Genetic Components of Variance for Winter Injury, Fall Growth Cessation, and Off-season Flowering in Blueberry Progenies

Carlos D. Fear¹, F.I. Lauer², J.J. Luby³, and R.L. Stucker⁴

Department of Horticultural Science and Landscape Architecture, University of Minnesota, St. Paul, MN 55108

Cecil Stushnoff²

Department of Horticulture Science, University of Saskatchewan, Saskatoon, Saskatchewan Canada S7N 0W0

Additional index words. blueberry breeding, Vaccinium spp., heritability, partial diallel cross

Abstract. Genetic variance components, narrow sense heritability, and combining ability effects of parents were determined for several traits from analysis of a partial diallel cross involving 17 parents. Parents included several *Vaccinium* species and interspecific hybrids. For fall growth cessation, general combining ability (GCA) effects were variable from year to year, and heritability was low. Variance due to GCA was more important than specific combining ability (SCA) variance for winter injury in each of the years. The heritability estimate over years was low for winter injury, although individual year estimates were higher. Lowbush parents had high GCA effects for winter injury in years with snow cover but low estimates for years without snow cover. Off-season flowering was observed in some progenies in both years studied. Certain *V. angustifolium* Ait. parents had high GCA effects for the occurrence of off-season flowering. The heritability estimate for off-season flowering in combined years was 0.47. Variation due to years and to GCA × year interaction was significant for all characters studied.

One of the primary limiting factors in temperate fruit production throughout the world is a lack of sufficient cold tolerance at some time during the year. Improved cold tolerance is, therefore, an important objective in many fruit breeding programs. Yet few studies have been made on the inheritance of cold hardiness in fruit crops (16).

Cold hardiness in peach flower buds (9) and in cambium and xylem tissues (2) was found to be quantitatively inherited. Broad sense heritability estimates were high for winter injury of peach [*Prunus persica* (L.) Batsch] cambium and xylem tissues (2), indicating good potential for selection for improved cold tolerance. In cloudberry (*Rubus chamaemorus* L.), broad sense heritability estimates for acclimation to cold tolerance ranged from 0.50 to 0.97 (12). Wilner (20) found maternal effects to be important in the inheritance of cold hardiness in apple (*Malus domestica* Borkh.). In one of the few studies to separate genetic components of variance, Watkins and Spangelo (19) found that additive variance was of major importance for several factors relating to plant survival in apple after cold stresses were applied.

In the Minnesota blueberry (*Vaccinium* spp.) breeding program, progress is being made for improved cold tolerance largely through the mating of superior parents followed by selection of superior transgressive segregates. Accelerated progress might be possible with an understanding of the inheritance of traits involved with cold tolerance, and of the relationship of winter

³Assistant Professor.

⁴Professor. Dept. of Agronomy and Plant Genetics.

injury to fall growth cessation or late summer and fall flowering (off-season flowering). The objectives of this study were to obtain estimates of components of variance for these traits and to examine their interrelationships in blueberry.

Materials and Methods

Each of 17 parents (Table 1) was crossed to 6 other parents according to the circulant partial diallel mating design described by Kempthorne and Curnow (6). The resulting 51 progenies were planted in 1976 at Becker, Minn., in a randomized complete block design with 4 replications. Each plot consisted of 12 seedlings spaced 1.2 m apart.

The parental material consisted of clones representing several species (*Vaccinium angustifolium* Ait., *V. angustifolium* var. *nigrum*, *V. corymbosum* L.) and species hybrids. The parents comprised a sample that might typically be used in a breeding program for improved cold tolerance and fruit quality. All parents are tetraploids (2n = 4x = 48). Meiosis was assumed to be normal in the parents. This was based on studies indicating a high percentage of bivalent pairing in several tetraploid blueberry species and interspecific hybrids (5, 8, 14), and on their fruit and seed set (unpublished data).

Individual plants were rated visually for growth cessation in late Sept. of 1979, 1980, 1981, and 1982. The rating scale used was a pretransformed scale (7) of 1 to 5 representing 100%, 85%, 50%, 15%, and 0% of the terminal buds, respectively, in active growth.

In the spring of 1980, 1981, and 1982, individual plants were visually rated for winter injury. The rating scale used was a pretransformed scale (7) of 0 to 10, where ratings represent the percentage of shoot dieback as follows: 0 = 100%; 1 = 97.5%; 2 = 90%; 3 = 79%; 4 = 65%; 5 = 50%; 6 = 35%; 7 = 21%; 8 = 10%; 9 = 2.5%; and 10 = 0%.

Plants were observed for occurrence of off-season flowering during the summer and early fall of 1981 and 1982. The date and number of shoots with open florets were determined for

Received for publication 19 Mar. 1984. Scientific Journal Series Paper No. 13,835. Minn. Agr. Expt. Sta., St. Paul. 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.

¹Former Research Assistant. Present address: Dept. of Horticulture, Iowa State Univ., Ames, IA 50011.

²Professor.

Table 1.	Identification and ancestry of Vaccinium clones used as par-
ents in	partial diallel cross.

Clone	Identification	Ancestry			
A	N66244 (Mn 84) ^{z,y}	Vaccinium angustifolium			
В	N70249 ^z	V. angustifolium			
С	GR V. $a.^{z}$	V. angustifolium			
D	GR 1 ^x	V. angustifolium X V. corym- bosum			
Ε	GR 2 ^x	V. angustifolium X V. corym- bosum			
F	N70220 ^w	V. corymbosum			
G	N70218 ^w	V. corymbosum			
Н	B 16	V. corymbosum (G65) X V. corymbosum ('Ashworth')			
Ι	B 10	V. corymbosum (G65) X V. corymbosum ('Ashworth')			
J	B 6	V. corymbosum (G65) x V. corymbosum ('Ashworth')			
К	B 11	V. corymbosum (G65) x V. corymbosum ('Ashworth')			
L	B 1-1	V. corymbosum (G65) x V. corymbosum ('Ashworth')			
М	R2P4 ^x	V. angustifolium X V. corym- bosum			
Ν	'Northsky'	B 6 x R2P4			
Ő	Mn 350	B 6 x R2P4			
P	Mn 61	V. corymbosum (USDA 11-93) X V. angustifolium var. ni- grum			
Q	'Bluetta'	(North Sedgwick lowbush x 'Coville') x 'Earliblue'			

^zCollected from wild stand in northern Minnesota.

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

"Clone provided by Fred Ashworth, Heuvelton, N.Y., believed to be primarily *V. corymbosum* with some lowbush genes.

each plant every 10-14 days from early July until the 1st fall frost.

The data were analyzed on a plot mean basis as a randomized complete block for individual years and as a split plot in time for the combined years analysis. In the combined years analysis, the appropriate error mean square derived from expected mean squares for a mixed model was used to test for significance of mean squares. The Satterthwaite approximation (15) was used to estimate error terms where necessary. A mixed effects model with years as a fixed effect and crosses and replications as random effects was assumed for estimating genetic variance components. Because of our interest in parental effects, GCA effects also were computed under the assumptions of a fixed effects model. One progeny failed to survive, so only 50 progenies were used in the analysis.

Estimates were obtained for the general (GCA) and specific combining ability (SCA) components of variance, $\sigma^2 g$ and $\sigma^2 s$, respectively. By assuming epistatic variance to be negligible, $\sigma^2 g$ and $\sigma^2 s$ then are related to the genetic components of variance (7):

$$\sigma_{g}^{2} = \frac{1}{4} \sigma_{A}^{2}$$
$$\sigma_{s}^{2} = \frac{1}{4} \sigma_{D}^{2}$$

where σ_A^2 = additive genetic variance, and σ_D^2 = dominance genetic variance.

For each character evaluated, individual year estimates of narrow sense heritability were obtained on a progeny mean basis by the formula:

$$h^2 = \frac{4\sigma_g^2}{4\sigma_g^2 + 4\sigma_s^2 + \frac{\sigma_e^2}{r}}.$$

Narrow sense heritability estimates for combined years analyses were estimated on a progeny mean basis as:

$$h^{2} = \frac{4\sigma_{g}^{2}}{4\sigma_{g}^{2} + 4\sigma_{s}^{2} + \frac{4\sigma_{gy}^{2}}{y} + \frac{4\sigma_{sy}^{2}}{y} + \frac{\sigma_{cr}^{2}}{r} + \frac{\sigma_{e}^{2}}{ry}}$$

where σ_{cr}^2 , σ_{gy}^2 , and σ_{sy}^2 are estimated variances due to interactions involving crosses with replications and years, respectively (10).

Results

Growth cessation. Crosses differed in percentage of shoots actively growing in early fall in both separate years and combined years analyses (Table 2). The highly significant crosses \times year interaction indicates crosses responded differently in different years. The GCA effects (not shown) of most parents for fall growth cessation ratings varied in ranking from year to year. However, P consistently was associated with late season shoot growth. Estimates of GCA and SCA components of variance for fall growth cessation were quite variable from year to year (Table 3). In 1979, 1981, and 1982, GCA estimates were greater than SCA; however, SCA was greater than GCA in the combined years and in 1980 estimates.

Winter injury. Analysis of variance of winter injury ratings indicated highly significant variation due to years, crosses, and the crosses \times year interaction (Table 2). Year to year variation was expected because the 3 winters were variable in time of onset of low temperatures, temperature extremes, and amount of snow cover. Over all years, parents M, N, and O were the best general combining parents for winter hardiness whereas parents E, F, G, and J had poor combining ability effects for winter hardiness. The combining ability effects for parents varied from year to year as would be expected considering differences in the 3 winters and components of winter hardiness likely associated with such differences. The differences in combining ability effects among years were most evident in comparing the 1980-81 winter with those of 1979-80 and 1981-82. In the winter of 1980-81, parents K, M, and Q had good combining abilities relative to other years, whereas parents B, C, and E had poor combining abilities. The variance components for winter injury show GCA to be more important than SCA in the individual years (Table 4).

Off-season flowering. Highly significant variation was observed due to crosses, years, and the crosses \times year interaction for the occurrence of off-season flowering (Table 2). In the summer and fall of 1981, at least 1 plant per progeny in 42 crosses flowered on current season's growth, whereas in 1982, only 25 of 50 progenies contained plants that flowered. Although more plants flowered and flowered earlier in 1981, the same parents had a high combining ability for off-season flowering in both years. The GCA effects indicate that parents B, C, and D were most responsible for the occurrence of off-season flowering, whereas parents H, I, and P had the least effect on its occurrence.

Correlation coefficients, both on a plant and progeny basis,

	Growth cessation		W	inter injury	Off-season flowering	
Source	df	Mean square	df	Mean square	df	Mean square
Replications	3	0.57**	3	1.31**	3	0.05**
Single crosses	49	0.39**	49	3.09**	49	0.14**
GCA	16	0.52	16	5.43	16	0.34**
SCA	33	0.33**	33	1.96	33	0.05
Error 'a'	143	0.16	143	1.78	143	0.03
Years	3	16.33**	2	327.00**	1	1.60**
Single crosses x years	147	0.24**	98	1.67**	49	0.05**
GCA x years	48	0.49**	32	3.78**	16	0.08**
SCA x years	99	0.11	66	0.66	33	0.03**
Error 'b'	383	0.10	283	0.66	143	0.01

Table 2. Analysis of variance for fall growth cessation, winter injury, and on-season nowering for partial ender cross of *vaccinium* over years.

**Significant at the 1% level.

Table 3. General and specific combining ability variance components (GCA and SCA) \pm se for *Vaccinium* progenies in combined and separate years.

	Combined		1979		1980		1981		1982	
Estimates	GCA	SCA	GCA	SCA	GCA	SCA	GCA	SCA	GCA	SCA
				Gı	rowth cessatic	on				
Variance	-0.0025	0.0118	0.0276	0.0236	0.0023	0.0059	0.0121	0.0044	0.0275	0.0185
SE	± 0.0029	± 0.0063	± 0.0120	± 0.0244	± 0.0020	± 0.0054	± 0.0060	± 0.0075	± 0.0140	± 0.0133
				,	Winter injury					
Variance	0.0052	0.0160	0.1085	0.0691	0.2556	-0.0241	0.0895	-0.0050		
SE	± 0.0332	± 0.0451	± 0.0610	± 0.0816	± 0.1180	± 0.1074	± 0.0390	± 0.0325		
				Off-	season flower	ing				
Variance	0.0092	0.0005		55		0	0.0137	0.0045	0.0021	0.0025
SE	± 0.0030	± 0.0020					± 0.0050	± 0.0029	± 0.0010	± 0.0021

were small and nonsignificant among the characters studied. We usually observed winter injury on shoots which had flowered the previous fall. Winter injury attributable to off-season flowering was confounded with a lack of cold tolerance in many progenies, thus reducing the correlation between the traits.

Narrow sense heritability estimates for the combined years analysis for fall growth cessation and winter injury are much lower than those for separate year analysis because of large cross \times year and cross \times replication interactions (Table 4). Epistatic variation, if present for these traits, may bias the heritability estimates upward. All genetic variation, however, was small compared to variation due to environment or genotype \times environment effects (Table 2).

Discussion

Growth cessation and winter injury. The cessation of growth early in the fall might be expected to be associated with fall hardening and development of good levels of cold tolerance, though growth cessation alone is not always associated with increased cold tolerance (4). In Minnesota, highbush cultivars frequently continue to grow late into the fall and are subsequently injured by fall freezes and/or low winter temperatures. Although differences exist in GCA effects for fall growth cessation among the parents studied, our results indicate that the order in ranking of GCA effects of parents was variable from year to year. GCA effects of parents for growth cessation were not closely associated with GCA effects of parents for winter injury. For example, parent P (USDA 11-93 x V. angustifolium var. nigrum) consistently had a low GCA effect for fall growth cessation, but did not have a low GCA effect for winter injury, as would be expected if early growth cessation was highly correlated with cold tolerance.

Several reasons may account for the poor correlation between

fall growth cessation and winter injury ratings. First, a wide range in cold tolerance levels exists among parents used in this study (3, 11, 17, unpublished data). Thus, progeny from some parents would have extensive winter injury regardless of when fall growth ceased. Second, differences in growth habit among progenies probably allowed lowbush-type plants to escape winter injury under snow cover, thus masking any effect of fall growth cessation. Third, growth cessation may be most important in early winter cold tolerance and not closely related to tolerance of low midwinter temperatures, fluctuating winter temperatures, or low temperatures in late winter and spring. All of these components of cold tolerance were evaluated in one rating of winter injury in late spring, making separation of the individual components impossible. On balance, the use of fall growth cessation as a selection criterion for increased cold tolerance would seem to have little usefulness in Minnesota and would not likely result in effective selection in the population studied.

The weather during the 3 years in which winter injury was evaluated differed markedly. The winters of 1979–80 and 1980–81 were mostly barren whereas as much as 46 cm of snow cover was present during most of the 1981–82 winter. The winter of 1981–82 was the coldest winter, with temperatures below -34° C recorded on several occasions in nearby St. Cloud, Minn. Favorable hardening conditions in the fall of 1981 and good snow cover in the 1981–82 winter resulted in less winter injury than in previous winters, despite much lower temperatures.

Over all 3 winters, the best combining parents for lack of winter injury were M, N, and O, all having the clone R2P4 in their ancestry. R2P4 is a half-high seedling which survived many years in northern Minnesota and thus may possess desirable genes for cold tolerance. The V. angustifolium clones, B and C, lacked consistency from winter to winter in their combining

Table 4.	Narrow sense	heritability	estimates	±	se for	Vaccinium	progenies. ^z
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Character	Years combined	1979	1980	1981	1982
Growth cessation	0.00 ^y	0.43 ± 0.05	0.19 ± 0.05	0.53 ± 0.07	$0.50~\pm~0.06$
Winter injury	$0.02~\pm~0.11$	$0.45~\pm~0.06$	0.76 ± 0.09	0.78 ± 0.08	
Off-season flowering	$0.47~\pm~0.14$			0.68 ± 0.06	0.35 ± 0.04

^zStandard error of heritability estimates computed by substituting the sE of the GCA variance component for the GCA variance component in the heritability formula.

^yHeritability was assumed to be zero when estimate of σ_A^2 was negative.

ability effects. In 1980–81, the winter without appreciable snow cover, they had low GCA effects but showed moderately high GCA effects in 1981–82, a winter with abundant snowcover. This supports the view of Brierley and Hildreth (1) that V. angustifolium clones are not inherently cold tolerant but are largely dependent on snow cover for their winter survival.

The GCA variance components for winter injury were consistently larger than SCA components in the individual year analyses (Table 3), suggesting that additive variance is more important than nonadditive variance in the inheritance of cold tolerance. When additive variance is high, the value of crosses should be predictable, based on parental phenotype, without the need of progeny testing to identify desirable parents.

Individual year estimates of variance components (Table 3) and heritability (Table 4) indicate sufficient genetic variability exists for selection for cold tolerance as measured by winter injury ratings. Estimates for the 1981-82 winter are probably inflated, because apparent genetic variability during that winter may be due to low temperature avoidance by low growing types under snowcover rather than to differences in inherent cold tolerance. Effects of winter injury avoidance by snow cover and variable types of stresses in different winters contributed to a large GCA \times year interaction. The large GCA \times year interaction and resultant low heritability for combined years analysis indicates that progress from selection would be slow and should be based on information obtained on genotypes grown in a number of environments (e.g., years and locations). Estimates of variance components and heritability from combined years data are less biased than individual year estimates, because genotype × year interaction effects are removed. The combined years estimate of GCA and SCA variance components and heritability for winter injury determined in this study have large SE, resulting from large cross \times replication and cross \times year interactions, and should be interpreted cautiously.

Genotype \times year interactions for a complex trait such as cold tolerance are not unexpected. Progenies possessing a single desirable component of cold tolerance, e.g., tolerance of extreme mid-winter low temperatures, might lack other important components, e.g., stability of hardiness under fluctuating winter temperatures. Since the critical component to survival may vary from winter to winter, so would the value of a genotype possessing desirable genes for only certain components. Estimates of heritability based on data from a single year would be upwardly biased relative to actual progress possible in selection for improved cold tolerance (due to the inclusion of genotype \times year interactions in the numerator of the h² formula). The low heritability estimate over years shows why progress from selection for improved cold tolerance has been slow compared to selection for other traits.

Off-season flowering. Blueberry literature contains little discussion of off-season flowering, but secondary flowering periods have been reported to occur in Vaccinium (13, 14, 18). Fallflowering occurs occasionally in the highbush cultivars 'Collins' and 'Earliblue' (J.N. Moore, personal communication) which are sister seedlings having one-sixteenth V. angustifolium parentage. In this study, clones B and C (V. angustifolium) and D (V. angustifolium \times V. corymbosum) were primarily responsible for most of the off-season flowering, although it was observed also in progenies from other parents. The genes for off-season flowering may be most common in V. angustifolium. We have observed wild V. angustifolium plants flowering in September in northern Minnesota but to a much lesser extent than we have observed under cultivation.

Undoubtedly, environmental factors contribute to the occurrence of off-season flowering. However, these data also indicate that there is a large genetic contribution associated with the occurrence of off-season flowering. Heritability estimates were 0.69 for 1981, 0.35 for 1982, and 0.47 for the combined years estimate. The estimate in 1982 is lower than 1981 because fewer progenies had flowering plants. Unfortunately, the importance of genotype \times location and genotype \times location \times year interactions, which may affect heritability estimates, could not be determined from the data.

Off-season flowering could be important in blueberry breeding. The trait should be strongly selected against in the development of normal fruiting cultivars. On the other hand, offseason flowering may allow the development of fall-fruiting blueberry cultivars similar to fall-fruiting red raspberries (Rubus idaeus L.). Certain V. angustifolium clones might serve as good parents for the trait, and heritability estimates suggest that successful selection should be possible. Mating the earliest clones followed by recurrent selection for early, intense fall-flowering should offer potential for some progress in exploiting the trait. Whether satisfactory levels of flowering and fruiting could be achieved before fall frosts is unknown. In areas where blueberry production is marginal due to extreme winter temperatures and lack of snow cover, this type of plant might be useful because the crop is produced on current season's growth thereby avoiding winter injury problems associated with exposure of reproductive and vegetative plant parts through the winter.

Genotype \times environment interactions. This study illustrates that genotype \times environment interactions potentially can limit progress from selection. Where adequate genetic variance for a trait exists, progress from selection could be increased by reducing the effects of genotype \times environment interaction. This reduction could be achieved by basing selection on data collected from a large number of environments (locations or years). However, when genotype \times environment is large, this approach may be impractical, severely limiting progress per year. Another approach to improve progress in selecting for traits having a large genotype \times environment interaction could be to base selection on data from environments where the full genotypic potential is expressed. In the case of winter injury of blueberries, this might be in locations or years characterized by snowless winters with low temperatures early in the fall, extreme low temperatures in midwinter, and fluctuating winter temperatures. These types of winters are, however, rare and unpredictable in target areas for blueberry cultivar development, resulting in slow progress based on selection following such winters. An approach with potential for overcoming problems of genotype \times environment interaction for complex traits would be to define the most critical components affecting expression of the trait under selection (e.g., cold tolerance or off-season flowering) and develop techniques allowing the screening of large numbers of seedlings for critical components under controlled conditions. This might best be done by screening very young seedlings, where the correlation between behavior of the young plant and the adult for expression of the trait can be established. Critical environmental components contributing to winter injury in blueberry in Minnesota are known (1, 17), but development of controlled screening technquees for breeding programs has lagged. Environmental factors associated with enhanced off-season flowering are not well understood at this time. Future research concerning breeding for complex traits such as cold tolerance or off-season flowering should define the critical environmental components limiting expression of the trait and allow development of rapid and efficient controlled environment screening techniques for those traits.

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