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Breeding Powdery Mildew Resistant Dogwoods and More at Rutgers University©

T.J. Molnar

Department of Plant Biology and Pathology, The School of Environmental and Biological Sciences, Rutgers University, 59 Dudley Road, New Brunswick, New Jersey 08901, USA.

Email: molnar@aesop.rutgers.edu

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INTRODUCTION

The Rutgers University Woody Ornamental Breeding Program began in 1960 under the direction of Dr. Elwin Orton. The early focus of the program was the breeding of hollies (*Ilex* sp.), with work on big-bracted dogwoods (*Cornus* sp.) starting in the 1970s. The program continues today with the addition of hazelnuts (*Corylus* sp.) for nut production and ornamentals. Over 40 cultivars have been released since the initiation of the program, and a number have become widely grown in the nursery and landscape trade. A list of releases can be found in Molnar and Capik (2013). The most noteworthy Rutgers introductions, at least from the perspective of plants propagated and sold thus far, are likely the hybrid dogwoods. These were largely the results of crossing *Cornus kousa* with *C. florida* to create a series of unique plants (subsequently named *Cornus* × *rutgersensis* [Mattera et al., 2015]) that combined traits of both parental species to create attractive, high-value landscape specimens. The hybrids generally exhibit increased vigor over their parental species and better drought tolerance than *C. florida.* However, their most important attribute is likely their resistance or increased tolerance to diseases such as dogwood anthracnose (*Discula destructiva*) and powdery mildew [(PM), *Erysiphe pulchra*) (Hibben and Daughtrey, 1998; Ranney et al., 1995)]. They also tend to get significantly fewer stem borers, extending their lifespan and reducing maintenance needs in the landscape.

Seven F_1 hybrids were released from the program, mostly from 1990-1991 (Orton, 1993), with the most popular and widely grown being 'Rutgan' Stellar Pink® (Fig. 1). Each cultivar differs in its floral attributes and growth habits and exhibits sterility, avoiding any concerns of naturalization in the landscape while also making them a dead-end for further breeding. While only the sterile selections were originally released, Dr. Orton did develop a small number of semi-fertile interspecific hybrids (trees that produced a very small number of fertile seeds) that formed the basis for further hybrid breeding.

POWDERY MILDEW IMPACTS *CORNUS FLORIDA*

In the 1990s, introduction of the PM pathogen *Erisyphe pulchra* caused major issues for *C. florida*, which is generally very susceptible to the disease (Li et al., 2009; Ranney et al., 1995). It causes a white bloom of mycelium on the leaves and can cause unattractive leaf distortion and red and brown coloration, leading to a significant reduction in overall aesthetic value, plant health, and vigor (Klingeman et al., 2004; Fig. 2). This damage is especially evident in nursery operations where plants are grown in dense rows in close proximity (Figs. 3 and 4). Individual trees in the landscape can vary in their reaction to PM, as environmental factors like wind and rainfall influence the severity of the disease. However, in general, susceptible cultivars lose leaf quality and health especially later in the summer, and the weakened trees tend to decline in vigor over subsequent years and succumb to stress-related disorders like stem borers, which ultimately can kill the trees.

Prior to the 1990s, in the absence of the disease, the breeding and selection for resistance to PM was not an objective of the Rutgers breeding program. The introduction of PM directly impacted several cultivars that were developed and released but which ultimately proved too susceptible for commercial production. An example includes *C. florida* 'D-376-15' Red Beauty®, which is a very attractive, dark-red bracted specimen tree (Figs. 5 and 6) that gets too much PM in liner production to be commercially viable (despite being patented it never became commercially available). A similar story could almost be told for 'Rutnut' Red Pygmy®. Fortunately, its unique dwarf form and deep red floral bracts make it novel enough to still be grown on a small scale despite its high susceptibility to PM. However, the disease generally makes the tree quite unattractive later in the summer, and likely reduces its lifespan in the landscape.

In 2006, with Dr. Orton's impeding retirement in 2008 approaching, the Rutgers ornamental program was bolstered by the knowledge that a new breeder (Dr. Tom Molnar) would be hired to continue the project. Working with Dr. Orton, we began by growing thousands of new seedlings derived from open-pollinated (OP) seed originating from a crossing block of unique breeding selections developed and amassed over the previous 40 years. This collection was largely made up of fertile advanced-generation interspecific hybrids, with genetic backgrounds spanning *C. kousa*, *C. florida*, and *C. nuttallii* in a variety of combinations (some known and others somewhat unknown due to open-pollination events in their pedigrees). Based on the out-crossing nature of *Cornus* and the wide diversity of plant material intercrossed, significant variation in many traits was expected in the offspring. The hopes were that some new cultivars might come from this process, or at least some interesting new breeding material to help continue improvement efforts.

As part of this new program, trees germinated from the OP seed were “screened” for tolerance to PM in the greenhouse, where this disease can become quite severe. This allowed for susceptible seedlings to be discarded prior to being field planted for further evaluation (about 25% of the seedlings were discarded at this stage). Several thousand OP trees were thus screened then field planted during 2006 to 2008.

The highest priority breeding goal at the time was to develop the coveted “dark pink” kousa or hybrid dogwood that Dr. Orton worked toward for much of his career (Orton, 1985). Fortunately, we had some very exciting developments on that front in this first generation of new seedlings, exemplified by the release of *C. kousa* ‘Rutpink’ Scarlet Fire®, which is described in more detail in Molnar (2017) and Molnar et al. (2017). Unexpectedly recovering many dark pink-bracted seedlings in the 2006-2008 planted OP populations reduced the attention put on breeding improved PM-resistant *C. florida*. These efforts were already impacted by the relatively limited germplasm base of PM resistant/tolerant *C. florida* available at Rutgers (Dr. Orton had not worked on *C. florida* since the early 1990s). These limitations, combined with the known rarity of PM resistance in the species (Windham and Witte, 1998), made developing a concerted effort to breed improved PM-resistant *C. florida* daunting and not likely achievable in the near term.

UNEXPECTED NEW SOURCE OF PM RESISTANCE

In 2011, 11 trees from an OP seed lot recorded to be from KF95-1, a *C. kousa* × *C. florida* breeding accession backcrossed to *C. florida* (BC_1), bloomed for the first time. By appearance, these trees looked 100% *C. florida*, despite a pedigree showing them as interspecific hybrids. They were pretty trees (mostly with white bracts, but a few with blush-pink) but not outstanding at first glance in comparison to other *C. floridas* in the nursery trade. The trees were not given a lot of attention, but since breeding records indicated they came from a hybrid mother tree (representing a possible BC_2 generation assuming their pollen parents were *C. florida*), they were not cut down and were allowed to grow on for further evaluation. A very bad PM year in 2013 highlighted this particular group of seedlings. Many trees in our program, including known hybrids and even some *C. kousa* selections expected to be highly tolerant to PM, showed disease symptoms that year. Amazingly, several seedlings in the KF95-1 OP seed lot remained free of PM and several others appeared highly tolerant (PM was found on only a relatively small percentage of their leaves). This was unexpected based on their pure *C. florida* phenotypes and the high disease pressure apparent in our fields. Their freedom from PM and the known rarity of PM resistance in the species indicated they might hold some previously unnoticed value for breeding.

Our first step was to clonally propagate the most attractive seedling that was free of PM, today known as selection Rutgers 15-25 (Figs. 7, 8, and 9), to see if the resistance held up in replication in our plots and at a different location. This was done with the help of Alex Neubauer at Hidden Hollow Nursery in Belvidere, TN. Multiple trees of Rutgers 15-25 were budded in the summers of 2014, 2015, and 2016 and evaluated for response to PM the following years in the nursery under standard practices and conditions generally suitable for high PM pressure. To our surprise, each year the trees came through evaluations with no signs or symptoms of PM, whereas the standard cultivars propagated at the nursery had their typical amounts of PM and seedling understocks for next year's budding needed significant fungicide applications to remain healthy. The resulting budded trees were dug and bare-rooted each year and sent back to Rutgers where they were lined out in the field or planted in containers for further evaluation. Here, our results showed they also remained free of PM in the greenhouse and field under what we considered high disease pressure, with no preventative fungicide applications. It should be noted that the original tree, Rutgers 15-25, also remains free of PM to date (October 2018) in the field, now spanning 11 growing seasons with no signs or symptoms of disease. Collectively, these trials provided a high level of confidence that this source of resistance was worthy of further exploration.

Looking to capitalize on the new source of PM resistance in breeding, we made a small number of controlled crosses with Rutgers 15-25 and some of its siblings in 2014, which were subsequently evaluated for PM response in the field. While the first populations were too small to examine genetic control, we did recover a significant number of resistant offspring, suggesting that the resistance is heritable and can be used in further breeding. In more recent years, many additional controlled crosses have been made and large populations are now growing in the field and greenhouse for evaluation and study.

WHERE DID THIS RESISTANCE COME FROM?

Breeding records indicate that Rutgers 15-25 and its siblings originated from seed collected from KF95-1, which is believed to be a backcross hybrid (BC_1) to *C. florida*. Interestingly, KF95-1 is the OP offspring of KF45-29 (Fig. 10), which is a full sibling of Stellar Pink®, whose shared parents are *C. kousa* K2 × *C. florida* 'Sweetwater Red' (Mattera et al., 2015). KF45-29 is unique in the fact that it is semi-fertile (Stellar Pink® is sterile). While most fruits are empty, a very small percentage (much less than 1%) set a viable seed. Dr. Orton took advantage of this fact and collected thousands of fruits over many years to search for seed. When he found them, he grew out the rare seedlings to add diversity to his breeding pool.

As a side note and point of reference, 'KF111-1' Hyperion® also originated from seed collected from KF45-29. Hyperion® is an extremely vigorous, white-bracted hybrid dogwood patented and released in 2011 (Fig. 11). It is believed to be a backcross hybrid to *C. kousa*, based on records that suggest KF45-29 bloomed later in the season the year the OP seed was harvested and would have been pollinated by *C. kousa* in the landscape at the research farm (Rutgers Gardens, New Brunswick, NJ). Note that *C. florida* and *C. kousa* bloom about a month apart, and the F_1 hybrids typically bloom at a date between the two parental species. Interestingly, Hyperion® is relatively fertile and can yield fertile offspring. Its fruit, especially when it contains a seed, clearly displays its hybrid background, expressing attributes of both *C. florida* and *C. kousa* (Fig. 12).

KF95-1, the recorded female parent of our source of PM resistance, is a half sibling of Hyperion®. As mentioned previously, it too is derived from an open pollination event of KF45-29. However, breeding records indicate flowering was during a year where KF45-29 bloomed early and during the late end of the *C. florida* bloom period. Thus, if the records are correct, KF95-1 is a BC_1 hybrid with *C. florida*. The phenotype of KF95-1 suggested this is the case, including its early bloom time closer to that of pure *C. florida*. Unfortunately, KF95-1 was cut down a few years ago before we realized its potential value, and a picture of the bracts are not available. However, an image of its fruit with viable seed was available that clearly shows its hybrid nature, similar in form to that of Hyperion® (Fig. 13).

Since the KF95-1 bloom period in 2006 overlapped that of the later end of *C. florida*, the OP seed collected are expected to be the result of pollination by *C. florida* and represent a possible BC_2 generation. With a significant portion of their genome now coming from *C. florida* (the genomic contribution of BC_2 hybrids would be approximately 87.5 % *C. florida*), we did not consider it unrealistic that the plants would look very much like *C. florida* in phenotype. As such, we operated under the assumption that the records were correct. However, considering that the PM resistance may have been derived from *C. kousa* (which would be of substantial breeding value since *C. kousa* is generally very resistant to PM), we decided to investigate further. Thus, we turned to molecular tools to examine this possibility with more certainty .

MOLECULAR TOOLS PROVIDE INSIGHT INTO THE ORIGIN OF PM RESISTANCE

The first glimpse of the genetic background of the PM resistant seedlings was completed as part of a Masters degree thesis by Robert Mattera (2016). In his study, 11 simple sequence repeat (SSR) markers were used to fingerprint 337 accessions, which included over 50 *C. floridas,* as well as many *C. kousa* and interspecific hybrids of diverse genetic backgrounds and combinations held in the Rutgers collection with some contributed by the University of Tennessee. While the primary goal was to examine the genetic diversity present in the Rutgers and University of Tennessee collections, the inclusion of the OP seedlings of KF95-1 was useful for shedding light on their inter-relationships and genetic background. Results showed that the seedlings were grouped tightly together in one clade, suggesting a common parent and supporting the hypothesis that they came from the same seed lot. This was an important finding—they most likely came from a single mother tree. However, the clade in which they were placed was clearly nested in the well-defined *C. florida* subgroup of the study, which was strongly supported and contained plants only known to be of *C. florida* species background. None of the known *C. kousa* or hybrids in the study were placed in the *C. florida* group (alternatively, and as even greater support for the groupings, no known *C. florida* accessions were place exterior to the *C. florida* group). This finding for the KF95-1 seedlings was unexpected based on their breeding history and was our first indication that the records could be wrong. Note that KF95-1 was unfortunately cut down and DNA not available for the SSR study.

While the SSR results made us question the origin of the KF95-1 seedlings and their reported connection to *C. kousa*, 11 SSR markers cannot clearly define the species background of a potential interspecific hybrid, especially those with a very high percentage of genetic composition from one parental species, such as in BC_2 hybrids. More work would need to be done to confirm their true origin. Regardless of this fact, one useful point was that the seedlings were shown to be genetically distinct from a number of the PM resistant and tolerant *C. florida* cultivars and selections included in the study (e.g., Appalachian Mist) that were developed at the University of Tennessee (Windham et al., 2003). The Tennessee-sourced plants were generally all placed in Subgroup 2 of the *C. florida* group in the dendrogram. This provided good evidence that the "KF95-1" seedlings are at least from a different, distinct genetic background and may possibly carry an unrelated source of PM resistance (Mattera, 2016).

Next, we considered a different approach to test the hypothesis that there are *C. kousa* genes present in the PM resistant seedlings. Knowing that chloroplasts are maternally inherited in most higher plants, we set out to identify if the chloroplasts of the seedlings were derived from *C. kousa* (the maternal line of KF95-1 is *C. kousa*). To do this, Muehlbauer et al. (2018) sequenced three conserved chloroplast genes in 11 of the PM resistant seedlings, as well as a panel of known *C. florida* and *C. kousa* cultivars and their reported mother KF95-1 (a dry herbarium specimen was identified and used to extract chloroplast DNA of KF95-1) to identify their maternal species lineage. The chloroplast genes included were *matK, rbcL*, and *ycf1,* which have been used previously in phylogenetic analysis of the Cornaceae family (Xiang et. al., 1998, 2002). The genes were successfully sequenced, and BLAST searches including the consensus sequence search revealed that each of the PM-resistant seedlings showed very close alignment with *C. florida* (again in contrast to our breeding records). However, there were some confounding sequencing results for the *C. kousa* controls where they did not explicitly discern *C. kousa* from *C. florida* cultivars in all cases, leaving some level of ambiguity. Further, gene sequence identities were also ambiguous for KF95-1, which made it hard to draw conclusions on its maternal origin (*C. kousa* or *C. florida*). However, since the results of KF95-1 were different from that of the 11 seedlings, the results provided some further evidence that they were not carrying a similar chloroplast origin. Unfortunately, due to the somewhat unclear results with *C. kou*sa, a deeper study with higher resolution would be needed to fully elucidate their maternal origin.

Fortuitously, in the research lab of Dr. Robert Trigiano at the University of Tennessee, Nowicki et al. (2018) was working on a study to analyze the chloroplast DNA diversity of *C. florida* and *C. kousa* using a high-resolution chlorotyping system developed for *C. florida* (Call et al., 2015). They agreed to include Rutgers 15-25 in their study, which included 332 accessions in total. Their recently published results clearly showed significant differences in chlorotype frequencies between the two species and placed Rutgers 15-25 with the *C. florida* accessions (Nowicki et al., 2018). Thus, the chloroplast in Rutgers 15-25, and likely all of its siblings, was derived from *C. florida*. This new, very well-supported evidence, combined with the previous two studies, make it clear that the seedlings do not fit their pedigree records. They are not the offspring of KF95-1 and most likely are pure *C. florida*. At some point, there must have been a mislabeling in the greenhouse or field. The results are humbling and a reminder of the value of clear notetaking and record keeping, as well as the value of molecular tools in clarifying and supporting breeding records.

PM RESISTANCE FROM UNCERTAIN ORIGIN, BUT IT STILL WORKS!

While the resistance might not come from the origin that was first thought, it appears to be extremely useful resistance that has held up across multiple locations and multiple years and is transmitted to its offspring. Very few other sources of PM resistance exist can claim to have held up completely free of PM in propagation nurseries in TN (most purported sources of resistance are in fact only tolerant; they get some PM in some years). While further testing is needed across a wider area, results to date are very promising. Now the question arises, where did this source of resistance come from? The Rutgers collection of *C. florida* was very small at the time the seed was collected, and none of the trees in the collection remain free of PM each year. Our SSR data tells us that the seedlings were likely collected from the same mother plant (or related plants), but we have no additional information on the source of the seed and no obvious suspects in our germplasm collection.

Regardless of its unknown origin, we are now using this source of resistance in a large-scale breeding program with the goal of developing a series of improved PM resistant plants with a variety of attractive plant types and bract colors. The current research objective is to study inheritance in a more systematic manner and characterize the gene or genes for resistance, similar to the work described by Parikh et al. (2016, 2017). We are also developing a large, full-sibling pseudo-F_2 mapping population to develop a genome-by-sequencing based genetic linkage map to hopefully identify quantitative trait loci associated with resistance. A more comprehensive diversity study, along with the creation of molecular tools to differentiate hybrid species composition, is also underway to help understand the hybrid plant material now being used in breeding at Rutgers. When used alongside the study of other genes for PM resistance (e.g., those discussed in Parikh et al. [2016, 2017]), molecular tools should help us design populations suitable for pyramiding genes and ultimately release improved, novel cultivars that express durable forms of resistance to PM.

CONCLUSIONS

A new source of PM resistance has been identified in the *Cornus* germplasm base held at Rutgers University. Breeding records indicated that the plants were of interspecific origin, but plant phenotypes and molecular studies strongly suggest otherwise. Although humbling, by using molecular tools, we have been able to better understand the species origin of the plant material in question and can now make better informed decisions about its use in breeding. Regardless of our records, resistance to PM is exceedingly rare in *C. florida*; thus, this new heritable source may hold significant value in breeding improved dogwood cultivars. Systematic breeding is now in progress alongside genetic studies to better understand the source of resistance with the goal of using it to develop a series of new, high-value dogwood plants that require reduced chemical inputs in the nursery - and live longer, healthier - and more attractive lives once planted into landscapes.

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Figure 1. *Cornus* × *rutgersensis* ‘Rutgan’ Stellar Pink® hybrid dogwood.

Figure 2. Powdery mildew caused by *Erisyphe pulchra* on leaf of *Cornus florida*.

Figure 3. Powdery mildew can cause significant damage, including twisting of leaves and young stems, to susceptible cultivars grown under nursery conditions without the use of fungicides.

Figure 4. *Cornus florida* var. *forma rubra* (center) and 'Cherokee Brave' (right) showing differential expression to powdery mildew caused by *Erisyphe pulchra*. Picture taken at Hidden Hollow Nursery, Belvidere, TN, October 25, 2018.

Figure 5. Close up of floral bracts of *Cornus florida* ‘D-376-15’ Red Beauty®, a cultivar developed at Rutgers University but never commercialized due to susceptibility to powdery mildew.

Figure 6. *Cornus florida* ‘D-376-15’ Red Beauty® at a distance.

Figure 7. Close up image of leaves of Rutgers breeding selection Rutgers 15-25 free of powdery mildew during high disease pressure year.

Figure 8. Grafted tree of Rutgers 15-25 free of powdery mildew in summer 2017, a year of very high disease pressure.

Figure 9. Floral bracts of Rutgers 15-25.

Figure 10. Blush pink floral bracts of KF45-29, a F_1 hybrid and full sibling to *Cornus* × *rutgersensis* 'Rutgan' Stellar Pink® dogwood.

Figure 11. Floral bracts of *Cornus* × *rutgersensis* ‘KF111-1’ Hyperion® dogwood.

Figure 12. Fruit of *Cornus* × *rutgersensis* ‘KF111-1’ Hyperion® dogwood containing viable seed represented as bulging fruitlet.

Figure 13. Fruit of KF95-1 dogwood containing viable seed.