An Analysis of Combining Ability for Height, Leaf Out, Bloom Date, and Flower Color for Crapemyrtle

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Abstract. Breeding of crapemyrtle (*Lagerstroemia*) in the United States has focused on developing hybrids between parents with disease or pest resistance and those with good floral characteristics. The objective of this work was to study the general and specific combining ability of several horticulturally important traits in crosses between pest-resistant parents and those with saturated flower colors. Ten crapemyrtle parents were tested in a factorial mating design including 25 of the 29 possible families. Analysis of variance revealed significant differences ($P \leq 0.05$) for all traits for the general combining ability of parents. The cross between 'Arapaho' and 'WHIT IV' displayed the best specific combining ability for a desirable combination of height, leaf-out time, bloom time, and flower color based on current breeding objectives. Overall, this study revealed the importance of both additive and nonadditive genetic variability in crapemyrtle, suggesting that an integrated breeding strategy to capture both additive and dominance variance would be appropriate for producing new, improved crapemyrtle clones for the four traits evaluated.

Crapemyrtles (*Lagerstroemia indica* L. and *L. indica* × *L. fauriei* Koehne hybrids) are small flowering trees that are widely cultivated in landscapes in the southern United States. Most cultivars selected before the latter part of the 20th century were chance seedlings chosen for unique color or growth habit (Egolf and Andrick, 1978). Today, commercial crapemyrtle production in the United States is primarily by means of asexual propagation of named clones (Byers, 1997). Many clones are now available that vary in ultimate size, growth habit, pest tolerance, and flower color to service various landscape objectives (Knox, 2000).

Breeding of crapemyrtle in the United States was primarily pioneered by Otto Spring of Okmulgee, OK, who released a number of cultivars through Monrovia Nurs-

ery of California, and by Donald Egolf at the U.S. National Arboretum. Both breeding programs focused initially on improving horticultural traits of *L. indica* by intraspecific hybridization. In 1963, a chance interspecific seedling ('Basham's Party Pink') between *L. fauriei* and *L. indica* was discovered in Conroe, TX (Egolf and Andrick, 1978). This discovery, in combination with research at the U.S. National Arboretum indicating that *L. fauriei* was resistant to powdery mildew, served as the impetus for introgression of *L. fauriei* into the U.S. National Arboretum breeding program as a source of powdery mildew resistance. No detrimental effects from this interspecific cross on fertility were recognized, and after the initial hybrids were selected for resistance, the program used half-sib and backcrosses to introduce resistance into predominantly *L. indica* germplasm. More than 20 cultivars with high levels of powdery mildew resistance (Egolf, 1981a, 1981b, 1986a, 1986b, 1987a, 1987b, 1990; Pooler, 2006; Pooler and Dix, 1999) have been released by the breeding program. Several of the releases have also demonstrated increased resistance to *Cercospora* leaf spot (Hagan et al., 1998), flea beetles (*Altica* sp.), and Japanese beetle (*Popillia japonica* Newman) (Pettis et al., 2004). Continued breeding with germplasm derived from Otto Spring's breeding program has resulted in the release

of several popular cultivars with unique flower colors (Whitcomb, 1985, 1999, 2000a, 2000b, 2004; Whitcomb et al., 1984).

Accurate and timely assessment of the genetic parameters underlying important traits is critical for predicting future gains and developing successful breeding strategies (Zobel and Talbert, 1984). Diallel mating designs have been researched extensively to optimize forest tree improvement (Foster and Bridgewater, 1986; Xiang et al., 2003). Such designs can efficiently estimate several genetic and environmental parameters for a population (Kempthorne, 1956; Pederson, 1972). Various studies using loblolly pine (*Pinus taeda* L.) have indicated that selection based on additive and dominance genetic variance for growth traits at early ages can be effective (Foster, 1986; Foster and Bridgewater, 1986; Li et al., 1991, 1992). Despite extensive application of diallel and factorial mating designs in forest genetics, few such studies have been conducted on perennial ornamental crops.

A factorial mating design (design II) (Comstock and Robinson, 1948) was used in this study to evaluate 10 clones of crapemyrtle as parents. The first objective was to determine additive (GCA) and dominance (SCA) variance components for height (HT), leaf-out (LO), initial seasonal bloom (BD), and flower color (FC). The second objective was to estimate GCA and SCA for the four traits for two subpopulations of parents to optimize future selection and breeding efforts.

Materials and Methods

Plant materials. The following crapemyrtle clonal cultivars were used as parents in this study: 'Arapaho' (Pooler, 2006), 'Biloxi' (Egolf, 1987a), 'Catawba' (Egolf, 1967), 'Osage' (Egolf, 1987b), 'Tonto' (Egolf, 1990), 'Tuscarora' (Egolf, 1981b), 'Tuskegee' (Egolf, 1986a), 'Velma's Royal Delight' (Dix, 1999), 'Whit II' (Whitcomb, 2000a), and 'Whit IV' (Whitcomb, 2000b). We consider these parents a random sample of modern, tree-form crapemyrtle clones that are widely produced commercially in the United States (Knox, 2000). Crosses were made between two subpopulations of these parents, one group selected for pest tolerance (PT) and the other for flower color (FL). PT clones originated from the U.S. National Arboretum breeding program, whereas FL clones were selected based on their purple or dark pink-red flowers. 'Biloxi', 'Osage', 'Tonto', 'Tuscarora', and 'Tuskegee' compose the PT subgroup based on published studies of disease (Hagan et al., 1998) and insect (Pettis et al., 2004) tolerance/resistance. The primary attribute of 'Catawba', 'Velma's Royal Delight', 'Whit II', and 'Whit IV' is their dark purple or red-dark pink flowers. 'Arapaho' has both improved disease resistance and desirable flower color (Pooler, 2006) and was classified with both groups in the mating design but was not selfed. Our objective was to cross a parent

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in one group (PT) with all parents in the other group (FL) without reciprocal crosses by using a factorial mating design (design II) (Comstock and Robinson, 1948) as outlined in Table 1. Pollinations were performed following previously published procedures (Pounders et al., 2006). Twenty-four of the 29 possible crosses in the 10-parent factorial were generated during Summer 2002.

Seeds were germinated in Spring 2003 and grown in pine bark substrate in 11.3-cm square pots (1 L) until Jan. 2004. Unselected progeny from each family were then planted in a Ruston sandy loam soil spaced 1.2 m apart in the row and 3.1 m between rows at Mississippi State University's McNeill Unit (latitude 30°39'N, longitude 89°38'W, elevation 66.14 m) located in southeast Mississippi. The planting was a randomized complete block design with six blocks, 24 families, and 15 individuals per family per block. All factors in the model were considered to be random.

Plants were exposed to ambient weather conditions and fertilized annually in early spring with 5 g of N per seedling as 13N-5.5 P-10.7K farm-grade fertilizer. Data were collected for LO, BD, and FC during the 2004 growing season and for 3-year HT after plants were dormant in 2005. Ratings for LO (1–5) were determined in 2004 by the week a seedling leafed-out, which ranged from the first week of March (1) through the first week of April (5). Ratings for BD (1–10) were based on seedlings initiating flowering over 9 weeks from the first week of June (1) through the first week of August (9). Plants that failed to flower were given a rating of 10. Flower color was based on a scale in which 1 = red–dark pink, 2 = purple, 3 = pink, 4 = lavender, and 5 = white. This scale was based on our breeding goal of selecting parents that produce high percentages of seedlings with saturated flower colors (red–dark pink or purple) rather than the white, lavender, and light pink flowers observed in initial crosses for introgression of pest resistance (Egolf, 1981a). Within each of these five broad color groups, additional variation was observed in hue and intensity. In other crops with complex flower color variation such as tulip (van Raamsdonk, 1993) and gladiolus (Cohen et al., 1986), intensive investigation indicates complex colors are the result of quantitative variation among multiple biochemical pathways on flower pigment saturation. A more complex rating scale for FC that reflected all observed variation was impractical under field conditions.

Data analysis. All computations were performed with SAS 9.1 (SAS Institute, Cary, NC). Analyses of variance to determine GCA and SCA mean squares with appropriate F-tests were generated with PROC GLM with all factors in the model designated as random effects. Correlations between the four traits were calculated with PROC CORR. Restricted maximum likelihood (REML) estimates of the variance components were obtained by using PROC MIXED. GCA effects and SCA effects (Griffing,

1956) were generated with Best Linear Unbiased Prediction (BLUP) (Harville, 1976).

Results and Discussion

The factorial mating design was implemented with 24 of the desired 29 families tested (Table 1). Survival and growth of the test families was high with 95% of the original planting of 2209 seedlings surviving for 3 years. Correlations between the four traits under evaluation was low with the highest association indicated between HT and BD ($r = 0.25$) and between LO and FC ($r = 0.14$); therefore, no strong relationship in the inheritance of the four traits is indicated.

Analyses indicated that both GCA and SCA were important sources of variation for the four traits (Table 2). The PT parents significantly affected the GCA for HT, whereas the FL parents did not. In contrast, PT and FL parents made similar GCA contributions to LO, BD, and FC. Additive variation exceeded dominance variation for all four traits for PT parents (Table 3). The ratios of additive to dominance variance were 5.2:1.0 for HT, 5.7:1.0 for LO, 2.9:1.0 for BD, and 7.8:1.0 for FC. The FL parent additive variation exceeded dominance variation for LO and FC and was equivalent for BD,

whereas dominance variation exceeded additive variation for HT. The ratios of additive to dominance variance were 0.5:1.0 for HT, 4.9:1.0 for LO, 1.0:1.0 for BD, and 7.5:1.0 for FC. The two independent estimations of additive variance generated by the factorial analysis should be attributed to the two subpopulations reflected in the PT and FL parents.

In an improvement program, GCA effects give an indication of how the additive variance generated for a trait by a tested parent is moving the mean value of its progeny when mated to other parents within the general population (Griffing, 1956). It is anticipated that selection of two parents representing each of the subpopulations with extreme effects on a trait should have the maximum effect on the mean of the progeny for that trait as reflected in SCA. Our current breeding goals are to develop large crapemyrtles (+GCA HT) that are late to leaf out (+GCA LO), bloom early (–GCA BD), and have red or purple flowers (–GCA FC). Best parents from the FL subpopulation to achieve each of these goals based on the GCA ranking in Table 4 are ‘WHIT VI’ for HT and LO, ‘Catawba’ for BD, and ‘Whit II’ for FC. Best PT parents to achieve the goals are ‘Tuskegee’ for HT, ‘Osage’ for LO, and ‘Arapaho’ for BD and FC. Based on GCA,

Table 1. Mating design for crosses between pest-tolerant (PT) (‘Arapaho’, ‘Biloxi’, ‘Osage’, ‘Tonto’, ‘Tuscarora’, and ‘Tuskegee’) and flower color (FC) (‘Arapaho’, ‘Catawba’, ‘Velmas Royal Delight’, ‘Whit II’, and ‘Whit IV’) crapemyrtle subpopulations.

Parents (FL) (PT)	Arapaho	Catawba	Velmas Royal Delight	Whit II	Whit IV
Arapaho		X	X	X	X
Biloxi	X	^z	^z	X	X
Osage	X	X	X	X	X
Tonto	X	X	X	X	X
Tuscarora	X	X	X	X	^z
Tuskegee	X	^z	^z	X	X

^zMissing families.

Table 2. Mean squares and F-tests for the crapemyrtle factorial analyses for height (HT), leaf out (LO), bloom date (BD), and flower color (FC).

Source	DF	HT	LO	BD	FC
GCA ^{PT}	5	66208**	70.7**	342.4**	58.3**
GCA ^{FL}	4	14794 ^z	63.2**	212.5**	55.4**
SCA	14	6706**	5.1*	43.0**	3.6 ^y
Error	113	2322	2.4	7.9	2.1

^{PT} = pest-tolerant parents; ^{FL} = flower color parents.

*Significant at $P \leq 0.05$; **significant at $P \leq 0.01$.

^zSignificant at $P = 0.12$.

^ySignificant at $P = 0.06$.

Table 3. Genetic parameter estimates for the crapemyrtle factorial analysis for four traits (height, leaf out, bloom date, and flower color).

Parameter	Height	Leaf-out	Bloom date	Flower color
$\sigma^2_{GCA^{PT}}$	250.3	0.179	1.147	0.163
$\sigma^2_{GCA^{FL}}$	24.83	0.146	0.421	0.157
σ^2_{SCA}	48.31	0.030	0.402	0.021
σ^2	892.6	0.936	4.720	0.808
V_A^{PT}	1001.2	0.716	4.588	0.652
V_A^{FL}	99.2	0.584	1.684	0.628
V_D	193.2	0.120	1.608	0.084
V_A/V_D^{PT}	5.2	5.7	2.9	7.8
V_A/V_D^{FL}	0.5	4.9	1.0	7.5

^{PT} = pest-tolerant parents; ^{FL} = flower color parents.

Table 4. Progeny means for each parent and estimates of general combining ability (GCA) effects for 10 crapemyrtle parents for four traits (height, leaf out, bloom date, and flower color).^z

Cultivar (PT)	Height		Leaf out		Bloom date		Flower color	
	Mean	GCA ^y	Mean	GCA	Mean	GCA	Mean	GCA
Arapaho	159	2.93	2.65	-0.42	6.29	-0.17	1.76	-0.33
Catawba	144	-0.19	2.87	-0.01	4.86	-0.63	2.46	0.55*
WHIT II	149	-3.02	3.16	0.16	7.35	0.92*	1.61	-0.31
WHIT VI	162	4.63	3.55	0.52*	5.90	-0.17	1.78	-0.14
Velma R.D.	136	-4.36	2.61	-0.25	5.73	0.05	2.1	0.22
Cultivar (FL)								
Arapaho	148	-3.95	2.35	-0.67*	4.85	-1.30*	1.43	-0.57*
Biloxi	169	12.82	3.29	0.22	7.84	1.25*	1.80	0.05
Osage	150	-3.04	3.54	0.54*	5.34	-0.83	2.45	0.45*
Tonto	137	-15.78	2.85	-0.12	5.84	-0.31	1.67	-0.28
Tuscarora	137	-13.29	2.73	-0.10	6.44	0.14	2.02	0.01
Tuskegee	179	23.23*	3.19	0.12	7.67	1.04	2.14	0.34

^zParents represent two subpopulations from the general population: pest-tolerant (PT) and dark flower colors (FL).

^y*Indicates the estimate of GCA effect significantly different from zero (positive and negative) based on *t* test ($P \leq 0.05$).

a cross between 'WHIT VI' and 'Arapaho' should move progeny means for the four traits in the desired directions.

In this study, parental GCA was a very good predictor for SCA means recorded for the families (Table 5). The cross between 'WHIT VI' and 'Tuskegee' had the greatest mean HT. The cross between 'WHIT VI' and 'Osage' had the latest mean LO. The cross between 'Catawba' and 'Arapaho' had the third earliest mean BD. The cross between 'Whit II' and 'Arapaho' had a FC mean nearest the desired red-dark pink rating of 1.

The cross between 'WHIT VI' (high HT GCA, high or late LO GCA, intermediate BD GCA, intermediate FC GCA) and 'Arapaho' (intermediate HT GCA, low or early LO GCA, low or early BD GCA, low FC GCA) should improve all four traits as desired to meet our current goal. The calculated SCA of this particular cross indicates the actual progeny means exceed the desired expected

change for all traits except HT. The rating scale used to quantify FC variation in families was effective in predicting flower color changes in progeny. Maximum genetic gain in progeny means for a trait is achieved when both additive and dominance variances are used. This can be achieved by selecting parents that have good GCA effects and that, when crossed with specific parents, consistently produce families with high SCA potential (or better-than-expected means based solely on GCA) (Foster and Bridgewater, 1986). The performance of the cross between 'WHIT VI' and 'Arapaho' conforms to these criteria for three of the four traits evaluated.

The high values of additive genetic variation identified for the four traits observed in this study indicate that either tandem selection or a weighted selection index can be effectively used to increase the frequency of elite individuals with the desired changes in these traits in advanced generations (Falconer,

1982). Clonal selection and vegetative propagation, which are standard production practices for commercial crapemyrtle production in the United States (Byers, 1997), also facilitate the capture of nonadditive genetic variation in selections. Because both GCA and SCA can be easily exploited for the four traits, genetic gains can be expected that are difficult to achieve through the more traditional seed propagation system used for woody plants that are difficult to propagate asexually.

Once combining ability parameters for a set of traits are obtained for a group of parents, the selection of parents for future crosses can be altered to reflect new breeding goals. Breeding goals for crapemyrtle will change over time to reflect changing consumer demands. The information generated on general and specific combining abilities can be used to select crosses that effectively move population means in the desired directions. Without such information, typically

Table 5. Family means and estimates of specific combining ability (SCA) effects for 10 crapemyrtle parents for four traits (height, leaf out, bloom date, and flower color).

Family ^z	Height		Leaf out		Bloom date		Flower color	
	Mean	SCA	Mean	SCA	Mean	SCA	Mean	SCA
ARA × BIL	168	-0.56	2.57	-0.11	6.82	-0.41	1.67	-0.03
ARA × OSA	165	7.65	3.20	0.06	5.24	5.90	2.15	0.03
ARA × TON	149	5.93	2.27	-0.08	5.15	-0.51	1.46	0.05
ARA × TUS	140	-1.94	2.52	0.03	6.90	0.55	1.81	0.07
ARA × TKE	177	-5.31	2.70	0.02	7.36	0.20	1.64	-0.18
CAT × ARA	150	0.95	2.06	-0.12	4.47	0.13	1.80	-0.07
CAT × OSA	143	-4.04	3.60	0.05	3.99	-0.66	3.10	0.06
CAT × TON	144	4.38	2.93	0.05	5.50	0.16	2.45	0.10
CAT × TUS	137	-1.67	2.90	0.02	5.47	-0.24	2.49	-0.01
WH2 × ARA	147	0.26	2.57	0.06	6.03	0.13	1.07	-0.01
WH2 × BIL	164	0.77	3.77	0.17	8.21	-0.18	1.52	-0.06
WH2 × OSA	148	0.95	3.43	-0.13	5.78	-0.45	2.16	0.03
WH2 × TON	120	-8.26	2.69	-0.18	7.60	0.59	1.28	-0.02
WH2 × TUS	140	2.49	3.22	0.09	7.86	0.44	1.55	-0.03
WH2 × TKE	170	-2.14	3.29	0.03	8.67	0.36	2.16	0.05
WH6 × ARA	145	-5.30	2.99	0.09	3.76	-0.84	1.06	-0.09
WH6 × BIL	175	2.27	3.68	-0.02	8.57	1.03	2.19	0.10
WH6 × OSA	153	-1.33	3.91	-0.06	5.43	0.15	2.08	-0.08
WH6 × TON	144	1.53	3.57	0.11	5.39	-0.31	1.29	-0.11
WH6 × TKE	200	11.94	3.64	-0.02	6.84	-0.19	2.56	0.17
VRD × ARA	150	3.32	1.80	-0.13	5.13	0.12	1.79	0.08
VRD × OSA	140	-3.81	3.57	0.16	6.28	0.67	2.74	0.03
VRD × TON	123	-6.63	2.74	0.08	5.93	-0.04	1.77	-0.06
VRD × TUS	133	-1.45	2.31	-0.16	5.59	-0.70	2.12	-0.03

^zParental abbreviations are Arapaho (ARA), Biloxi (BIL), Osage (OSA), Tonto (TON), Tuscarora (TUS), Tuskegee (TKE), Catawba (CAT), Velmas Royal Delight (VRD), Whit II (WH2), and Whit IV (WH6).

selected crosses would be based solely on parental expression of the trait, greatly reducing breeding efficiency for quantitative traits.

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