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# Inheritance of Ripening Uniformity and Relationship to Crop Load in Blueberry Progenies

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*Additional index words.* *Vaccinium corymbosum, V. angustifolium,* heritability, partial diallel, fruit breeding

*Abstract.* **The intervals, in days, between 10%, 50%, and 90% ripened fruit, as well as crop load, were estimated over 2 years in progenies from a partial diallel cross among 17 blueberry (*Vaccinium corymbosum* L., *V. angustifolium* Ait., and *V. corymbosum* x *V. angustifolium* hybrids) parents. General combining ability (GCA) mean squares were highly significant for all ripening intervals and for crop load, while specific combining ability mean squares were nonsignificant, indicating a large proportion of additive genetic variance. Narrow-sense heritability estimates were about 0.50 for the three ripening intervals (10–50%, 50–90%, and 10–90%). Several parents had large positive GCA effects, indicating their contribution to a long ripening interval. Most progenies with large crop loads required >15 days between 10% and 90% ripened fruit. Despite the consistently positive relationship between ripening interval length and crop load, variation among families and the potential for within-family segregation suggest the possibility of obtaining genotypes with high yield potential and improved uniform ripening.**

A high degree of ripening uniformity could improve efficiency of hand or machine harvest of blueberry (*Vaccinium* spp.) fruit, although a grower also may be placed at greater risk from adverse environmental conditions.

Galletta (5) suggested that concentrated ripening may be achieved by selecting for a short bloom period, or a uniform ripening period, or for the tendency to maintain mature fruit on the bush in prime condition. He noted that certain highbush (*V. corymbosum* L.) cultivars like Croatan, Collins, Morrow, and Earliblue will mature >80% of their crop in a 7-day period with appropriate weather conditions. Likewise, Darrow and Scott (2) indicated that several highbush cultivars can mature 70–100% of their crop within a 2-week period.

Half-high (*V. corymbosum* x *V. angustifolium* Ait. derivatives) blueberry genotypes developed by the Univ. of Minnesota breeding program have a high yield potential (4–5 kg/bush), but may require 3–5 weeks to ripen their fruit, depending on environmental conditions and crop load (see ref. 11; unpublished data). The long ripening period may be due in part to use of parental genotypes only one or two generations removed from wild ancestors (11). While an extended ripening period may be an advantageous adaptation for wild genotypes to minimize risk from adverse environmental conditions, it is less desirable in commercial production where some environmental factors can be managed. Maintaining high yield potential with greater ripening uniformity would be desirable in future half-high cultivars.

Our objectives were to examine the inheritance of ripening uniformity and the relationship between crop load and ripening uniformity in a population of half-high blueberries. This information will provide guidance for effective selection and for planning future crosses to increase ripening uniformity.

## Materials and Methods

Each of 17 parents (Table 1) was crossed with six other parents in a circulant partial diallel mating design (8). The parents were tetraploid ($2n = 4x = 48$) clones representing *V. corymbosum, V. angustifolium,* and hybrids between the species. The resulting progenies were planted in 1976 at Becker, Minn.

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

| Parent | Ancestry |
|---|---|
| N70249[z,y] | *Vaccinium angustifolium* |
| GRVa[z] | *V. angustifolium* |
| MN-84[x] | *V. angustifolium* x *V. corymbosum* |
| R2P4[w] | *V. angustifolium* x *V. corymbosum* |
| GR-1[w] | *V. angustifolium* x *V. corymbosum* |
| GR-2[w] | *V. angustifolium* x *V. corymbosum* |
| MN-61 | *V. corymbosum* (USDA 11-93) x *V. angustifolium* var. *nigrum* |
| Northsky (MN-332) | B6 x R2P4 |
| Northcountry (MN-350) | B6 x R2P4 |
| Bluetta | (North Sedgewick lowbush x 'Coville') × 'Earliblue' |
| N70220[v] | *V. corymbosum* |
| N70218[v] | *V. corymbosum* |
| B-16 | *V. corymbosum* (G65 x 'Ashworth') |
| B-10 | *V. corymbosum* (G65 x 'Ashworth') |
| B-6 | *V. corymbosum* (G65 x 'Ashworth') |
| B-11 | *V. corymbosum* (G65 x 'Ashworth') |
| B1-1 | *V. corymbosum* (G65 x 'Ashworth') |

[z] Collected from wild stand in northern Minnesota.

[y] N numbers are Minnesota fruit accession numbers; Mn, B, and GR prefixes indicate selections from the Minnesota program.

[x] Probable *V. angustifolium* x *V. corymbosum* derivative (4, 10).

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

[v] Clone provided by F. Ashworth, Heuvelton, N.Y.; believed to be *V. corymbosum* with some lowbush genes.

on a Hubbard loamy sand with 2% organic matter and a pH of 4.8–5.2. The experimental design was a randomized complete block design with four replications. Each plot consisted of 12 seedlings spaced 1.2 m apart within rows 2.4 m apart. Single plants of each parent, except for N70220, which perished, were planted in an unreplicated adjacent block at a spacing of 1.5 × 2.4 m.

During 1984 and 1985, the dates at which 10%, 50%, and 90% of the fruit were ripe were estimated visually for each parent and progeny plant. Plants were evaluated every 3 or 4 days from late June through early August. The intervals (in days) between 10% and 50% (10/50), 50% and 90% (50/90), and 10% and 90% (10/90) ripened fruit were calculated for each plant to estimate degree of ripening uniformity. Crop load, relative to plant size, was estimated each year on a rating scale from 1 = very light crop to 9 = very heavy crop.

The data were analyzed on a plot mean basis for a randomized complete block design as a split-plot in time assuming a mixed effects model with crosses and replications as random effects and years as a fixed effect. The Satterthwaite approximation (14) was used where necessary to calculate F values. None of the plants from one cross survived; hence, only 50 progenies were used in the analyses. Narrow sense heritability estimates and their SEs were derived as previously described by Fear et al. (3). Normal disomic inheritance was assumed based on reports of predominantly bivalent pairing in tetraploid species (6, 7, 9, 12, 13), although quadrivalents have been observed with varying frequency in several genotypes (6, 7, 12). Estimation of narrow sense heritability also necessitated the assumptions of negligible epistatic genetic variance and independent distribution of genes in the parents (1, 3). Because of our interest in parental genotypes, GCA effects were computed under the assumptions of a fixed effects model (1).

## Results and Discussion

Parental genotypes varied considerably for length of ripening intervals (Table 2). Length of the 10/90 interval ranged from 7 to 28 days. The 10/50 interval was shorter than the 50/90 interval for all the parents. GRVa, a lowbush genotype, and 'Bluetta' had the shortest 10/90 intervals, but GRVa also had a very light crop load. The cultivars introduced by the Minnesota program ('Northsky' and 'Northcountry') had 10/90 intervals of about 3 weeks.

Progeny means and ranges (Table 3) indicated that crop loads were generally reduced in 1984 following a winter with temperatures reaching −42°C on two occasions. Most flower buds above the snowline were killed, reducing potential yield. While the temperature reached −35° in Jan. 1985, flower bud injury was not as severe as in 1984. In spite of this difference in crop loads, the overall mean 10/90 interval was similar in both seasons. The 10/50 interval was slightly shorter in 1985 compared to 1984, while the 50/90 interval was 1 day longer. As with the

Table 2. Mean intervals between 10%, 50%, and 90% ripened fruit and estimated crop load rating of blueberry parent plants (means over 1984–1985).

| | Ripening interval (days) | | | |
|---|---|---|---|---|
| Clone | 10/50 | 50/90 | 10/90 | Crop load[z] |
| N70249 | 4.0 | 14.5 | 18.5 | 6.5 |
| GRVa | 2.5 | 4.5 | 7.0 | 2.5 |
| MN-84 | 9.0 | 11.0 | 20.0 | 5.0 |
| MN-61 | 11.5 | 16.5 | 28.0 | 5.0 |
| R2P4 | 4.5 | 10.5 | 15.0 | 4.5 |
| GR-1 | 6.0 | 10.0 | 16.0 | 3.0 |
| GR-2 | 6.5 | 7.5 | 14.0 | 4.5 |
| Northsky | 8.5 | 9.5 | 18.0 | 5.0 |
| Northcountry | 6.5 | 16.0 | 22.5 | 6.5 |
| B-6 | 8.0 | 10.0 | 18.0 | 5.5 |
| B-10 | 4.0 | 8.0 | 12.0 | 2.5 |
| B-11 | 6.5 | 10.0 | 16.5 | 4.5 |
| B-16 | 5.5 | 13.0 | 18.5 | 4.0 |
| B1-1 | 5.0 | 8.0 | 13.0 | 3.0 |
| N70218 | 6.0 | 14.5 | 20.5 | 6.0 |
| N70220 | --- | --- | --- | --- |
| Bluetta | 3.5 | 7.0 | 10.5 | 4.5 |

[z] Estimated crop load relative to plant size. Rating scale ranged from 1 = very light crop to 9 = very heavy crop.

Table 3. Mean and range of blueberry progenies for intervals between 10%, 50%, and 90% ripened fruit and estimated crop load in 1984, 1985, and combined years.

| | | Ripening interval (days) | | | |
|---|---|---|---|---|---|
| Year | Statistic | 10/50 | 50/90 | 10/90 | Crop load[z] |
| 1984 | Mean | 6.9 | 7.4 | 14.3 | 2.5 |
| | Range | 4.1–11.3 | 3.7–11.2 | 7.8–19.3 | 1.3–6.6 |
| 1985 | Mean | 6.3 | 8.3 | 14.6 | 4.6 |
| | Range | 3.3–12.3 | 5.2–12.3 | 9.4–21.9 | 2.9–6.6 |
| Combined | Mean | 6.6 | 7.9 | 14.5 | 3.6 |
| | Range | 4.1–11.8 | 4.8–10.5 | 9.4–19.9 | 2.2–6.6 |

[z] Estimated crop load relative to plant size. Rating scale ranged from 1 = very light crop to 9 = very heavy crop.

parents, the overall progeny mean for the 10/50 interval was shorter than the 50/90 interval. This difference may be due to a bias in the subjective visual estimations or to unknown physiological limitations in ripening the latter portion of the crop. The ranges for the ripening intervals indicated considerable variation existed among the progenies for ripening uniformity.

Analysis of variance (Table 4) indicated significant ($P \leq 0.01$) year effects for the 10/50 and 50/90 intervals as well as crop load. The 10/90 intervals showed no year effect because of cancelling effects of the 10/50 and 50/90 intervals between years. All traits exhibited significant ($P \leq 0.05$ or 0.01) cross × year interactions, but mean squares were small relative to those for the crosses component.

The GCA mean squares were significant ($P \leq 0.01$) for all traits and were 5 to 7 times larger than the nonsignificant ($P > 0.05$) SCA mean squares. This relationship between GCA and SCA mean squares indicates a high proportion of additive genetic variance for ripening uniformity and crop load. Parental performance should be predictive of progeny performance for these traits.

Heritability estimates and their SEs were 0.52 ± 0.23 for the 10/50 interval, 0.50 ± 0.23 for the 50/90 interval, and 0.48 ± 0.21 for the 10/90 interval. The moderately high heritability estimates suggest that progress in reducing ripening interval length could be accomplished through recurrent phenotypic (mass) selection. These heritability estimates should, however, be interpreted cautiously because of potential upward bias by genotype × location interaction and because the assumptions of negligible epistasis, independent distribution of genes among parents, and completely disomic inheritance may be invalid (1).

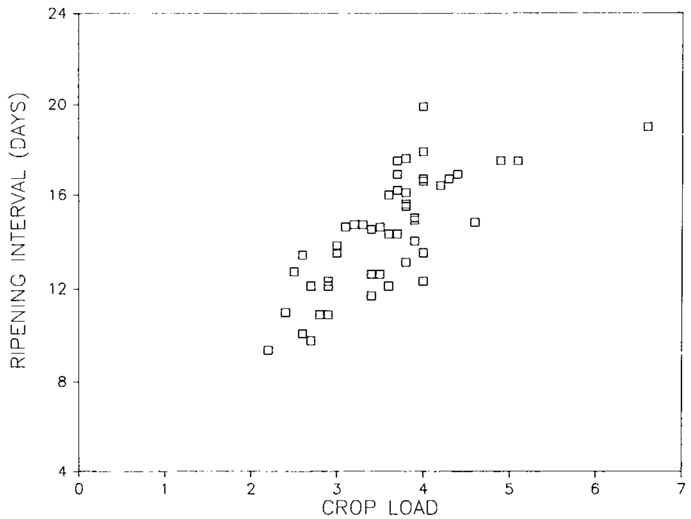

Fig. 1. Relationship between estimated crop load (1 = very light to 9 = very heavy) and length of interval between 10% and 90% ripened fruit based on family means over 1984–1985 ($r = 0.74$, $P \leq 0.01$).

The large positive GCA effects (Table 5) for the cultivars Northsky and Northcountry and several other genotypes (MN-84, MN-61, R2P4, and GR-1) used extensively as parents in the Minnesota program indicated that these parents contributed to longer ripening intervals in their progeny. 'Bluetta', N70218, and N70220 had the largest negative GCA effects for ripening interval. These three genotypes also were noted for their GCA effects for short fruit development (bloom to ripening) interval (4). Their potential for use in increasing ripening uniformity must be tempered because they also had the largest negative GCA effects for crop load. These negative effects probably are because their large-statured progeny (10) suffered increased winter injury to flower buds above the snowline. The use, as parents, of other highbush cultivars noted for their ripening uniformity (2, 5) may be warranted if this trait can be combined with cold hardiness and/or low stature.

The relationship between ripening uniformity and crop load was indicated by the size of the correlation coefficients between crop load and the various ripening intervals (Table 6). The higher-yielding families tended to have longer ripening intervals. Crop load variation was apparently more closely related to variation for the 50/90 interval than for the 10/50 interval. Whether this difference was due to bias in our subjective estimation procedures or to actual physiological relationships is unknown.

Variability among progenies (means over 1984–1985) for estimated crop load and the length of the 10/90 ripening interval and the relationship between these traits are depicted in Fig. 1. Thirty of the 50 families were estimated to ripen 80% of their

Table 4. Analysis of variance for intervals between 10%, 50%, and 90% ripened fruit and estimated crop load for blueberry partial diallel mating design over years (1984–1985).

| | | Mean squares | | | |
|---|---|---|---|---|---|
| | | Ripening interval | | | Crop |
| Source | df | 10/50 | 50/90 | 10/90 | load |
| Replications | 3 | 17.2** | 36.8** | 103.8** | 20.5** |
| Crosses | 49 | 15.7** | 14.3** | 48.6** | 4.6** |
| GCA | 16 | 34.0** | 34.4** | 115.9** | 11.1** |
| SCA | 33 | 6.9 | 4.5 | 16.0 | 1.5 |
| Error "a" | 147 | 3.1 | 3.8 | 9.9 | 0.8 |
| Years | 1 | 38.9** | 78.8** | 7.0 | 476.1** |
| Crosses × years | 49 | 2.7* | 5.0* | 9.9** | 1.7** |
| GCA × years | 16 | 2.1 | 6.6 | 11.6 | 3.0** |
| SCA × years | 33 | 3.0** | 4.2* | 9.1** | 1.0* |
| Error "b" | 150 | 1.4 | 2.6 | 4.9 | 0.6 |

*,** F value significant, $P \leq 0.05$ and 0.01, respectively.

Table 5. General combining ability effects of blueberry parents for intervals between 10%, 50%, and 90% ripe fruit and estimated crop load (1984–1985).

| | Ripening intervals | | | Crop |
|---|---|---|---|---|
| Clone | 10/50 | 50/90 | 10/90 | load[z] |
| N70249 | −0.4 | 1.1 | 0.7 | 1.1 |
| GRVa | −1.0 | 1.0 | 0.0 | 0.3 |
| MN-84 | 1.5 | 0.2 | 1.7 | −0.1 |
| MN-61 | 1.1 | 0.7 | 1.8 | 0.8 |
| R2P4 | 1.0 | 0.4 | 1.4 | 0.3 |
| GR-1 | 0.5 | 0.8 | 1.3 | 0.2 |
| GR-2 | 0.1 | 0.9 | 0.9 | −0.2 |
| Northsky | 1.4 | 0.5 | 1.9 | 0.4 |
| Northcountry | 1.2 | 0.7 | 1.9 | 0.4 |
| B-6 | −0.3 | −0.4 | −0.7 | −0.3 |
| B-10 | −0.4 | −0.6 | −1.0 | −0.4 |
| B-11 | −0.9 | −0.7 | −1.6 | −0.4 |
| B-16 | 0.1 | −0.4 | −0.3 | −0.2 |
| B1-1 | 0.1 | −0.1 | 0.0 | −0.1 |
| N70218 | −1.1 | −1.1 | −2.2 | −0.5 |
| N70220 | −1.1 | −1.1 | −2.2 | −0.7 |
| Bluetta | −1.8 | −1.9 | −3.7 | −0.6 |
| SE | 0.3 | 0.3 | 0.5 | 0.3 |

[z] Estimated crop load relative to plant size. Rating scale ranged from 1 = very light crop to 9 = very heavy crop.

Table 6. Correlation coefficients ($r$) between estimated crop load and intervals between 10%, 50%, and 90% ripened fruit in 1984, 1985, and combined years (family mean basis).

| | Ripening interval | | |
|---|---|---|---|
| Year | 10/50 | 50/90 | 10/90 |
| 1984 | 0.39[z] | 0.56 | 0.56 |
| 1985 | 0.51 | 0.61 | 0.65 |
| Combined | 0.57 | 0.77 | 0.74 |

[z] All $r$ values were significant ($P \leq 0.01$, df = 49).

crop in $\leq$15 days. Only six families with an estimated crop load higher than the overall mean (3.6) had 10/90 intervals of $<$15 days. Nevertheless, there was up to a 5- to 7-day range for 10/90 interval length among families with similar mean crop load levels. Given the potential for segregation within families, the prospect exists for selection of genotypes with both a high yield potential and relatively short ripening interval in spite of the general positive relationship between these traits.

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# Genotypic Differences in the Effect of Temperature on $CO_2$ Assimilation and Water Use Efficiency in Blueberry

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*Additional index words.* *Vaccinium darrowi, V. corymbosum,* gas exchange, temperature tolerance

***Abstract.*** **To determine if the net $CO_2$ assimilation and water use efficiency (WUE) of highbush blueberry under high temperature can be improved genetically, gas exchange determinations were made for a selection of *Vaccinium darrowi* Camp (Florida 4B), a highbush cultivar (Bluecrop) (*V. corymbosum* L.), their $F_1$ hybrid (US75), and two crosses of the $F_1$ hybrid to another improved genotype (US239 and US245). All genotypes responded parabolically to increasing temperature at vapor pressure deficits <1 kPa. Maximum $CO_2$ assimilation of US75 ($15\ \mu mol\cdot s^{-1}\cdot m^{-2}$) was 30% to 40% higher than either parent. Carbon dioxide assimilation of US75 and Florida 4B was optimum at 30°C and that of 'Bluecrop' at 20°. The optimum for US239 was similar to 'Bluecrop', and that of US245 to Florida 4B. Florida 4B had higher WUEs than 'Bluecrop' at both 20° (5.64 $\mu$mol $CO_2$/mmol $H_2O$ to 4.01) and 30° (3.73 to 2.53). US239 and US245 had significantly ($P < 0.05$) higher WUEs at 30° than did 'Bluecrop'. Residual conductance to $CO_2$ ($g_r$) decreased in 'Bluecrop' when temperature was raised from 20° to 30°, but increased in all other genotypes. Due to the favorable gas exchange properties of US75 and US245 at 30°, we suggest that the high temperature tolerance of *V. darrowi* may be heritable and that US245 may be used to improve the heat tolerance of highbush blueberry.**

*Vaccinium corymbosum* L. grows well under relatively cool, moist conditions (4), while *V. darrowi* often occurs on hot, dry, sandy scrublands in central Florida (10, 17). As such, they may possess physiological adaptations that improve their net $CO_2$ assimilation and water use efficiency under the temperature conditions of their respective habitats.

One selection of *V. darrowi* (Florida 4B) has a temperature optimum for net $CO_2$ assimilation about 8° to 10°C higher than that of 'Bluecrop', a cultivar of *V. corymbosum* (14, 16). Although *V. corymbosum* ($4\times = 48$) and *V. darrowi* ($2\times = 24$) differ in ploidy, one of us (A.D.D.) has developed a series of

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