

Quantitative Inheritance of Plant Growth Habit in Blueberry Progenies

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Abstract. Genetic variance components, narrow-sense heritabilities, and general combining ability (GCA) effects were estimated for plant growth habit traits from a partial diallel cross among 17 blueberry (*Vaccinium corymbosum* L., *V. angustifolium* Ait., and *V. corymbosum* × *V. angustifolium* hybrids) parents. Plant height, plant diameter, and a subjective stature rating were recorded for parent and progeny plants in 1984 after 9 growing seasons at Becker, Minn. General and specific (SCA) combining ability variances were significant for all traits. GCA variance components were larger than SCA components for height and stature rating, and heritabilities (family-mean basis) were 0.68 and 0.64, respectively, indicating the relative importance of additive genetic variance for these traits. Desired stature or height in this population should be recoverable through recurrent phenotypic selection. SCA variance components were much larger than GCA components for plant diameter measures, and heritability was low. *Vaccinium angustifolium* parents had very negative GCA effects for plant height and stature ratings, while parents with largely *V. corymbosum* ancestry had positive effects. Coefficients of determination between parental phenotype and GCA effects indicated that progeny performance should be predicted by parental phenotype for stature or height but not for diameter.

Galletta (6) described 4 blueberry bush types of current or potential commercial importance: a) large-fruited, low-growing (<1 m), rhizomatous matted rows, b) intermediate height (1 m) hedgerows, c) 1.5- to 2-m-high bushes with stocky, unitary canes, and d) very high (2.25- to 3-m) bushes for over-the-row mechanical harvesters. Blueberry breeders have been concerned with the inheritance of plant stature in crosses of highbush and lowbush since Coville's (2) earliest hybridizations of wild selections. Coville noted that most of the hybrids were similar in height to the natural hybrids between these 2 species, ranging from 0.6 to 0.9 m. Darrow et al. (3) later evaluated some of Coville's F₁ hybrids and found them intermediate in height between their respective lowbush and highbush parents, ranging generally from 0.75 m to 1.20 m. Johnston (9) reported that only 3% of the F₁ hybrids between highbush genotypes and Michigan lowbush selections did not have a low growth habit. He considered the lowbush habit almost completely dominant (9, 10). Meader et al. (13) observed bush types in F₁ progenies from crosses between highbush cultivars and lowbush clones and in F₂ progenies derived from open-pollinated F₁ plants. All F₁ plants were intermediate in height after 11 years. The height of F₂ progeny as 4-year-old plants ranged from 0.13 to 1.09 m, showing considerable segregation. Likewise, segregation was also noted for the spreading rhizomatous growth habit characteristic of *V. angustifolium*.

The Univ. of Minnesota blueberry breeding program has employed 2 strategies in developing cultivars adapted to northern regions where commercial blueberry culture is currently limited by cold winter temperatures. One approach has been to select for early fall acclimation and flower bud hardiness (4, 16). In addition, low-statured "half-high" plants have been sought that

escape winter injury by maintaining much of the fruiting volume beneath the snow (9, 16).

Our objective was to estimate genetic variance components, narrow-sense heritability, and parental general combining ability (GCA) effects for plant growth habit traits to provide guidance for improving selection and for planning of future crosses.

Materials and Methods

Each of 17 parents (Table 1) was crossed with 6 other parents

Table 1. Identification and ancestry of *Vaccinium* clones used as parents in partial diallel cross.

Parent	Ancestry
N70249 ^{zy}	<i>Vaccinium angustifolium</i>
GRVa ^z	<i>V. angustifolium</i>
MN-84 ^z	<i>V. angustifolium</i>
R2P4 ^x	<i>V. angustifolium</i> × <i>V. corymbosum</i>
GR-1 ^x	<i>V. angustifolium</i> × <i>V. corymbosum</i>
GR-2 ^x	<i>V. angustifolium</i> × <i>V. corymbosum</i>
MN-61	<i>V. corymbosum</i> (USDA 11-93) × <i>V. angustifolium</i> var. <i>nigrum</i>
Northsky (MN-332)	B6 × R2P4
Northcountry (MN-350)	B6 × R2P4
Bluetta	(North Sedgewick lowbush × Coville) × Earliblue
N70220 ^w	<i>V. corymbosum</i>
N70218 ^w	<i>V. corymbosum</i>
B-16	<i>V. corymbosum</i> (G65 × Ashworth)
B-10	"
B-6	"
B-11	"
B1-1	"

^zCollected from wild stand in northern Minnesota.

^yN numbers are Minnesota fruit accession numbers; Mn, B, and GR prefixes indicate selections from the Minnesota program.

^xClone resulting from open-pollination of a half-high plant of unknown origin growing in the Harvard Forest (Massachusetts); selected at Grand Rapids, Minn.

^wClone provided by F. Ashworth, Heuvelton, N.Y.; believed to be *V. corymbosum* with some lowbush genes.

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in a circulant partial diallel mating design (11). The parents were tetraploid ($2n = 4 \times = 48$) clones representing *V. corymbosum*, *V. angustifolium*, and hybrids between the species. The resulting progenies were planted in 1976 at Becker, Minn. (Hubbard loamy sand, 2% organic matter, pH = 4.8 to 5.2) in a randomized complete block design with 4 replications. Each plot consisted of 12 seedlings spaced 1.2 m apart in rows 2.4 m apart. Parents, except for N70220, which perished, were planted in an unreplicated adjacent block at a spacing of 1.5 m $\times$ 2.4 m.

In Oct. 1984, after 9 growing seasons, plant height, plant diameter in the direction of the row (diameter 1), and plant diameter perpendicular to the direction of the row (diameter 2) were measured on each parent plant and on each plant within a progeny. In addition, each plant also was rated subjectively for plant stature on a scale ranging from 1 = the low, spreading, rhizomatous habit characteristic of *V. angustifolium* to 9 = upright erect stature of most *V. corymbosum* cultivars.

The data were analyzed on a plot mean basis assuming a random effects model for crosses and replications. Estimates for general and specific (SCA) combining ability variance components and for narrow sense heritability were derived as previously described by Fear et al. (4). Normal disomic inheritance was assumed based on reports of predominantly bivalent pairing in tetraploid species (7, 8, 12, 14, 15), although quadrivalents have been observed with varying frequency in several clones (7, 8, 14). Estimation of narrow sense heritability also necessitated the assumptions of negligible epistatic genetic variance and independent distribution of genes in the parents (1, 4). Because of our interest in parental effects, general combining ability effects were computed under the assumptions of a fixed effects model (1).

Results and Discussion

The parents varied considerably for all traits (Table 2), although parents with largely *V. angustifolium* ancestry were generally shorter and smaller in diameter than *V. corymbosum* parents. MN84 was collected from a wild stand in northern Minnesota and was presumably *V. angustifolium*. Compared with the more

Table 2. Plant height, plant diameter in the row (diameter 1), plant diameter across the row (diameter 2), and plant stature rating of blueberry parent plants.

Clone	Height (cm)	Diam 1 (cm)	Diam 2 (cm)	Stature ^z
N70249	35	80	65	1
GRVa	30	50	50	1
MN-84	70	105	100	6
MN-61	90	140	120	5
R2P4	55	100	90	5
GR-1	75	85	80	6
GR-2	55	100	100	2
Northsky	50	65	80	3
Northcountry	60	110	105	4
B-6	90	100	90	7
B-10	65	40	35	7
B-11	90	70	95	7
B-16	90	100	100	7
B1-1	65	115	105	6
N70218	80	130	120	6
N70220	---	---	---	---
Bluetta	85	135	120	6

^zPlant stature rating scale: 1 = prostrate to 9 = erect.

phenotypically authentic *V. angustifolium* clones, GRVa and N70249, it was much larger in stature (Table 2), later to bloom and ripen, and larger in fruit size (5). This clone appears to be an introgressant with *V. corymbosum*. The highbush parents were all less than 1 m tall at this location, reflecting stunting caused by repeated winter injury. Because of this stunting, subjective stature ratings probably describe the relative stature potential of the parents better than height measurements.

Analysis of variance indicated that GCA and SCA terms were significant ($P \leq 0.01$) for all traits. GCA variance components for plant height and stature were considerably larger than SCA variance components (Table 3). However, SCA components were larger for diameter measurements. Narrow-sense heritability estimates (Table 3) were moderately high for height and stature and low for the 2 diameter measurements. There was greater variance for diameter 2 (across the row) than for diameter 1 (within the row), probably induced by the narrow 1.2-m spacing within the row restricting growth as the plants matured. Because of this space limitation, the full extent of variability among the families was not expressed in the diameter 1 measure.

The significant SCA variance for height and stature support the observations of other researchers (3, 9, 10) that dominance (and possibly epistatic) genetic effects are important in the inheritance of plant height. Nevertheless, the large narrow-sense heritability estimates (Table 3) reflect the importance of GCA and additive genetic variance for height or stature in this population. A large proportion of additive variance suggests that progress toward recovering desirable stature, high or low, could be made using recurrent phenotypic selection.

In addition to height, plant spread is an important determinant of the plant's fruiting volume and, ultimately, of the yield potential. In this population, variation for plant diameter was due primarily to nonadditive genetic variance as indicated by the relative magnitudes of GCA and SCA variance components (Table 3). Thus, in contrast to plant height, mean progeny performance for plant diameter would not be predicted accurately based on parental phenotypes.

Estimates of heritability and genetic variance components in this study should be interpreted cautiously because of the probability that assumptions of negligible epistasis, independence of genes in parents (no linkage), and completely disomic inheritance may be invalid (1). In addition, heritability estimates are probably biased upward because of our inability to estimate genotype $\times$ location interaction variance. Resources did not permit replication of the experiment at additional locations. At the Becker, Minn. location, high-statured genotypes are injured frequently by low winter temperatures while low-statured genotypes are protected by snow cover (4). Stunting of high-statured

Table 3. General (GCA) and specific (SCA) combining ability variance components and heritability estimates for plant height, plant diameter in the row (diameter 1), plant diameter across the row (diameter 2), and plant stature rating from blueberry partial diallel mating design.

Estimates	Height	Diam 1	Diam 2	Stature
GCA	27.8	6.9	22.7	0.35
SE	10.4	7.0	13.0	0.13
SCA	10.6	39.2	52.4	0.17
SE	4.7	16.8	20.2	0.06
Heritability	0.68	0.13	0.27	0.64
SE	0.26	0.13	0.16	0.24

genotypes within a progeny could have inflated apparent dominance for low stature. Had this experiment been conducted at locations with milder or harsher winter climates than the test site, stature differences between high- and low-growing progenies probably would have been more or less pronounced, respectively. Selection for a particular plant habit in this type of *V. angustifolium* × *V. corymbosum* population should be most effective at a location with relatively mild winter temperatures within that target population of environments, because variation for stature would be most fully expressed.

Large, negative GCA effects for all traits for the 2 authentic lowbush parents, GRVa and N70249, indicated that they contribute to diminutive plant size in their progenies (Table 4.) This finding agrees with the observations of other researchers (3, 9, 10, 13) concerning the short stature of progenies with one *V. angustifolium* parent. Other parents with lowbush ancestry, GR-2, 'Northsky', and 'Northcountry', also had negative GCA effects for plant height and stature. Three clones with lowbush ancestry—MN-84, R2P4, and GR-1—had fairly large, positive GCA effects for height and stature. These clones also had relatively large height and stature readings (Table 2). 'Bluetta' had the largest positive GCA effects for height and stature (Table 4). Other parents with largely highbush ancestry, except B-6, had smaller, but positive GCA effects.

The coefficients of determination (r^2) between parental phe-

notype (Table 2) and GCA effects (Table 4) were 0.71 ($P \leq 0.01$) for stature, 0.43 ($P \leq 0.01$) for height, 0.14 (NS) for both diameter 1 and diameter 2. These relationships indicate that parental phenotypes would more accurately predict progeny performance for plant stature rating or height than for diameter in these types of crosses. The larger coefficient of determination for stature compared to height, and the similar heritability estimates (Table 3), suggest that subjective stature ratings are at least as useful as more time-consuming height measurements for studying the inheritance of plant habit.

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Table 4. General combining ability effects of blueberry parents for plant height, plant diameter in the row (diameter 1), plant diameter across the row (diameter 2), and plant stature.

Clone	GCA effects			
	Height (cm)	Diam 1 (cm)	Diam 2 (cm)	Stature (rating)
N70249	-15.5	-10.9	-8.9	-1.74
GRVa	-7.1	-9.8	-16.9	-0.73
MN-84	3.2	0.0	5.9	0.57
MN-61	1.1	2.9	5.6	0.07
R2P4	4.2	8.4	8.4	0.24
GR-1	4.3	0.5	3.4	0.34
GR-2	-1.6	3.4	4.0	-0.43
Northsky	-7.4	-0.4	-5.8	-0.74
Northcountry	-3.6	-1.0	0.2	-0.47
B-6	-1.3	-7.5	-5.0	-0.19
B-10	4.3	3.1	9.2	0.57
B-11	1.8	0.7	-4.5	0.41
B-16	2.4	2.8	4.3	0.21
B1-1	3.6	2.3	1.4	0.38
N70218	1.0	2.1	-4.5	0.32
N70220	2.4	-0.4	-1.6	0.40
Bluetta	8.3	2.9	4.8	0.79
SE	1.6	3.4	3.6	0.17