0.7308
CF701	0.1954	66.0	325.0	23.0	0.8795	0.7323	0.8682
CF1001	0.4682	21.0	346.0	11.0	0.6686	0.3815	0.6149
CF1020	0.5820	26.0	317.0	11.0	0.6155	0.4132	0.5832
CF1045	0.5721	22.0	333.00	10.0	0.6175	0.4204	0.5798

Marker	Major Allele Frequency	Genotype No	No. of obs.	Allele No	Gene Diversity (H <sub>e</sub> )	Heterozygosity (H <sub>o</sub> )	PIC
Mean	0.3975	44.36	322.27	15.45	0.7452	0.5314	0.7177



**Table 5.** Unidentified accessions (n=11) with suggested pedigree information based on the UPGMA dendrogram clustering, STRUCTURE analysis. \*Indicates strong support from allelic data.

Accession Name	STRUCTURE ID	Proposed Genotype
D226*	91	<i>C. florida</i> 'Rainbow'
RGC200	136	<i>Cornus</i> × <i>rutgersensis</i> 'Rutcan' Constellation®
RGC199	148	<i>Cornus</i> × <i>rutgersensis</i> 'Rutban' Aurora®
RGC210	150	<i>Cornus</i> × <i>rutgersensis</i> 'Rutfan' Stardust®
D224*	24	<i>C. florida</i> 'Sweetwater Red'
RGC209	111	<i>Cornus</i> × <i>rutgersensis</i> 'Rutgan' Stellar Pink®
D233	131	<i>Cornus</i> × <i>rutgersensis</i>

Accession Name	STRUCTURE ID	Proposed Genotype
		‘KF111-1’ Hyperion®
D039	134	<i>Cornus</i> × <i>rutgersensis</i>
		‘KF111-1’ Hyperion®
D242	149	<i>Cornus</i> × <i>rutgersensis</i>
		‘Rutfan’ Stardust®
DB02	108	<i>Cornus</i> × <i>rutgersensis</i>
		‘Rutlan’ Ruth Ellen®
D220	109	<i>Cornus</i> × <i>rutgersensis</i>
		‘Rutlan’ Ruth Ellen®

**Table 6.** Matrix of the pairwise  $F_{ST}$  values (below the diagonal) and the probability values (above the diagonal) for the five consensus groups. Group 1 – *C. florida* group; Group 2 – *Cornus* × *rutgersensis* group; Group 3 – *Cornus* × *elwinortonii* group; Group 4 – *C. kousa* inter-specific hybrid group; Group 5 – Pink-bracted *C. kousa* group

Group 1	Group 2	Group 3	Group 4	Group 5	
-	0.001	0.001	0.001	0.001	Group 1
<b>0.120</b>	-	0.001	0.001	0.001	Group 2
<b>0.229</b>	0.163	-	0.001	0.001	Group 3
<b>0.282</b>	0.201	0.118	-	0.001	Group 4
<b>0.305</b>	0.199	0.140	0.114	-	Group 5