11-11-2016

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Recommended Citation

Lipi Parikh, M.T. Mmbaga, S. Kodati, M. Blair, D. Hui, G. Meru, "Broad-sense heritability and genetic gain for powdery mildew resistance in multiple pseudo-F2 populations of flowering dogwoods (Cornus florida L.)", Scientia Horticulturae, Volume 213, 2016, Pages 216-221, ISSN 0304-4238, https://doi.org/10.1016/j.scienta.2016.09.038.

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Abstract

Powdery mildew caused by *Erysiphe pulchra* is one of the most destructive diseases of flowering dogwoods (*Cornus florida* L.). Control of powdery mildew relies heavily on chemical fungicides. Developing genetic resistance and planting powdery mildew resistant cultivars is a desirable long term control strategy for the disease. Information on inheritance characteristics associated with powdery mildew resistance in *C. florida* is needed to facilitate development of breeding strategies for a new generation of powdery mildew resistant cultivars. The objectives of this study were to determine broad-sense heritability, genetic gain and minimum number of effective genes associated with resistance to powdery mildew in *C. florida*. Progeny segregating for powdery mildew resistance were developed through controlled crosses between susceptible cultivar [Cherokee Princess (CP)], resistant selection (R14) and moderately resistant cultivars [MI9 and Cherokee Brave (CB)]. The parents and progeny were evaluated for resistance/ susceptibility to powdery mildew under greenhouse conditions and estimates for broad-sense heritability, genetic gain and minimum number of effective genes was determined. Broad-sense heritability ranged from 60% to 88% while corresponding narrow-sense heritability ranged from 53% to 86.6%. The highest predicted genetic gain for powdery mildew resistance was obtained in the R14 x CP (78%) and CB x MI9 (61%) crosses while the lowest genetic gain was observed in the CP x MI9 (34%) and MI9 x CB (36%) crosses. These results indicate that CB x MI9 and R14 x CP crosses are best parental lines for developing resistance to powdery mildew among the genotypes tested. Use of these parental lines and understanding the gene flow of resistance to powdery mildew in dogwoods will help researchers to develop a targeted breeding approach in generating new generation of resistant cultivars.

Keywords: flowering dogwoods, broad-sense heritability, genetic gain, pseudo-F_2, powdery mildew

Introduction

Flowering dogwoods (*Cornus florida* L.) is native to the U.S and is one of the most popular and economically important ornamental trees in the southeastern U.S with total annual sales of 30 million dollars (United States Department of Agriculture, 2009). The state of Tennessee contributes approximately 23.2% of dogwood sales in the U.S, thus disease constraints that impact dogwood production have ripple effect on the state's economy especially in rural communities. Powdery mildew caused by *Erysiphe pulchra* a (Cook & Peck, Braun & Takamatsu) is the most important constraint in the production of flowering dogwoods (Mmbaga and Sauve, 2004). Powdery mildew fungus produces white mycelia that cover plant foliage thus reducing the total surface available for photosynthesis. This leads to stunted growth, seedling death, reduced aesthetic value and negative impacts on plant sales (Li et al., 2009; Mmbaga, 1998; Mmbaga and Sauve, 2004; Windham et al., 2005). To mitigate these losses, dogwood production requires an effective and consistent strategy for controlling powdery mildew. Currently, disease control relies heavily on the use of chemical fungicides which has in turn increased the production costs and reduced grower profits. As a result of the rising cost in dogwood production, many small-scale nursery growers have reduced or terminated dogwood production (Fulcher and White, 2012; Klingeman et al., 200). In addition, there is a rising concern over the impact of chemical fungicides on the environment. Development and adoption of cultivars resistant to powdery mildew is the most preferred strategy for managing the disease. However, most of the commercially available dogwood cultivars are susceptible to powdery mildew with an exception of a few that are resistant. It is estimated that growers can save approximately $0.148 per tree and $593 per acre by planting powdery mildew resistant dogwood cultivars that do not require routine fungicide applications (Gardner et al., 2004; United States Department of Agriculture, 2002). Furthermore, a survey has shown that consumers are willing to pay $13.35 more for powdery mildew resistant dogwood cultivars than the susceptible cultivars (Gardner et al., 2004). Unfortunately, the few powdery mildew resistant cultivars that are available commercially including 'Cherokee Brave' (Hagan et al., 1998; Mmbaga and Sauve, 2004; Windham et al., 1998), 'Jean's Appalachian Snow', 'Karen's Appalachian Blush', and 'Kay's Appalachian Mist' (Windham et al., 2003) are not resistant across multiple environments and their resistance has not been stable over time (Mmbaga and Sauve, 2004). Therefore, there is an urgent need to develop more cultivars that are resistant to powdery mildew. In addition, there is also a need to understand the total phenotypic variance for the powdery mildew resistance trait as a function of genotype, environment and genotype by environment interactions so as to effectively design targeted breeding programs or selection procedures for genetic improvements (Acquaah, 2011). Heritability is the proportion of the observed phenotypic variation in the progeny that is inherited (Poehlman and Sleper, 1995) while variance due to environmental factors occurs when expression of the genotype is not stable across multiple target environments. In cases where genotype by environment interactions are important, breeding strategies may include the identification of parental lines that can perform well in targeted environments (Fox et al., 1997). Powdery mildew resistance in dogwood has been reported to vary across different environments over multiple years (Mmbaga and Sauve, 2004). Such observations suggest a need for additional studies to better understand the variance components for powdery mildew resistance in dogwood. However, tree crops have long generation time and genetic studies take a long time; furthermore, flowering dogwood have obligatory cross pollination and are highly heterozygous. Fehr (1987) suggested the use of F1 as Pseudo F2 when progeny is derived from controlled crosses for highly heterozygous trees. This was supported by Allard (1999) who explained that when parents are highly heterozygous at many loci due to repeated cross pollination, progeny derived from controlled crosses of such highly heterozygous parents are considered Pseudo F2 and are not true F1's. Thus, phenotypic evaluation of F1 as pseudo F2 has been reported in several other cross pollinated crops including mulberry (Banergee et al., 2012), cassava (Aravanopoulous, 2010), tall fescue (Majidi et al., 2009) and willows (Owolade, 2006).

Broad sense heritability is the fraction of total phenotypic variance that is genetic due to additive, dominance and epistatic effects (Poehlman and Sleper, 1995). Estimates of broad sense heritability have been useful in understanding the extent to which a trait is influenced by the genotype as opposed to the environment. For example, high broad-sense heritability values found for turf quality, crown density, mowing quality, and genetic color in tall fescue (*Festuca arundinacea* Schreb) (Bokmeyer et al. 2009a; Burton and Devane, 1953) and native prairie junegrass (*Koeleria macrantha* Ledeb) (Clark and Watkins, 2012) indicate that these traits are largely influenced by the genotype as opposed to the environment. Despite the significance of broad sense heritability in trait improvement, such information has not been determined for powdery mildew resistance in dogwoods. Recent reports on narrow sense heritability estimates (70% - 90%) for powdery mildew resistance in flowering dogwoods (Parikh et al., 2015) indicate the importance of additive gene effect (Nyquist, 1991) on this trait.

Heritability estimates are useful in estimating genetic gains as prediction parameters of progeny performance (Allard, 1960). While it is easy to breed and predict performance of progeny for qualitatively inherited traits controlled by a few genes (Flor, 1971), predicting progeny performance for quantitatively inherited traits is often difficult and requires estimation of genetic gain (Browning and Frey, 1969; Hooker, 1967). Since powdery mildew resistance in dogwood is quantitatively inherited (Parikh et al., 2015), it is critical to estimate genetic gain for the trait to effectively predict performance of progeny derived from particular crosses.

Based on previous crosses between susceptible cultivar [Cherokee Princess (CP)], resistant selection (R14) and moderately resistant cultivars [MI9 and Cherokee Brave (CB)] (Parikh et al., 2015), the objective of the current study was to estimate broad sense heritability, genetic gain and the minimum number of effective genes involved in powdery mildew resistance in dogwood.

Materials and Methods

Population development.

Controlled crosses were conducted between four parental clones that included powdery mildew resistant (R), moderate resistant (MR) and susceptible (S) genotypes. These crosses were conducted at Tennessee State University Nursery Research Center (TSU-NRC), McMinnville, TN using combinations of R X MR (MI9 x CB), R X S (MI9 x CP and R14 x CP) and their reciprocal crosses (CB x MI9 and CP x MI9) done over a three year period (2004, 2011, and 2012).

Controlled crosses were achieved by the hand pollination as described by Reed (1999). After pollination, plant inflorescences remained covered until seeds were harvested. Processing of the harvested seeds involved removal of the red soft seed-coat followed by washing and drying for about 30 days. Seed dormancy was broken by vernalization at 4^oC for three months as described by Chouard (1960). Germinants with visible radicals were sown in a Morton's potting mix (Morton's Horticultural Supplies Inc., McMinnville, TN) in 3.75 L pots. MI9 x CB generated 177 progeny plants in 2005, and its reciprocal cross CB x MI9 generated 186 progeny plants in 2013. In, 2005 CP x MI9 generated 79 progeny plants whereas MI9 x CP generated 97 progeny plants in 2012. The controlled cross between R14 and CP generated 155 progeny seedlings in 2012. Seedlings of the parental plants and their progeny were maintained in a greenhouse-controlled environment at $26/20^oC \pm 3$ (day/night) and 70-90% RH at the TSU-NRC, McMinnville, TN and at the TSU main campus research facilities, Nashville, TN. All plants were fertilized using Nutricote Total™ (Florikan ESA LLC, FL, USA) 18-6-8 (N-P-K) at a rate of 12 g per plant, equivalent to 2.16 g nitrogen, 2.62 g phosphorus and 6.30 g potassium per potted plant and watered daily by overhead sprinkler system to promote powdery mildew disease development.

Plant inoculation.

Naturally infected plants of susceptible plants were placed in the study area as a source of air-borne inoculum. These plants were placed strategically in the greenhouse to allow even distribution of air-borne spores on the parents and the progeny. Disease severity rating was assessed in 2005, 2012 and 2013 on a scale of 0 to 5 adapted from Horsfall and Barrat (1945), in which a score of 0 represented plants showing 0% symptoms in the foliage, while a score of 1, 2, 3, 4 and 5 represented plants showing 1-10%, 11-25%, 26-50%, 51-75% and 76-100% symptoms in the foliage respectively. A visual representation of the disease scale from 0-1 on flowering dogwoods is presented in Figure 1. Disease evaluations were conducted monthly in June, August and September and the highest disease severity was used for subsequent data analysis.

Figure 1: Powdery mildew disease severity on flowering dogwoods, rating of 0-5 in which 0= No disease (a), 1= 1-10% (b), 2= 11–25% (c), 3= 26-50% (d), 4= 51-75% (e), 5= 76-100% (f).

Heritability.

Broad sense heritability was measured using the variance component method (Fehr, 1987). For this method, the formula, $H = \sigma^2 g / \sigma^2 p$; where, $\sigma^2 g$ = Variance due to genotype (additive, dominance or epistatic) and $\sigma^2 p$ = Variance due to phenotype was used (Toker, 2004). This analysis used Proc MIXED restricted maximum likelihood (REML estimation of VARCOMP) SAS Institute, NC (2002-2010). Narrow sense heritability was estimated using mid-parent-progeny regression analysis (Poehlman and Sleper, 1995) in which the means of the pseudo F_2 progeny were regressed against mid-parent values from the two parents used in the cross and the slope of the regression line was equal to the narrow sense heritability.

Genetic Gain.

The top 5% of the population was chosen for the selection intensity. Genetic advancement was calculated using the formula from Bonos (2006) and Bonos et al., (2003):

$$G= (i) (\sqrt{\sigma^2_p}) (h^2)$$

In this formula, *i* is the selection intensity in top 5% (2.06), σ^2_p is parental variance among the replicates of parental clone and h^2 is narrow sense heritability calculated as described above.

Minimum number of effective genes.

The minimum number of effective genes controlling powdery mildew resistance in flowering dogwoods was calculated based on the formula by Wright (1968):

$$N= (P_1 – P_2)^2/8 (\sigma^2_{F2} - \sigma^2_e)$$

Where, N= Number of genes, P1 = Mean resistance of parent 1, P2 = Mean resistance of parent 2, σ^2_{F2} = Variance of F_2 population, σ^2_e = Environmental variance among the replicates of parental clone pooled for all parental clones. This estimation method makes an assumption that genes have equal effects, no dominance or epistasis present, and that no two loci are on the same chromosome (Poehlman and Sleper, 1995).

Results and Discussion

Parental and progeny response to powdery mildew:

There were significant differences in disease severity between the resistant and susceptible parents in all the years (Table 1). For each year, disease severity varied over time (June, August and September). Cherokee Princess showed the highest amount of disease (disease severity ≥3) in all the three years indicating highest susceptibility, while R14 selection showed the lowest disease severity (disease severity ≤1) indicating highest resistance. As expected, both CB and MI9 selections displayed moderate disease severity (disease severity of 1.5-3.5) indicating moderate resistance. Although CB was released as a highly resistant cultivar (Hagan et al., 1995; Ranney et al., 1994), the results in the current study suggest that this cultivar has moderate resistance as previously reported by Mmbaga and Suave (2004). Based on progeny means for each cross, there was no significant differences in progeny mean disease severity from crosses between R x R, S x R or R x S crosses. The reciprocal crosses did not indicate significant influence of maternal or paternal inheritance on powdery mildew resistance. As reported previously (Parikh et al., 2015), powdery mildew resistance in pseudo F_2 population showed quantitative inheritance with a continuous distribution of disease severity.

Heritability

The estimates for genotype, year and residual effects varied across the 5 crosses (Table 2). Variance due to genotype ranged between 0.56 and 2.06 across all the populations (Table 2). The highest variance due to genotype was from MI9 x CP and R14 x CP followed by MI9 x CB. Variance across the years was generally small and not significant. Similarly, variance resulting from interaction between genotype and year (Genotype*Year) was not significant for CB x MI9, CP x MI9, MI9 x CP and R14 x CP crosses. Variance due to Genotype*Year interaction was highest in MI9 x CB (0.76) and low in the other crosses (Table 2). Residual variance/environmental variance (σ^2_e), ranged from 0.07 to 0.60 and was lower than variance due to genotype (Table 2). Similar results for genotypic variance (0.1 - 366.74), variance due to genotype*year interaction (0 - 56) and residual variance (0.07 - 143.08) have been reported for various morphological and fruit color traits in open-pollinated half-sib mango families (Brown et al., 2009).

The two-year estimates for broad-sense heritability were 88.9%, 60%, 66%, 80%, and 87.2% for the CB x MI9, MI9 x CB, CP x MI9, MI9 x CP and R14 x CP crosses respectively (Table 3). These high broad-sense heritability values (60% - 88.9%) indicate that the total phenotypic variance observed for powdery mildew resistance in flowering dogwoods is mainly accounted for by the genotype (additive, dominance or epistasis effects). Similar high broad-sense heritability has been reported for brown patch resistance in tall fescue (*Festuca arundinacea* Schreb) (74%) (Bokmeyer et al., 2009a). Other quantitative traits with high broad-sense heritability include yield (69% - 99%) in safflower (*Carthamus tinctorius*) (Camas and Esendal, 2006) and leaf size (99.79% - 99.97%) in tobacco (Alekoska and Aleksoki, 2009).

Narrow sense heritability (additive gene effects) estimates for powdery mildew resistance in flowering dogwoods using mid-parent progeny means regression ranged from 53.3% to 86.6% (Table 3). The populations that showed high narrow sense heritability of 86.7%, 70.3% and 75% were derived from CB x MI9, MI9 x CP and R14 x CP crosses respectively. High narrow-sense heritability (70% - 97%) has been observed for quantitative traits in tobacco (Alekoska and Alekoski, 2012). Fahlini et al. (2010) also reported estimates of narrow-sense heritability (88% - 98%) for agro-morphological traits like grain breadth, plant height, and grain shape and grain length. The level of narrow sense heritability observed for MI9 x CB (53.30%) and CP x MI9 (62.50%) crosses was moderate and is similar to estimates for brown patch resistance (57% - 62%) in tall fescue (Bokmeyer et al., 2009b). These values are also similar to the values (14% - 98%) reported by Stommel and Griesbach (2008) and (76% - 79%) reported by Banerjee et al. (2012) for leaf length and leaf color of capsicum and bacterial leaf spot resistance in mulberry respectively.

Estimates for broad-sense heritability in the current study exceeded those of the corresponding narrow-sense heritability. This was expected because broad-sense heritability takes into account total genetic variance (additive + dominance + epistasis effects) as opposed to narrow-sense heritability which only accounts for additive genetic effects (Allard, 1960). The high heritability values reported in this study suggest that most of the phenotypic variance in powdery mildew resistance observed in the five crosses is attributable to genetic effects. Similar results were observed for quantitative traits in tall fescue (Bokmeyer et al., 2009b) and tobacco (Aleksoka and Aleksoki, 2012), where it was concluded that high broad-sense and narrow sense heritability were indicative of traits being controlled by genetic factors as opposed to environmental effects.

Genetic Gain

Estimates for broad-sense and narrow-sense heritability are useful tools for predicting the genetic gain resulting from a specific bi-parental cross. Estimates for genetic gain calculated using broad-sense heritability take into account all components of genotypic variance (additive, dominance and epistasis effects) and are typically higher than those derived from narrow-sense heritability which accounts only for additive gene effects (Bonos et al., 2003). Since breeders are more interested in the additive gene effects for a given trait, estimation of genetic gain from narrow-sense heritability is prevalent. In our current study, genetic gain for powdery mildew resistance was estimated using values for narrow-sense heritability (Table 4). The genetic gain observed in all the crosses ranged from 33.9% to 77.7%. This genetic gain was calculated with an assumption that the top 5% of the pseudo F_2 plants would be selected for further propagation. The expected genetic gain was highest in the R14 x CP and CB x MI9 crosses with an expected gain of 77.7% and 60.9% respectively. High genetic gains of up to 68% have been reported for dollar spot resistance in tall fescue (Bonos et al., 2006). In the current study, low genetic gain was observed for the MI9 x CB (36.1%), CP x MI9 (33.9%) and MI9 x CP (37.3%) crosses. Such low genetic gains are not uncommon in disease resistance traits. For instance, in creeping bent-grass, low genetic gains (28% and 44%) have been previously reported for dollar spot resistance (Bonos, 2006).

Minimum number of effective genes

The minimum number of effective genes contributing to powdery mildew resistance was calculated for all the S x R and R x S crosses and ranged from 1.27 to 3.01 (Table 5). These results support the idea that powdery mildew resistance in flowering dogwood is inherited quantitatively (Parikh et al., 2015). Similar results in number of genes (1.0 - 3.2) has been reported for brown patch resistance in tall fescue (Bokmeyer et al., 2009b). However, the high broad-sense heritability values in this study suggest a possibility of other minor non-additive gene effects. Thus, estimates for the minimum number of effective genes in this current study may be slightly biased. This type of biasness has been reported in turfgrass patho-systems (Bonos et al., 2006; Han et al., 2006).

Conclusion

The findings from this study show high broad-sense heritability for powdery mildew resistance in flowering dogwoods, which strongly suggest that the observed phenotypic variance is largely a function of genetic effects (additive, dominance or epistasis). Conversely, environmental effects are expected to have little influence on expression of this trait. The high narrow-sense heritability for powdery mildew resistance observed in the current study indicates that additive gene effects are more important than non-additive effects (dominance and epistasis) for powdery mildew resistance. The highest genetic gains were observed for the R14 x CP and CB x MI9 crosses which suggest the usefulness of these parental combinations in breeding for powdery mildew resistance in flowering dogwood. The minimum number of effective genes segregating in the S x R and R x S crosses ranged from 1 - 3 genes and support previous findings that powdery mildew is inherited quantitatively in flowering dogwoods.

Acknowledgements

The author’s gratefully acknowledge Dr. Lucas Mackasmiel, Terri Simmons and Terry Kirby with their assistance throughout this project. This project was partly funded by USDA Capacity building grant No 010-38821-21532.

References

Acquaah, G., 2011. *Principles of plant genetics and breeding. 6.* Carlton, Australia: Blackwell publishing.

Aleksoska, A.K., Aleksoski J., 2012. Heritability of Quantitative Traits in F1 and F2 Progenies of some Domestic and Foreign Tobacco Varieties. Agriculturae Conspectus Scientificus 77: 207-210.

Allard, R.W., 1960. *Principles of plant breeding*. John Wiley & Sons. Inc. New York.

Allard, R.W., 1999. *Principles of plant breeding*. New York: Wiley.

Aravanopoulos, F.A., 2010. Contribution of leaf morphometricsin the study of genetic entries in Salix L. In (1st Ed)*ElectronicJournal of Plant Breeding*, 1320–1328.

Banerjee, R., Das, N.K., Doss, S.G., Saha, A.K., Bajpai, A.K., Bindroo, B. B., 2012. Narrow sense heritability estimates of bacterial leaf spot resistance in pseudo F2 (F1) population of mulberry (Morus spp.). *European Journal of Plant Pathology*.*133:* 537 - 544.

Bokmeyer, J.M., Bonos, S.A., Meyer W.A., 2009a. Broad-sense heritability and stability analysis of brown patch resistance. *HortSci 44*: 289-292.

Bokmeyer, J.M., Bonos, S.A., Meyer, W.A., 2009b. Inheritance characteristics of brown patch resistance in tall fescue. *CropSci 49*: 2302-2308.

Bonos, S.A., 2006. Heritability of dollar spot resistance in creeping bentgrass. *Phytopathology 96*: 808-812.

Bonos, S.A., Clarke, B.B., Meyer, W. A., 2006. Breeding for disease resistance in cool season turfgrass. *Annu. Rev. Phytopathol. 44*: 213-234.

Bonos, S.A., Casler, M.A., Meyer, W.A., 2003. Inheritance of dollar spot resistance in creeping bentgrass. *Crop.Sci. 43*:2189-2196

Brown, S.J., Schnell, R.J., Ayala-Silva, T., Moore, J.M., Tondo, C.L., Winterstein, M.C., 2009. Broad-sense Heritability Estimates for Fruit Color and Morphological Traits from Open-pollinated Half-sib Mango Families HortScience 44: no. 6 1552-1556.

Browning, J.A., and Frey, K.J., 1969. Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* 7355–382.

Burton, G.W., Devane, E.H., 1953. Estimating heritability in tall fescue (Festuca arundinacea) from replicated clonal material.

Camas, N., Esendal, E., 2006. Estimates of broad-sense heritability for seed yield and yield components of safflower (Carthamus tinctorius L.). Hereditas, 143: 55-7.

Chouard, P., 1960. Vernalization and its Relations to Dormancy. *Annual Review of Plant Physiology, 11*, 191-238.

Clark, M.D., and Watkins, E., 2012. Broad-sense heritability estimates of turfgrass performance characteristics in native prairie junegrass germplasm. *HortSci 47*: 1228-1233.

Fahlini R.A., Khodambashi, M., Houshmand S., Arzani A., 2010. Estimation of the heritability of agro-morphological traits in rice (*Orzya sativa* L.) using F_2:$_3$ families. *African Journal of Agricultural Research 5*: 1297-1303

Fehr, W.R., 1987. Theory and technique. *Principles of cultivar development*, *In Vol 1*. New York: Macmillan Publishing Co.

Flor, H.H., 1971). Current status of the gene-for-gene concept. *Annu. Rev. Phtopathol. 9*: 275-296.

Fox, P.N., Crossa, J., Ramagosa, I., 1997. Multi-environment testing and genotype x environment interaction. In: Kempton, R.A and Fox, P.N. (eds), *Statistical methods for plant variety evaluation.* Chapman & Hall, p. 117-138

Fulcher, A.F., White, S.A., 2012. IPM for select Decidious trees in southeastern US nursery production, Ch.7: *Dogwood-Cornus spp*.

Gardner, J.G., Eastwood, D.B., Hall, C.R., Brooker, J.R. 2004. $0.148/tree. *Production and marketing Reports, 14*, 114-119

Hagan A.K., Hadin, B., Gilliam, C.H., Keever, G.J., Williams J.D., Eakes, J., 1998. Susceptibility of cultivars of several dogwood taxa to powdery mildew and spot anthracnose. *J. Environ. Hort. 16*: 147-151

Hagan, A.K., Gilliam, C., Keever, G., Williams J.D., 1995. Reaction of dogwood selections to powdery mildew. Ornamental Research Report Series No. 10. *Alabama Agricultural Experiment Station.* Auburn University, Auburn, AL. 50 pp

Han, Y., Bonos, S.A., Clarke, B.B., Meyer, W.A., 2006. Inheritance of resistance to gray leaf spot disease in perennial ryegrass. *Crop science, 46*, 1143-1148.

Hooker, A.L., 1967. The genetics and expression of resistance in plants to rusts of the genus Puccinia. *Annu. Rev. Phytopathol. 5*: 163–182.

Horsfall, J.G., Barrat, R.W., 1945. An improved grading system for measuring plant diseases. (Abstract.) *Phytopathology 35*:655.

Klingeman, W.E., Brooker, J.R., Eastwood, D.B., Riley, l.B., Belie, B.K., Knight, P., 2001. Consumer perceptions of landscape characteristics, disease and pest problems, and the value of powdery mildew resistant dogwood. *Univ. Tennessee Inst. Agr. Agr. Econ. Res. Serv*. 07-01

Li, Y., Mmbaga M.T., Windham, A.S., Windham, M.T., Trigiano R.N., 2009. Powdery mildew of dogwoods: Current status and future prospects. *Plant disease. 93*, 1084-092.

Majidi, M., Mirlohi, A., & Amini, F., 2009. Genetic variation, heritability and correlations of agro-morphological traits in tall fescue (Festuca arundinacea Schreb.). *Euphytica, 167*(3), 323-331.

Mmbaga, M.T., 1998. Effect of powdery mildew on growth of dogwood. *Tenn. Nurserymen's Assoc. News*. 8:16–17.

Mmbaga, M.T., Sauve, R.J., 2004. Multiple disease resistance in dogwoods (Cornus spp.) to foliar pathogens. Journal of Arboriculture, 30(2), 101-107

Nyquist, W., 1991. Estimation of heritability and prediction of selection response in plant populations. *Crit. Rev. Plant Sci. 10*: 235-322.

Owolade, O.F., 2006. Line x Tester analysis for resistance to cassava anthracnose disease. *World Journal of AgriculturalSciences, 2*, 109–114.

Parikh, L.P., Mmbaga, M.T., Kodati, S., Zhang G., 2015. Estimation of Narrow sense heritability of powdery mildew resistance in pseudo-F2 (F1) population of flowering dogwoods (Cornus florida L) *European Journal of Plant Path*. DOI 10.1007/s10658-015-0806-5

Poehlman, J.M., Sleper, D.A., 1995. Breeding field crops. *Iowa State Univ. Press, Ames, IA*.

Ranney, T.G., Grand, L.F., Knighten, J.L., 1994. Resistance of Cornus kousa taxa to dogwood anthracnose and powdery mildew. *Proc. South. Nurserymen's Assoc. Res. Conf. 39*:212–216.

Reed, S.M., 1999. Development of a labor-efficient hand pollination procedure for flowering dogwood. *J. Environmental Horticulture 17*, 92-94.

SAS Institute. 2002-2010. SAS/STAT user's guide, *Version 9.3* Cary, NC.

Stommel, J.R., Griesbach, R.J., 2008. Inheritance of fruit, foliar, and plant habit attributes in Capsicum. *Journal of the American Society for Horticultural Science*, *133*, 396-407.

Toker, C., 2004. Estimates of broad-sense heretability for seed yield and yield criteria in faba (Vicia faba L.). *Hereditas 140*: 222-225

United States Department of Agriculture. 2009. *2007 census of agriculture*, Washington DC.

United States department of labor. 2002. Producer price index for fungicidal preparations primarily for agriculture, garden or health service. Series PCU2879#7, Bur. Labor Stat., Wash., D.C

Windham, M.T., Witte, W.T., 1998. Naturally occurring resistance to powdery mildew in seedlings of Cornus florida. Journal of Environmental Horticulture, 16, 173-175.

Windham, M.T., Witte, W.T., Trigiano, R.N., 2003. Three white bracted cultivars of Cornus florida resistant to powdery mildew. HortScience 38:1253–1255

Windham, M.T., Trigiano, R.N., Windham, A.S., 2005. Susceptibility of Cornus species to two genera of powdery mildew. Journal of Environmental Horticulture, 23(4), 190 - 192.

Wright, S., 1968. Evolution and the genetics of populations. Vol. 1. Genetic and biométrie foundations. Evolution and the genetics of populations. Vol. 1. Genetic and biometrie foundations.

Table 1: Powdery mildew severity in Cherokee Princess, MI9 and R14 in 2005, 2012 and 2013 in controlled greenhouse environment

Year of evaluation	Greenhouse progeny evaluation[a]	Parents	Mean disease severity[b]
2005	GH-1	Cherokee Princess	4.5a
		Cherokee Brave	2.5 cd
		Selection MI9	1.5 ef
2012	GH-1	Cherokee Princess	4.5 a
		Selection R14	1.0 gf
		Selection MI9	1.5 ef
2013	GH-1	Cherokee Princess	3.0 cb
		Selection R14	0.5 g
2013	GH-2	Cherokee Brave	3.5 b
		Selection MI9	2.0 ed

LSD 0.05* = 0.661

[a] GH-1 – Greenhouse at Tennessee State University Otis Floyd Nursery Research Center, McMinnville , GH-2- Greenhouse at Tennessee State University main campus (Nashville, TN)

[b] Mean disease severity assessed on 0-5 scale in which 0= No disease, 1= 1-10%, 2= 11–25%, 3= 26-50%, 4= 51-75%, 5= 76-100% of the plant covered with powdery mildew. Numbers followed by same letters are not significantly different (SAS Institute, 2002-2010)

Table 2: Estimates for genotype, year, genotype x year and residual variance components in populations derived from CB x MI9, MI9 x CB, CP x MI9, MI9 x CP and R14 x CP crosses for the years 2005, 2012 and 2013

Sources of Variation	**Variance components**[a]				
	CB x MI9	MI9 x CB	CP x MI9	MI9 x CP	R14 x CP
Genotype	0.56	0.75	0.47	1.15	2.06
Year	0	0	0	0.04	0
Genotype*Year	0	0.76	0.15	0.12	0.12
Residual	0.07	0.51	0.12	0.60	0.30

[a] Variance components estimated using Proc MIXED REML VARCOMP Method in SAS Inc.

Table 3: Variance components and heritability estimates (broad-sense and narrow-sense) for CB x MI9, MI9 x CB, CP x MI9, MI9 x CP and R14 x CP crosses

Cross	**σ^{2}_{g}**[a]	**σ^{2}_{e}**[b]	**σ^{2}_{p}**[c]	**BSH**[d]	**NSH**[e]
CB x MI9	0.56	0.07	0.63	88.88	86.66
MI9 x CB	0.75	0.51	1.26	60.00	53.30
CP x MI9	1.15	0.60	1.75	66.00	62.50
MI9 x CP	0.47	0.12	0.59	80.00	70.30
R14 x CP	2.06	0.30	2.36	87.20	75.00

[a] Variance due to genetic component (σ^{2}_{g})
[b] Environmental variance (σ^{2}_{e})
[c] Phenotypic variance (σ^{2}_{p})
[d] Broad-sense heritability estimates ($H = \sigma^{2}g / \sigma^{2}p$)
[e] Narrow-sense heritability (h^2 = Slope of mid-parent vs progeny mean regression)

Table 4: Predicted gain from selection (Gs) for powdery mildew disease resistance in CB x MI9, MI9 x CB, CP x MI9, MI9 x CP and R14 x CP crosses. Estimates assumed that only the top 5% of the progeny was be advanced.

Cross	Genetic gain from selection of top 5%	Expected genetic gain in % of the mean	Mean disease severity[a]
CB x MI9	1.31	60.9	2.13
MI9 x CB	1.12	36.1	3.10
CP x MI9	1.16	33.9	3.42
MI9 x CP	1.00	37.3	2.68
R14 x CP	2.23	77.7	2.87

[a] Mean disease severity assessed on 0-5 scale in which 0= No disease, 1= 1-10%, 2= 11–25%, 3= 26-50%, 4= 51-75%, 5= 76-100% of the plant covered with powdery mildew.

Table 5 Estimates for the minimum number of genes controlling powdery mildew resistance in S x R (CP x MI9) and R x S (MI9 x CP and R14 x CP) crosses.

Cross	Minimum No. of effective Genes[a]
CP X MI9	1.27
MI9 X CP	3.01
R14 X CP	2.9

[a] Minimum number of effective genes $[N = (P_1 – P_2)^2/8\ (\sigma^2_{F2} - \sigma^2_e)]$

Figures