

Combining Ability for Plant and Fruit Traits of Interspecific Blueberry Progenies on Mineral Soil

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Additional index words. *Vaccinium corymbosum*, *V. ashei*, *V. myrtilloides*, *V. atrococcum*, *V. darrowi*, *V. myrsinites*, *V. angustifolium*, interspecific hybrids, fruit breeding

Abstract. Data from a four-parent diallel, involving one highbush (*Vaccinium corymbosum* L.) clone and three interspecific hybrids grown on mineral soil unamended with organic matter, were analyzed to determine combining ability effects for six traits: plant size, berry size, the number of days between flowering and fruiting (# DBF&F), the ratio of total fruit weight to canopy volume (TFW : CYV), days to fruit ripe, and yield. General combining ability effects were significant for all characters tested, except yield and berry size in 1984. Specific combining ability effects were significant for plant size in 1983, #DBF&F in 1984, TFW: CYV in 1984, and berry size in 1985. Vigorous and productive highbush cultivars can be developed for mineral soils by using the interspecific clones from this study and their selected recombinant to combine the genes for plant vigor with the high-quality fruit traits of highbush cultivars.

Highbush blueberries are produced in a wide range of climatic conditions but generally are limited to well-drained, moist, acidic soils high in organic matter. Production is possible on mineral (upland) soils if amended by the addition of sulfur, peatmoss, irrigation, and mulch. These strict soil requirements limit the areas for highbush production or increase management costs when blueberries are grown on upland soils that are low in organic matter. The addition of organic matter to mineral soils for blueberry production can account for almost 45% of planting costs (Fowler et al., 1981). Rabbiteye and lowbush blueberry plants are also vigorous and productive on well-drained, high-organic soils, and on upland soils low in organic matter, they are more vigorous than highbush blueberry plants (Chandler et al., 1985b; Korcak, 1986; Korcak et al., 1982). In addition, other blueberry species, such as *Vaccinium myrsinites*, *V. atrococcum*, and *V. darrowi*, have been observed growing on mineral soils and are considered potential sources for upland soil adaptation (Galletta, 1975). Selection on acidic, well-drained, sandy organic soils for the past 80 years and the small germplasm pool from which present highbush cultivars descended probably are responsible for the narrow soil adaptation of most of these cultivars. Only two cytoplasm are present in 48 of the most popular cultivars (Hancock and Krebs, 1986). Genetic improvement of highbush blueberries for upland soil adaptability is the best way to increase production on mineral soils because neither fertilization nor peatmoss incorporation influence growth on a mineral soil as much as the genetic composition of the plant (Korcak, 1986). Blueberry breeders now are developing highbush cultivars adapted to upland soils by using the considerable genetic variability present in *Vaccinium*. With the genetic bridges now existing between ploidy levels (Chandler et al., 1985a), the major steps to genetic advancement are the identi-

fication of important traits and determination of the inheritance of these traits.

This study was designed to examine combining ability effects for both plant and fruit traits in interspecific hybrid blueberry seedlings developing on mineral soil unamended with organic matter. Information from this Study will allow evaluation of one species and three interspecific hybrid clones for transfer of traits important for plant growth and fruit production. Our research continued work started by Chandler et al. (1985b) by using their four-parent diallel.

Materials and Methods

The mature blueberry plants used were established in the field in 1982, as a four-parent (G362, US226, US75, and JU11) (Table 1) diallel set of crosses and three additional crosses involving JU64 (JU64 x G362, JU64 x JU11 and G362 x JU64), on a Galestown fine sandy loam reddish-brown udult soil (0.7% to 1.0% organic matter) at Beltsville, Md. The soil pH was lowered with S to =4.2 before planting and no organic matter was added at any time.

A randomized complete-block design with 10 blocks was used. Each block consisted of progeny plots of 10 seedlings spaced

Table 1. Ploidy level ($x = 12$) and species included in the parentage of the five parental *Vaccinium* clones.

Clone	Ploidy	Constitution
JU11	6x	Tifblue (<i>Vaccinium ashei</i> Reade) x US 41 (<i>V. atrococcum</i> Heller) (Colchiploid)
JU64	4x	<i>V. myrsinites</i> Lamark x <i>V. angustifolium</i> Aiton
US75	4x	Fla-4B (<i>V. darrowi</i> Camp) x Bluecrop (<i>V. corymbosum</i> L.)
US226	4x	<i>V. myrtilloides</i> Michaux x <i>V. atrococcum</i> (Colchiploid)
G362	4x	<i>V. corymbosum</i>

Received for publication 28 June 1989. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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Abbreviations: BS, berry size; CYV, canopy volume; DFR, days to fruit ripe; DIF, differences in canopy volume; #DBF&F, number of days between flowering and fruiting; GCA, general combining ability; SCA, specific combining ability; TFW, total fruit weight.

0.5 m within and 1.0 m between rows and parental plots containing two clones of each parent. In 1983 and 1984, all the parent and progeny plots in the field were evaluated. In 1985, only the parents and seedlings from the plots of one set of F₁ plants from the four-parent diallel plus the plots of G362 x JU64 and JU64 x JU11 were evaluated.

The plants were fertilized in 1982 with 25 kg N/ha (1.87 g N/plant) applied as (NH₄)₂SO₄ and watered periodically with overhead sprinklers. The field received no fertilizer in 1983, but was irrigated, and weeds were controlled by cultivation and herbicide. In both 1984 and 1985, 28 kg N/ha, 12.3 kg P/ha, and 23.3 kg K/ha were applied in mid-May and 23 kg N/ha of (NH₄)₂SO₄ in early July. Total nutrients added per plant in 1984 and 1985, were 4.65 g N, 1.2 g P, and 2.3 g K. The plants were drip-irrigated using a 8-mil twin-wall lateral with holes punched every 30 cm. In 1985, soil tension was monitored with tensiometers. Four blocks of the field were irrigated when the soil tension reached 0.03 to 0.04 MPa at a depth of 15 cm, and the remaining six blocks were irrigated when soil tension reached 0.08 to 0.09 MPa at a depth of 25 cm. After a stress period, plants were irrigated for 8 to 12 hr to bring soil tension to 0 MPa.

In Fall 1983, 1984, and 1985, plant size was determined by calculating CYV from height, width, and breadth measurements of all the parent plants and a random sample of at least three seedlings per progeny plot. These CYV values were converted to DIF by subtracting the previous year's CYV from the current year. Data on fruiting traits were collected in 1984 and 1985: DFR, TFW, BS, and TFW : CYV. In 1984, data were also recorded for days to flower, so #DBF&F could be determined. DFR was determined by recording the number of days from 1 Jan. to ripen 50% of the fruit. TFW was the weight of all the fruit on a plant when 50% of the fruit was ripe. BS was determined by weighing 10 randomly selected ripe berries. Days to flower was recorded as the number of days from 1 Jan. for 50% bloom.

Data for 1983 and 1984 were subjected to a complete diallel analysis using the Schaffer and Usanis (1969) computer program; F ratios and GCA and SCA effects were calculated according to Griffing's method 3, model I analysis (Griffing, 1956). Diallel analysis was performed on the 1985 data in a similar manner, except that Griffing's method 4, model I analysis for a half-diallel was used (Griffing, 1956).

Results and Discussion

No maternal or reciprocal effects were found in 1983 and 1984, so a half-diallel design was chosen for 1985. The GCA x location effects in 1985 were not significant; thus, the data from the wet and dry sides of the field were combined. GCA was highly significant for DIF and TFW : CYV in all years analyzed (Table 2). SCA was highly significant for DIF 83 and significant for TFW : CYV 84. JU11 was the highest in GCA effects for DIF 83, 84, and 85, and US75 was second in DIF 85 (Table 3). US226 was the highest and G362 was second in GCA effects for TFW : CYV 84 and 85. Because only three progenies of JU64 were present in the field and data was only collected from two of these in 1985, a reliable estimate of GCA could not be determined, but data presented in Table 4 indicate that JU64 can transmit mineral soil tolerance to its offspring. The progeny means of JU11 x US75, JU64 x JU11, and G362 x JU11 for DIF 85 and G362 x JU64 for TFW : CYV (Table 4) were significantly higher than the parental means, indicating

Table 2. Summary of analyses of variance for DIF, TFW : CYV, DFR, #DBF&F, and BS.

Trait	Year	Source	MS	F
DIF	1983	GCA	423 × 10 ⁸	8.10**
		SCA	278 × 10 ⁸	5.32**
DIF	1984	GCA	421 × 10 ⁹	8.45**
		SCA	931 × 10 ⁸	1.87 ^{NS}
DIF	1985	GCA	157 × 10 ¹⁰	26.66**
		SCA	114 × 10 ⁹	1.91 ^{NS}
TFW : CYV	1984	GCA	731 × 10 ³	13.30**
		SCA	194 × 10 ³	3.54*
TFW : CYV	1985	GCA	109 × 10 ⁴	5.34**
		SCA	150 × 10 ³	0.73 ^{NS}
DFR	1984	GCA	6447	8.85**
		SCA	553	0.76 ^{NS}
DFR	1985	GCA	4101	233.80**
		SCA	14	0.82 ^{NS}
#DBF&F	1984	GCA	3808	32.27**
		SCA	486	4.63*
BS	1985	GCA	194	94.00**
		SCA	67	32.13**

NS, *, **Nonsignificant or significant at P = 0.01 or 0.05, respective y.

either heterosis for these traits or a difference resulting from seed vs. clonal propagation.

JU11 is a hybrid of two upland-soil-adapted species (*V. ashei* and *V. atrococcum*) (Galletta, 1975; Lyrene and Sherman, 1980), and US75 is descended from one upland-soil-adapted species (*V. darrowi* Camp) (Galletta, 1975; Lyrene and Sherman, 1980). JU64 and US226 are from the cross of two upland-soil-adapted species, but they and their progenies did not produce large plants on this mineral soil. Undoubtedly, this outcome is due partly to JU64 being a product of two lowbush species (*V. myrsinites* Lamarck and *V. angustifolium* Aiton) (attainable height for lowbush is <0.5 m) (Galletta, 1975) and US226 originating from the cross of a lowbush and highbush species (*V. myrtilloides* and *V. atrococcum*, respectively) (attainable height for a halfhigh is 0.5 to 1.0 m) (Galletta, 1975). This height discrepancy was partly compensated for by analyzing DIF. In the case of G362, genes for plant height are not a complicating factor because it is a highbush type (*V. corymbosum* L.) and produces a smaller DIF than US75, a lowbush (*V. darrowi*) and highbush (*V. corymbosum*) cross. In a study of five blueberry interspecific progenies evaluated in three upland soils and one traditional blueberry organic sand (3% organic matter and 95% sand), Korcak (1986) reported that there was a tendency for growth of progenies in the mineral soils to increase as the amount of *V. corymbosum* in their parentage decreased. This trend was not as apparent in our data because of the complication due to the height effect.

The significant GCA for DIF and TFW : CYV demonstrates that genetic variability exists for mineral soil adaptability and that selection should result in genetic improvement for these traits. Because GCA was higher than SCA, these traits are probably governed primarily by additive gene action; therefore, parental performance should predict hybrid progeny performance. The significant SCA estimates indicate that, for certain traits, a large sample of seedlings from particular crosses should be screened to identify the individuals with the best combination of GCA and SCA. Heritability estimates could not be obtained using the GCA and SCA effects because the analytical method presumed a fixed model (Griffing's model 1). In addition, interpretation of the gene action associated with these traits is limited to the parents and progeny used and can not be extrapolated to the population level. However, we hypothesize that other geno-

Table 3. Estimates of GCA effects for DIF in 1983, 1984, and 1985, TFW: CYV in 1984 and 1985, #DBF&F in 1984, BS in 1985, and DFR in 1984 and 1985 and SCA effects for DIF in 1983, TFW : CYV in 1984, #DBF&F in 1984, and BS in 1985.

Parent	DIF 83	DIF 84	DIF 85	TFW : CYV 84	TFW : CYV 85	#DBF&F 84	BS 85	DFR 84	DFR 85
<i>GCA effects</i>									
JU11	60,525	185,325	349,775	-115	-148	13.7	-3.6	22.4	20.6
US75	2,980	-2,575	56,575	-180	-219	-5.4	2.3	-6.6	-2.9
G362	-13,625	-13,425	-84,975	51	65	-3.9	2.9	-2.6	-5.9
US226	-49,880	-169,325	-321,375	244	301	-4.3	-1.7	-13.1	-11.9
SE ²	23,996	77,574	141,177	98	123	4.6	1.8	7.9	7.2
<i>SCA effects</i>									
Cross									
US75 x US226	34,447			-64		2.1	-0.9		
G362 x JU11	34,447			-64		2.1	-0.9		
JU11 x US75	5,132			111		-0.7	-1.2		
US226 x G362	5,132			113		-0.7	-1.2		
JU11 x US226	-39,578			-48		-1.3	2.1		
G362 x US75	-39,578			-48		-1.3	2.1		
SE	14,712			37		0.7	0.6		

²Standard error of the difference between two effects.

Table 4. DIF, TFW : CYV, TFW, and BS means for parental clones and interspecific hybrid progenies grown on a mineral soil in 1985.

Entry	N ²	Trait ³			
		DIF (m ³)	TFW : CYV (g·m ⁻³)	TFW (g)	BS (g/10 berries)
JU11 x US75	10	1.03 a	465 de	618 ab	8.7 f
JU64 x JU11	9	0.92 a	369 de	428 bcde	5.2 i
G362 x JU11	10	0.88 a	614 cde	707 ab	9.6 ef
US75	10	0.61 b	168 e	133 de	17.0 c
JU11	10	0.59 b	1373 b	946 a	9.2 f
JU11 x US226	10	0.50 bc	1027 bcd	573 abc	8.0 fg
G362 x US75	10	0.45 bcd	705 cde	451 bcd	18.6 b
US75 x US226	10	0.35 cde	779 bcde	457 bcd	10.8 de
G362 x JU64	10	0.22 de	1990 a	743 ab	9.4 ef
JU64	10	0.22 de	927 bcd	197 cde	5.4 hi
US226 x G362	10	0.19 e	1193 b	339 bcde	11.2 d
G362	10	0.15 e	991 bcd	151 de	23.3 a
US226	5	0.10 e	483 de	36 e	6.8 gh

²Either the number of progeny plots per cross or the number of parental clones sampled.

³Mean separation by Duncan's multiple range test, $P = 0.05$.

types of *V. ashei*, *V. darrowi*, *V. angustifolium*, *V. atrococcum*, and *V. myrsinites* also possess genes for tolerating upland soil situations because of the habitats that these species occupy in nature (Galletta, 1975; Lyrene and Sherman, 1980). To ensure the use of species with the best possible combination of genes for upland soil tolerance, species populations should be screened for important traits in replicated agricultural situations.

Chandler et al. (1985b) reported a high GCA for CYV on these plants in 1982 but a low narrow-sense heritability (h^2) estimate from mid-parent offspring regression ($h^2 = 0.10$). In 1983, 1984, and 1985, mid-parent offspring regression estimates of h^2 were 0.53, 0.34, and 0.71, respectively. The h^2 estimates were probably higher in this study because the parental clones established more slowly than their seedling progeny. These high h^2 values indicate that CYV production on this mineral soil is primarily genetically determined.

The TFW : CYV ratio is an estimate of efficiency for partitioning photosynthate into fruit; US226 and G362 possess traits for higher efficiency than the other parents. Highbush selection G362 would be expected to have genes for efficient partitioning of biomass into fruit because it was selected for large fruit and

productivity. JU11 progeny means for TFW : CYV 85 were all lower than the JU11 clonal mean, possibly because they are pentaploids, which are generally less fertile than diploids, tetraploids, or hexaploids (Chandler et al., 1985a).

The yearly combining abilities for the fruiting traits show that TFW 84, TFW 85, and BS 84 had nonsignificant GCA and SCA values (Table 2). GCA was highly significant for DFR 84, DFR 85, #DBF&F 84, and BS 85; SCA was highly significant for BS 85 and significant for #DBF&F 84. US226 was lower in GCA for DFR 84 and 85 than G362 and JU11 (Table 3). G362 and JU75 were highest in GCA for BS 85 and only JU11 was highest in #DBF&F. In other inheritance studies with blueberries, BS (Darrow et al., 1939; Draper and Scott, 1969; Edwards et al., 1974; Finn and Luby, 1986), DFR (Darrow et al., 1939; Finn and Luby, 1986; Lyrene, 1983), and #DBF&F (Draper et al., 1982; Finn and Luby, 1986; Lyrene, 1983) were all found to be highly heritable. Large fruit size was found not to be associated with low yield, and small fruit size was reported to be dominant (Draper et al., 1982; Finn and Luby, 1986). These relationships might be the case for only *V. corymbosum* and *V. angustifolium* species or interspecific hybrid populations. We found that US75 had large fruit and low yield (Table 4). Fla-4B, one of the parents of US75, has small fruit and low yield, while the other parent, 'Bluecrop', has large fruit and high yield. No heterosis for BS occurred (Table 4) and G362 x JU64 was the only progeny that had a higher mean for TFW than its parents.

The highly significant GCA for DIF, TFW : CYV, and the fruiting traits indicate that genetic diversity for upland soil tolerance is present and heritable in the *Vaccinium* clones used in this study. The traits necessary for vigorous growth and high productivity on mineral soils are present in the germplasm examined in this study. US75 was second in GCA for almost all the traits evaluated, and we conclude that it has the best combination of genes for breeding upland-soil-adapted plants. US75 can also be used to breed for a shortened interval between flowering and fruiting. High TFW : CYV, the major trait lacking in US75, can be transferred in crosses to US226 and JU64. In addition, US226 was identified as a source for earliness on a mineral soil. JU11 was the best parent for transfer of plant vigor and this increased vigor should be useable after one or two additional backcrosses to a tetraploid. The low yield and vigor of G362 on this mineral soil does not reduce its potential as a

genetic source of productivity, especially if combined with US75, JU11, or JU64. Some of the seedlings from the crosses of G362 x US75, US75 x US226, and US226 x G362 with commercial potential have been selected and propagated for advance testing. Because GCA was higher than SCA for DIF and all fruiting traits except TFW, a recurrent selection program to develop vigorous and productive highbush blueberry cultivars for mineral soils, unamended with organic matter, should be effective by using the genetic material from this study and other related species material.

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