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Combining Ability for Seedling Root System Size and Shoot Vigor in Interspecific Blueberry Progenies

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Abstract. **Interspecific blueberry (*Vaccinium* spp.) progenies were examined to determine combining abilities and genetic variability for seedling root system size and shoot vigor and to establish whether a large root system is correlated with good growth when plants are grown on a mineral soil and exposed to a moderate soil water deficit. General combining ability (GCA) variance components for root system size and shoot vigor and specific combining ability variance components for shoot vigor were significant. US226, a tetraploid hybrid of *V. myrtilloides* Michaux x *V. atrococcum* Heller, had the highest GCA effect for root system size and the lowest GCA effect for shoot vigor. US75 (*V. darrowi* Camp x *V. corymbosum* L.) had the highest GCA effect for shoot vigor and was second in GCA effect for root system size. Comparison of the crosses containing G111 (*V. corymbosum*) with those containing G362 (*V. corymbosum*) indicates that selecting for the best *V. corymbosum* clone to start a breeding program seems as important as selecting the mineral soil-adapted parent. Root system ratings were highly correlated with total dry weight of field-grown plants ($r = 0.89$). The method used in this study to evaluate seedlings for root system size and shoot vigor could be used to eliminate the less vigorous plants from a population before field planting and to evaluate mineral soil adaptability.**

Current highbush blueberry (*Vaccinium corymbosum*) cultivars were selected from progenies growing on irrigated, acidic, sandy soils with high organic matter levels and, thus, are well adapted to these growing conditions. However, the occurrence of these types of soils is limited. Growing highbush cultivars on high pH (>pH 5.5), low organic matter, droughty, mineral soils is successful when soil amendments and irrigation are used (Korcak, 1983; Moore, 1976). The accepted recommendation for establishing highbush blueberries on a mineral soil include 1) incorporating enough S before planting to lower the pH into the acceptable range; 2) incorporating peat into the soil at time of planting; 3) after transplanting, applying 8 to 13 cm of an organic mulch around the base of each plant; 4) installing a drip-irrigation system; and 5) continuing mulch applications in subsequent years. However, adding organic matter in the form of peat at planting may account for as much as 45% of planting costs (Fowler et al., 1981). Sulfur applications are inexpensive but, over time, the pH may rise above the desired level making reapplication necessary. Rabbiteye blueberries (*V. ashei* Reade), which are more drought resistant than highbush blueberries (Erb et al., 1988b; Galletta, 1975), can be successfully grown on acidified mineral soils by either adding organic matter or irrigating (Cummings et al., 1981; Spiers, 1986). Because of the importance of adequate moisture for successful blueberry production and the relation between moisture stress and mineral soil adaptability in blueberries (Erb et al., 1993), any genetic improvement in water-use efficiency in blueberry cultivars would be beneficial for commercial producers.

Through breeding and selection, highbush blueberries may be developed that are genetically buffered against adverse growing conditions. *Vaccinium* species are found growing over a wide range of soil and climatic conditions (Galletta, 1975; Lyrene and Sherman, 1980), a characteristic that indicates that the genetic diversity for drought resistance, heat tolerance, and mineral soil adaptability exists in the genus. Genetic bridges between ploidy levels and different species now exist (Chandler et al., 1985a), and what remains to be developed are more ways to screen plants for their adaptation to specific conditions.

Brown and Draper (1980) identified genetic differences in *Vaccinium* for higher Fe-use efficiency in a nutrient solution with a high pH (5.5 to 6.6). Iron-efficient plants remained green under low levels of Fe by releasing H^+ from their roots, allowing Fe accumulated on their roots to be available for plant use. In an in vitro screen for high pH (6.0) tolerance (Finn et al., 1991), genetic variation was significant for vitality and dry weight. The progenies containing the most *V. angustifolium* Aiton performed the best. Variation for adaptation to mineral soils has been shown to occur in *Vaccinium* interspecific populations (Chandler et al., 1985b; Erb et al., 1990; Korcak, 1986; Korcak et al., 1982). General combining ability (GCA) and specific combining ability (SCA) variance components were significant for producing a large canopy when blueberry progenies were grown on a mineral soil low in organic matter (Chandler et al., 1985b; Erb et al., 1990). In previous studies (Erb et al., 1988a, 1988b), a seedling screening technique for drought resistance was developed and the existence of genetic diversity for drought resistance was demonstrated. In

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another moisture stress study (Erb et al., 1991), field-grown mature blueberry clones and progenies subjected to a moderate water deficit differed in canopy growth. Combining-ability analysis indicated that only SCA effects were significant for the difference in canopy volume between moisture-stressed and control plants.

This study was conducted to determine combining abilities and genetic variability for seedling root system size and shoot vigor and to establish whether a large root system is correlated with good growth when plants are grown on a mineral soil and exposed to a moderate soil water deficit.

Materials and Methods

Greenhouse experiment. Seed of 15 blueberry crosses were germinated in February and the seedlings were transplanted in May into 5.7-cm-square × 5.7-cm-deep peat pots containing Jiffy mix (Jiffy Products, Shippegan, Canada). The ancestry of the parental clones is described in Table 1. The potted seedlings were placed on a sand bed in two unheated greenhouses. During the growing season, the outside average maximum temperature ranged from a low of 21.2C in April to a high of 32.2C in September. On cloudy days, greenhouse temperatures were 1 to 2 degrees warmer than outside and on sunny days they were 3 to 6 degrees warmer. The Jiffy mix and the sand bed had a pH of ≈6.0 at the beginning of the experiment. The plants were arranged in a randomized complete-block design consisting of four replications of each progeny with replications nested in greenhouses. In each replication, 16 seedlings of each progeny were lined up pot to pot in a row. A guard row was placed around the entire experiment.

The plants were grown for 3 months and fertilized every week with 21N–3.1P–5.8K fertilizer (Peters Acid Special; W.R. Grace & Co., Fogelsburg, Pa.) until the last week of August. Every other week, Fe chelate was added to the mix, and every month complete fertilizer ($g \cdot liter^{-1}$) (0.37N–0.68P–0.77K–0.35Ca–0.004B–0.008Cu–0.006Fe–0.007Mn–0.003Mo–0.006Zn–0.009Mg) (VHPF; Miller Chemical & Fertilizer Co., Baltimore, Md.) was added to the mix at rates we used previously (Erb et al., 1988a).

The plants overwintered in the unheated greenhouses. In late March, they were evaluated for root growth into the sand bed and for shoot vigor. A 1 to 9 rating scale was developed to estimate root system size and shoot vigor. Figure 1 illustrates some of the classes on the scales. A 9-scored root would penetrate ≈12 cm into the sand and a 9-scored shoot would have two or more stems 40 cm long, with the longest stem having a basal stem diameter about the size of a pencil or greater. The illustration in Fig. 1B does not accurately depict the increase in basal stem diameter going from class 3 to class 9. A score of 1 in the root rating scale indicated no roots penetrated into the sand and a score of 1 in the shoot rating indicated a dead plant.

Table 1. Ploidy level (x = 12) and species included in the parentage of the nine *Vaccinium* clones used as parents.

Clone	Ploidy level	Constitution
JU10 and JU11	6x	Tifblue (*V. ashei* Reade) x US41 (*V. atrococcum* Heller) (colchiploid)
JU62 and JU64	4x	*V. myrsinites* Lamark x *V. angustifolium* Aiton
US75	4x	Fla-4B (*V. darrowi* Camp) x Bluecrop (*V. corymbosum* L.)
G111	4x	*V. corymbosum* (Selection from U.S. Dept. of Agriculture breeding program)
US226	4x	(*V. myrtilloides* Michaux x *V. atrococcum*) (colchiploid)
G362	4x	*V. corymbosum* (Selection from U.S. Dept. of Agriculture breeding program)

Root and shoot evaluation scores from one set of F_1s of a four-parent (G362, G111, US75, and US226) diallel were subjected to diallel analysis using the Schaffer and Usanis (1969) computer program. F ratios and GCA and SCA effects were calculated according to Griffing's method 4, model I analysis (Griffing, 1956). The assumptions for this method and model are that parental effects are fixed and maternal and reciprocal effects are nonsignificant.

Field experiment. After the seedlings were rated for root size and shoot vigor, the progeny from 12 crosses were planted in mid-April on a field of Galestown sandy, clay loam (Psamnaentic Hapludult) soil (0.7% to 1.0% organic matter) at Beltsville, Md. The experiment was arranged in a randomized incomplete-block design with six blocks and four replications per cross. Each replication consisted of 15 seedlings spaced 0.5 m within and 1.0 m between rows. No organic matter was added to the field. Six months before planting, S was applied to the field to lower the pH from 6.5 to 4.5 and the field was fumigated with 403 $kg \cdot ha^{-1}$ of methylbromide and chloropicrin (2:1). In March, the soil pH was 6.0, so additional S was added to the field to bring the pH to 4.5.

The plants were fertilized with 11.5 kg N/ha (1.85 g N/plant) of $(NH_4)_2SO_4$ in May and July. The plants were allowed 2 months to acclimate before drought stress was imposed by allowing the soil tension level to reach 0.08 to 0.09 MPa on four occasions (21 June, 22 July, 14 Aug., and 9 Sept.) before overhead irrigation was applied to lower the soil tension level to 0 MPa. Soil tension was monitored with six tensiometers placed 12 cm deep. Tensiometers were examined twice a week when tension was low and every day when soil tension was >0.05 MPa. The average maximum temperature for May, June, July, August, and September was 30.3, 31.8, 32.8, 32.9, and 31.8C, respectively. The rainfall total for May, June, July, August, and September was 9.6, 5.1, 11.7, 5.6, and 10.7 cm, respectively.

In late September, four crosses (G362 x JU64, G362 x G111, G362 x US75, and US226 x G362) were dug, and shoot and root dry weights were taken. Data from these four crosses were used in correlation analysis to determine the relationship of seedling root system ratings to total dry weight, shoot dry weight, root dry weight, and shoot : root ratio. Resources only permitted taking total dry weight on four crosses in the study. These four G362 crosses were chosen because they are at least half the crosses used in the diallel analysis in the greenhouse experiment and they represent a straight *V. corymbosum* cross (G362 x G111) and progeny from three interspecific hybrids that have been previously evaluated for mineral soil adaptability (Erb et al., 1990) and drought resistance (Erb et al., 1988b, 1991).

Statistical analysis. Analyses of data for both experiments were determined by analysis of variance (PROC GLM) (SAS Institute, 1985), and means were separated by LSD for unequal sample size in the greenhouse experiment and by Duncan's multiple range test in the field experiment.

Results and Discussion

Greenhouse experiment. The progeny from seven crosses had a higher root rating mean than a straight *V. corymbosum* cross (G111 x G362), and two additional crosses were higher than the reciprocal cross (G362 x G111) (Table 2). These data indicate that

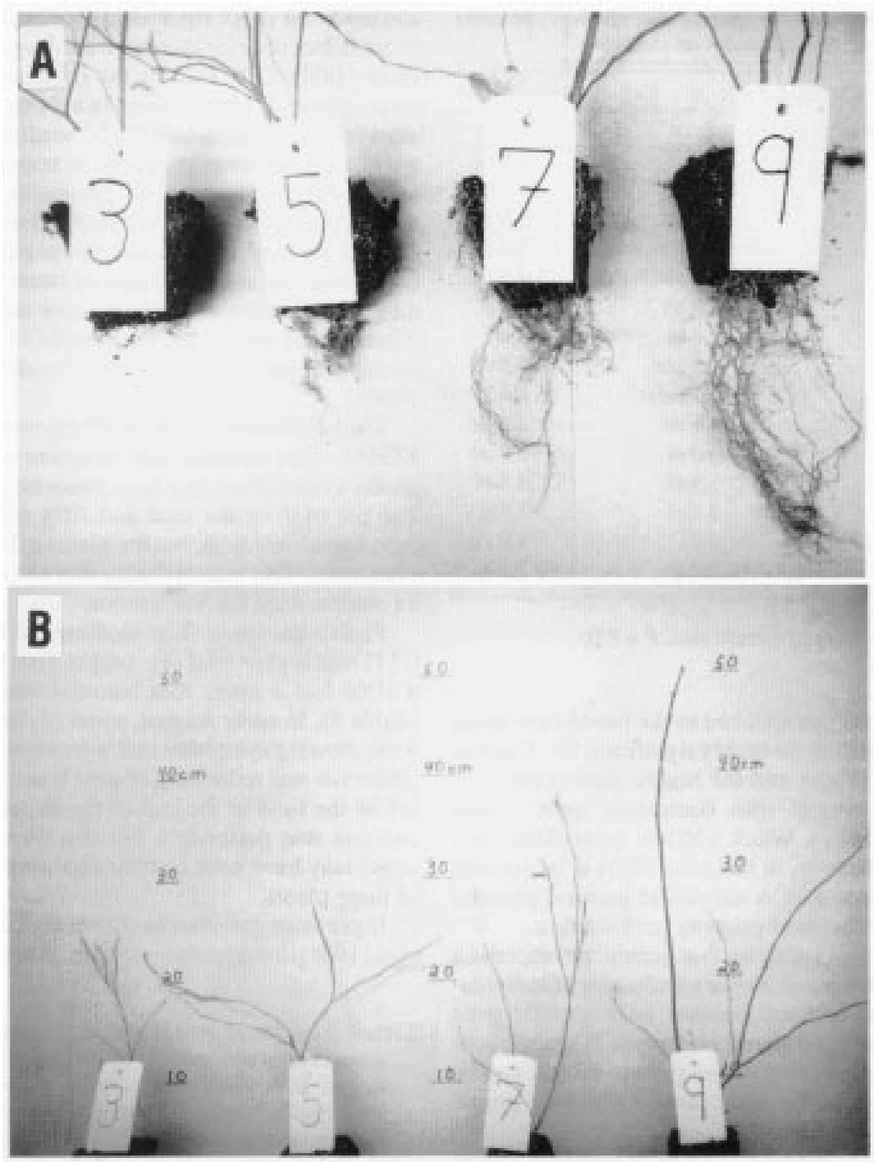

Fig. 1. (**A**) Root rating scale and (**B**) shoot rating scale used to score seedlings in the greenhouse experiment.

advancement in blueberry seedling root system size is possible if the right genotypes are crossed. In the two crosses with the highest root rating means, >50% of their germplasm came from mineral soil-adapted species. The progeny of JU11 x G111 should be pentaploid, with 3x of their genome coming from JU11, which is composed of two mineral soil-adapted species (*V. ashei* and *V. atrococcum*) (Galletta, 1975). US226 x US75 is one-fourth *V. corymbosum* and three-fourths mineral soil-adapted species (*V. atrococcum, V. myrtilloides,* and *V. darrowi*) (Galletta, 1975). *Vaccinium ashei* is considered to be a source of good root characters (Galletta and Fish, 1971). The percentage of mineral soil-adapted germplasm in a cross is not the only factor contributing to the high mean root rating of a cross. The cross G362 x JU10 was not significantly different from G111 x G362. JU10 x JU11 and JU64 x JU62 were the only crosses in the study in which 100% of the germplasm was from mineral soil-adapted species. However, inbreeding depression was probably influencing the performance of these full-sib crosses (Table 1). *Vaccinium corymbosum* reportedly produces small root systems (Coville, 1921; Gough, 1980; Kramer et al., 1941) and has low tolerance for mineral soils (Galletta, 1975; Galletta and Fish, 1971; Lilly et al., 1975). However, comparison of the crosses containing G111 with those containing G362 indicates that G111 is a better source for improving root system size. Selecting the best *V. corymbosum* clone to initiate a breeding program seems to be as critical as selecting the mineral soil-adapted parent.

Only two crosses had a higher shoot rating mean than G362 x G111 and two additional ones were higher than G111 x G362 (Table 2). Four crosses had high shoot and root ratings: G111 x US75, G111 x JU64, US226 x US75, and G362 x JU11. The root and shoot ratings correlation ($r = 0.56$, $P = 0.0001$) revealed that selection for just shoot vigor would exclude a significant amount of germplasm that has good root system size characters.

Analysis of variance tables for root and shoot ratings for one set of F_1s are presented in Table 3. For root ratings, location and GCA were highly significant and for shoot ratings, location, SCA, and GCA were highly significant. The plants performed differently in the two greenhouses, but there was no significant genotype × environment interaction.

Because a fixed model was used for analysis, variance components could not be estimated, and the interpretation of the gene action associated with these traits is limited to the parents and

Table 2. Mean root and shoot ratings for interspecific blueberry progeny growing in two greenhouse compartments on sand beds.[z]

Cross	No. of samples	Rating mean Root	Shoot
JU11 x G111	64	4.2 a[y]	3.5 ef
US226 x US75	96	4.2 a	4.2 bc
G362 x JU11	56	4.1 ab	4.0 bcd
US226 x G111	128	3.9 ab	3.4 fg
G111 x JU64	128	3.8 ab	4.3 bc
G111 x US75	128	3.8 ab	5.0 a
JU10 x JU11	128	3.6 bc	3.4 f
US226 x G362	128	3.5 bcd	3.5 ef
G362 x JU10	96	3.5 bcd	4.4 b
G111 x G362	128	3.1 de	3.8 de
G362 x US75	125	3.0 ef	3.9 cd
G362 x JU64	128	2.9 ef	3.5 ef
G362 x JU62	128	2.8 ef	3.1 g
G362 x G111	128	2.7 f	4.0 cd
JU64 x JU62	128	2.2 g	2.2 h

[z]Rating scales are illustrated in Fig. 1.
[y]Mean separation by LSD for unequal sample size, $P = 0.05$.

progeny used and cannot be extrapolated to the population level. However, it can be assumed that the highly significant GCA values are due to additive gene effects and the highly significant SCA values are associated primarily with dominance gene effects (Hallauer and Miranda, 1981). When additive gene effects are larger than dominance effects or, in this case, GCA is larger than SCA, then selection for that trait is simplified because parental performance is a good predictor of progeny performance.

Significant SCA for a trait indicates that genetic advancement can be made by selecting for a trait, but large numbers of individuals per cross need to be screened because only specific gene combinations will produce the superior phenotype. Through continual selection and recombination, these genetic effects can be fully exploited, and because blueberries are vegetatively propagated, genetic variability can be fixed.

The large positive GCA effect for US226 for root system size and US75 for shoot vigor identifies these plants as the best parents to use in breeding for increased seedling root system size and shoot vigor (Table 4). In US226, the good root characters are probably coming from *V. atrococcum*. In a drought-screening study (Erb et al., 1988b), where 6-month-old seedlings and 3-month-old softwood cuttings were grown on a mineral soil and exposed to a severe soil moisture deficit, progenies and clones containing *V. atrococcum* germplasm had higher mean root biomass fractions than an open-pollinated species population of *V. myrtilloides*. US75 was the most drought-resistant clone when grown on a mineral soil under a moderate water deficit (Erb et al., 1991) and it had the second largest positive GCA effect for canopy volume production on a mineral soil (Chandler et al., 1985; Erb et al., 1990).

The best crosses for SCA effects were G111 x US75 and G362 x G111. This indicates that selection within *V. corymbosum* can produce individuals that have genes for good seedling shoot vigor. The pH (6.0) of the sand and Jiffy mix at the beginning of the experiment was high, but the plants exhibited no visible pH stress symptoms. This was probably due to the Peters Acid Special and Fe chelate used for fertilization.

Field experiment. The seedlings of G362 x JU64 and G362 x G111 had higher total dry weight than US226 x G362, and G362 x JU64 had a lower root biomass fraction than US226 x G362 (Table 5). In early August, some of the plants in this experiment were showing symptoms that were more characteristic of pH stress (chlorosis and reddening of new leaves) than drought stress. The pH of the field at the end of the experiment was 4.9. No tissue analysis was performed, but this observation suggests that pH stress may have been another factor influencing the performance of these plants.

In previous greenhouse (Erb et al., 1988a, 1988b) and field (Erb et al., 1991) drought-stress studies, JU64 clones were more drought

Table 3. Analysis of variance for root and shoot ratings from a diallel system of blueberry crosses involving two interspecific hybrids and two *Vaccinium corymbosum* clones grown in two greenhouse compartments on sand beds.

Source[z]	Rating df	MS	F
		Root	
Location (L)	1	3.3	11.24**
GCA	4	4.1	14.27**
SCA	3	0.1	0.52[NS]
GCA × L	4	0.4	1.38[NS]
Error	43	0.3	
		Shoot	
L	1	4.4	23.16**
GCA	4	3.1	16.31**
SCA	3	0.9	4.84**
GCA × L	4	0.3	1.63[NS]
Error	43	0.2	

[z]GCA = general combining ability, SCA = specific combining ability.
[NS],**Nonsignificant or significant at $P = 0.01$, respectively.

Table 4. Estimates of general combining ability (GCA) effects for root and shoot ratings and specific combining ability (SCA) effects for shoot ratings from a diallel system of blueberry crosses involving two interspecific hybrids and two *Vaccinium corymbosum* clones grown in two greenhouse compartments on sand beds.

Parent	GCA effects Root	Shoot	Cross	SCA effects Shoot
US226	0.51	–0.32	G111 x US75	0.43
US75	0.22	0.66	G362 x G111	0.30
G111	–0.08	–0.12	US226 x G362	0.03
G362	–0.65	–0.22	US226 x US75	–0.11
SE	0.25	0.23	US226 x G111	–0.14
			G362 x US75	–0.51
			SE	0.14

Table 5. Mean total dry weight (TDW) and root biomass fraction for interspecific blueberry progenies grown on a mineral soil and exposed to a moderate water deficit.

Cross	No. of samples	TDW mean (g)	Mean root biomass fraction
G362 x JU64	60	7.2 a	0.29 b
G362 x G111	60	7.1 a	0.32 ab
G362 x US75	60	5.2 ab	0.31 ab
US226 x G362	60	3.1 b	0.33 a

[z]Mean separation by Duncan's multiple range test, $P = 0.05$.

resistant than those of US226, and the JU64 progenies were almost always more drought resistant than those of US226. JU64 is the product of a cross between two species reported to be adapted to mineral soils (Galletta, 1975) and drought resistant (Davies and Albrigo, 1983). There is no previously published information on the performance of G111, but G362 was intermediate in drought resistance to JU64 and US226 when evaluated in a greenhouse (Erb et al., 1988b) and field drought-stress study (Erb et al., 1991). This indicates that the good performance of G362 × G111 may be primarily due to G111. The superior root system size of the G111 crosses compared to the G362 crosses in the greenhouse portion of this study provides some support for this theory.

The seedling root system ratings from the greenhouse experiment were highly correlated with the total dry weight ($r = 0.89$, $P = 0.0001$), root dry weight ($r = 0.86$, $P = 0.0001$), and stem dry weight ($r = 0.90$, $P = 0.0001$) of the field-grown plants. They were negatively correlated with shoot : root ratio ($r = -0.23$, $P = 0.0001$). In this study, the root ratings from the greenhouse experiment were good predictors of growth in a moderately dry mineral soil. The high correlation coefficients between data from these two experiments indicate that the transplanted seedlings with a large root system developed better under the adverse conditions of the field. Ekanayake et al. (1985) confirmed that root thickness, root dry weight, and root length density were important characters in maintaining high leaf water potentials when rice was under water stress. They also showed that these characters are highly heritable. The root rating scale used in the greenhouse experiment takes root size and root length density into account (Fig. 1). The high GCA for seedling root system size indicates that this trait in blueberries is probably highly heritable.

A previous study (Erb et al., 1993) established that there was a relationship between growth on a mineral soil and soil moisture stress. This indicated that drought stress could be used as a method to screen blueberries for mineral soil adaptability. In this study, the two best parents at transmitting good seedling root growth characters to their progenies were US226 and US75. In addition, root system size of young seedlings was highly correlated with total dry weight after one season of growth on a moderately drought-stressed mineral soil. US75 has been identified (Chandler et al., 1985b; Erb et al., 1990) as a parent that transmits genes for mineral soil adaptability to its progeny. However, both US75 and US226 were drought susceptible when grown on a mineral soil and exposed to a severe soil moisture deficit (Erb et al., 1988b), a result that indicates that screening for severe drought stress would not identify all the mineral soil-adapted germplasm available. The data from this study indicate that the procedure developed in the greenhouse experiment could be used to eliminate the less vigorous plants from a population before field planting and to evaluate for mineral soil adaptability. This would enable breeders to capitalize on the mineral soil-adapted germplasm that is not related to severe drought-stress resistance.

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