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Floral Bud Cold Hardiness of *Vaccinium ashei*, *V. constablaei*, and Hybrid Derivatives and the Potential for Producing Northern-adapted Rabbiteye Cultivars

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Abstract. **From 2004 to 2006, cold hardiness assays were performed to evaluate the relative winterhardiness of flower buds in selections of pure *Vaccinium ashei* Reade and *V. constablaei* Gray as well as in selections/families composed of various combinations of *V. ashei* and *V. constablaei* germplasm. Significant differences were observed among entries with LT_{50} values ranging from –17.2 to –28.4 °C. An analysis of LT_{50} versus percent *V. constablaei* yielded a regression of LT_{50} (°C) = (–0.08 × *V. constablaei* percentage) – 21.57. Families or selections with 50% (or greater) *V. constablaei* and some with 25% *V. constablaei* had LT_{50} values equivalent to or better than 'Bluecrop'. Based on this information, a 25% *V. constablaei* constitution appears suitable to develop northern-adapted rabbiteye types if proper parents are selected and if sufficient selection pressure for winterhardiness is exercised.**

The observed floral bud cold hardiness (or lack of) in blueberry (*Vaccinium* sp.) plants containing southern-adapted germplasm is a result of both midwinter cold hardiness and deacclimation rates (Rowland et al., 2005). Southern U.S. blueberry growers like the growth habit of rabbiteye (*V. ashei* Reade, syn. *V. virgatum* Ait.) because it is vigorous and relatively easy to care for in addition to being productive. Rabbiteye is not naturally found in areas north of ≈37°N latitude in the eastern and midwestern United States as a result of its limited winterhardiness and rapid rate of deacclimation (loss of cold acclimation) once chilling requirements are satisfied (USDA hardiness zone 7). Along the Pacific coast, rabbiteye is limited by a lack of heat during the production season rather than cold in the dormant season, but they are capable of growing fruitfully as far north as ≈48°N latitude.

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In Georgia and many parts of the southern United States, there is a move toward growing more southern highbush blueberry (predominantly *V. corymbosum* with a low chilling trait from *V. darrowi* Camp.) because it is earlier ripening than rabbiteye blueberry. However, there is also a desire for earlier ripening rabbiteye blueberries to bridge the ripening interval between southern highbush and the current rabbiteye cultivars. One goal of the cooperative breeding program between the USDA-ARS and the University of Georgia is to develop rabbiteye cultivars that are earlier ripening without being earlier flowering. It has long been recognized that the introduction of *V. constablaei* Gray (syn. *V. corymbosum* forma *constablaei*) germplasm into *V. ashei* concomitantly makes rabbiteye later to flower, earlier to ripen, and overall more cold-hardy (Brightwell et al., 1949; Darrow et al., 1952). Such hybrids are being pursued to achieve these goals.

Vaccinium constablaei is a highbush-like hexaploid species found at higher elevations in northern Georgia, western North Carolina, and eastern Tennessee (Galletta and Ballington, 1996). Its main characteristics are exceptional levels of midwinter cold-hardiness, slow deacclimation (Rowland, et al., 2005), late flowering, a short fruit development interval (at least relative to *V. ashei*), moderate vigor, and a nonsuckering growth habit. Its fruit are small, aromatic, not objectionably seedy, and can have very good quality.

Vaccinium ashei is a hexaploid species traditionally grown commercially in southern areas with mild winters (Galletta and Ballington, 1996). In the current cultivated germplasm base, its main characteristics are cold sensitivity, rapid deacclimation (Rowland et al., 2005), relatively early flowering (in areas with sufficient heat units), and a long fruit development interval. *V. ashei* is vigorous, high-yielding, adaptable to upland soils, and many cultivars have a tendency toward "suckering" (spreading by underground shoots). Its fruit are relatively large, as are the seeds, and it can be excessively seedy or gritty, possessing stone cells (Gough, 1983; Yarbrough and Morrow, 1947). The organic acid composition of the fruit, with malic acid predominating, can result in a blander tasting fruit than that of northern highbush (Ehlenfeldt et al., 1994).

Hybrids of *V. ashei* with *V. constablaei* can yield more desirable rabbiteye types for the southern United States because these rabbiteye-derivative hybrids often have a later flowering time and an earlier fruit ripening time than *V. ashei* selections (Ballington et al., 1986). Successful crosses among these hybrid types have yielded the earlier ripening rabbiteye cultivar 'Snowflake' (Lyrene, 1993). However, in other combinations, *V. constablaei* introgression can yield rabbiteye derivatives suitable for the North. 'Little Giant', a hardy processing hybrid grown in Michigan, is a 50:50 hybrid of *V. ashei* and *V. constablaei* (U.S. Dept. of Agriculture, 1996).

In our breeding program, representative subfamilies of *V. ashei–V. constablaei* breeding populations produced for Georgia were grown in New Jersey and were found to be generally hardy and potentially suitable for growth in similar northern areas. We also evaluated six genotypes from 100% *V. constablaei* breeding population and found them to have very good cold-hardiness and very late deacclimation (Rowland et al., 2005). The late deacclimation of *V. constablaei* is reflected in its late flowering date, typically lagging 2 or more weeks behind 'Bluecrop'. These attributes led us to consider the possibility that northern-adapted hexaploid types could be developed from *V. ashei–V. constablaei* hybrids. Just as (northern) highbush yielded "southern highbush" through *V. darrowii* introgression (Sharpe and Sherman, 1976), (southern) rabbiteye might yield "northern rabbiteye" through *V. constablaei* introgression. The particular value of this approach is that there is no sterility in the F_1 hybrids as a result of inequality of ploidy levels as often occurs in highbush × rabbiteye hybrids.

The concept of "northern rabbiteye" holds great potential because *V. ashei* and

V. constablaei are complementary for many characteristics. Ballington et al. (1986) reviewed various *V. ashei–V. constablaei* hybrids under North Carolina conditions and found "significant differences among progenies for all traits, with sufficient variability for selection within most progenies." It is particularly notable that most hybrids with up to 75% *V. ashei* germplasm exhibit none of the objectionable grittiness in the fruit so often observed in rabbiteye (Ehlenfeldt, personal observation). Ballington et al. (1986) did not evaluate cold-hardiness among the traits they examined, and this is a critical issue to the concept of "northern rabbiteye." Among selections we have made of "northern rabbiteye" thus far, their characteristics can be summarized as 1) excellent vigor, 2) high potential productivity, 3) late flowering (relative to rabbiteye), 4) winter-hardiness (greater than most rabbiteye), 5) good/interesting fruit quality, often somewhat dark in color, 6) late ripening (compared with highbush but earlier than rabbiteye), and 7) possessing moderate fruit size.

To determine the most suitable compositions needed for hardiness under northern conditions, we evaluated the relative winter-hardiness of pure *V. ashei* and *V. constablaei* as well as selections and families composed of various percentages of *V. ashei* and *V. constablaei* germplasm.

Materials and Methods

In 2004, 2005, and 2006, we evaluated midwinter flower bud cold-hardiness in a range of materials, including *V. ashei* cultivars, *V. constablaei–V. ashei* hybrid families and clones with varying species compositions, and *V. constablaei* families (Table 1). Materials were grown at the Philip E. Marucci Center for Blueberry and Cranberry Research and Extension at Rutgers University, Chatsworth, NJ. In general, 35 terminal shoots were collected from each sampled clone or cultivar within the study. For rabbiteye cultivars, samples came from two plants; for US selections, from single plants; and for 'Little Giant', five plants. For sampled families, six to eight sufficiently budded clones were selected and sampled equally to make up the 35 shoots. The shoots were bulked and randomly distributed when the freezing assay was conducted. Sampled clones within families were tagged, and the same clones were used in subsequent years provided they had sufficient flower buds. If a marked clone did not have sufficient flower buds, a different clone would be substituted. Substitutions were seldom more than one or two clones per family. The *V. constablaei* families were less well-adapted to Atlantic coastal conditions, and obtaining uniformly distributed samples was considerably more difficult. For these families, shoots from six or more relatively vigorous and well-budded plants were sampled and bulked. Numbers of sampled clones varied from six to 11, with two to three bushes often providing one-third to two-thirds of the stems. For all experimental entries, shoots were collected in the morning and immediately packed with frozen cold-packs and sent by overnight shipment to Beltsville, MD, where they were assayed the next day for cold-hardiness.

Table 1. *Vaccinium constablaei* Gray germplasm composition, partial pedigrees, and samples used in cold hardiness evaluations, 2004 to 2006.

Germplasm or selection	*V. constablaei* ancestry (%)	LT_{50} estimates/yr[z] 2004	2005	2006
NC 86-40-2 × NC 86-28-3 (*V. constablaei* family)	100	*	*	*
NC 86-40-2 × US 831 (*V. constablaei* family)	100	2	*	*
US 1112 = NC 86-40-2 × US 866[y]	75	2	2	2
US 1080 (5x) = NC 86-28-3 × US 861[x]	60	*	*	*
ARS 99-89 = NC 86-40-2 × DeSoto	50	2	2	2
Little Giant	50	*	*	*
US 1043 = US 866 × Beckyblue	25	2	1	2
Delite × Little Giant (family)	25	2	—	1
US 1056 = US 874[w] × Premier	25	2	2	2
Climax × Little Giant (family)	25	2	2	2
Baldwin	0	1	—	2
Climax	0	—	—	2
Delite	0	—	—	2
Tifblue	0	1	1	—

[z]Asterisks indicate clones/selections/families that had LT_{50} estimates that fell below the lowest evaluation temperatures of the assay (i.e., less than –28 °C). Dashes indicate clones/selections/families that had more than 50% damage on the sample date; hence, no LT_{50} could be calculated or those that had highly variable anomalous results. Similar problems (damage or variability) existed in samples for which only one sample set was used in a given year.

[y]US 866 = NC 86-40-2 × NJ 89-158-8. NJ 89-158-8 is a hexaploid and is a hybrid of two triploids (Ehlenfeldt and Vorsa, 1994). NJ 89-158-8 is ≈70% *V. corymbosum* L., 18% *V. darrowi* Camp, 9% *V. angustifolium* Ait., and less than 1% each of *V. tenellum* Ait. and *V. ashei* Reade.

[x]US 861 = Bluecrop × N 8527#1 (G 434 × *V. ovatum* Pursh). US 861 is presumably tetraploid and is ≈68% *V. corymbosum*, 25% *V. ovatum*, 4% *V. angustifolium*, 1% to 2% *V. darrowi*, and less than 1% each of *V. tenellum* Ait. and *V. ashei*.

[w]US 874 = NC 86-40-2 × NJ 89-58-8.

Cold-hardiness was assayed using a detached shoot assay as described by Arora et al. (2000, 2004). Detached shoots of listed materials (Table 1) were assayed on 24 Feb. and 3 Mar. in 2004, on 24 Feb. and 2 Mar. in 2005, and on 11 and 18 Jan. in 2006. Shoots were collected relatively late in the winter in 2004 and 2005, a time that in previous studies was found to represent a period of maximum cold-hardiness. In 2004, this yielded suitable readings, but 2005 was a colder winter, and by late February/early March, several selections had already sustained more than 50% damage, rendering it impossible to calculate LT_{50} values (see Table1). Samples were collected earlier in 2006 to avoid similar damage. In 2005, samples of the cultivar 'Bluecrop' were included as a representative northern highbush standard. Five- to 6-cm-long shoots with three to eight flower buds were subjected to a freeze–thaw protocol that consisted of placing three randomly sampled shoots/treatment–temperature from each genotype in test tubes (three shoots/tube) with 0.5 mL of water and subjecting them to controlled freezing in a glycol bath (Model 2325; Forma Scientific, Marietta, OH) for each sampling date. Ice nucleation was initiated at –1 °C, samples were allowed to equilibrate for ≈45 min, then further cooled at 0.5 °C/30 min down to –4 °C, at 1 °C/30 min down to –8 °C, and at 2 °C/30 min thereafter to respective final treatment temperatures. Bud temperature was monitored by copper-constantan thermocouples (TT-T-30) attached to a thermometer (DP465; Omega Engineering, Stamford, CT). Initial treatment temperatures chosen for fully cold-acclimated buds covered a range from –10 to –28 °C (the lowest temperature that the glycol freezing bath would consistently reach) at 2 °C increments to represent 0% to 100% injury to blueberry buds for most genotypes (Arora et al., 1997). Controls in both years consisted of similarly handled shoots that were kept at 4 °C with no exposure to glycol bath freezing regimes. Shoots were removed from the freezing bath at respective treatment temperatures and samples were allowed to thaw overnight at 4 °C followed by 24-h incubation at 20 °C. Subsequently, buds were dissected and observed for injury (visual browning) of the ovaries in individual flowers (Arora et al., 2000; Flinn and Ashworth, 1994), and a percent damage value was calculated for each bud.

Bud cold-hardiness was defined as the temperature causing 50% injury overall (LT_{50}). A probit model with a logistic distribution was used to fit to percent damage versus temperature data observed for each (genotype, year, replicate) and the LT_{50} was estimated using Proc Probit (SAS Institute, Inc., 2005). Table 1 lists the number of LT_{50} value estimates used in subsequent analysis of variance (ANOVA) and regression analyses. Some LT_{50} estimates were omitted because the observed data did not visually indicate that a probit model was an appropriate model for these data (i.e., the LT_{50} value was not attained as a result of the occurrence of more than 50% damage before the assay) or because the sample produced results judged to be highly variable and anomalous in the freezing assay. Other LT_{50} estimates were omitted because their estimates fell below the range of temperatures actually

observed (i.e., below –28 °C). Nonsignificant genotype × year interactions indicated year-to-year LT_{50} consistency among genotypes based on examination of the five genotypes observed in all 3 years, the six genotypes observed together in 2004 and 2005, the seven genotypes observed together in 2004 and 2006, and the five genotypes observed together in 2005 and 2006. Significant differences among genotypes/families were evaluated with a Sidák-adjusted means comparison (to protect against inflation of type I error above $\alpha = 0.05$). A linear regression was fit to a $Y = LT_{50}$ versus x = % *V. constablaei* model using 1/variance as a weighting factor (i.e., the variance among LT_{50} values as a function of specific *V. constablaei* percentages). This variance was of comparable size for *V. constablaei* percentages of 0, 25, and 50, larger for percentages of 75, and largest for *V. constablaei* percentages of 100. Hence, LT_{50} values at *V. constablaei* percentages of 0, 25, and 50 contributed the greatest weight to fitting the regression line.

Results and Discussion

Across the 3 years of the study, LT_{50} values ranged from –17.2 to –28.4 °C (Table 2; N.B., –28 °C was the lowest value we could measure with our apparatus). Significant differences were statistically observed among 12 entries in the study (including 'Bluecrop') (ANOVA, F = 14.06, 33 df, $P < 0.0001$). Another three entries, US 1080, 'Little Giant', and one of the two *V. constablaei* families, had less than 50% damage at –28 °C; thus, they had extrapolated LT_{50} values lower than –28 °C. These selections were excluded in further analyses. A regression of LT_{50} values versus percent *V. constablaei* produced a highly significant regression (F = 23.28, 43 obs, $P < 0.0001$, adjusted $r^2 = 0.35$). The regression equation described by the values was LT_{50} (°C) = (–0.08 × *V. constablaei* percentage) – 21.57. The r^2 indicates that the predictive value of this regression is low, but with this precaution, one may calculate that, on average, a composition of 55% *V. constablaei* germplasm might yield an LT_{50} value roughly equivalent to that of 'Bluecrop'. In summary, any selection/family with 50% or more *V. constablaei* was hardy at or below –25 °C, but when percentages of *V. constablaei* dropped to 25%, considerably more variability for cold-hardiness was observed. If we examine LT_{50} values, some selections with as little as 25% *V. constablaei* germplasm had LT_{50} values equivalent to 'Bluecrop' (e.g., the LT_{50} of the 'Climax' × 'Little Giant' family was within 0.1 °C of the value for 'Bluecrop'). Numerous entries, including some that were 100% *V. ashei*, were not statistically different from 'Bluecrop'.

Percentages of other germplasms did not appear to be consistently significant factors, but specific ancestry did. US 1043 (–17.3 °C) and US 1056 (–24.4 °C) are identical percentagewise with respect to species composition (Table 2) but have different specific ancestors. Both are 50% *V. ashei*, 25% *V. constablaei*, 18% *V. corymbosum*, plus small components of other species. However, US 1043 has 'Beckyblue' as its *V. ashei* ancestor, whereas US 1056 has 'Premier' as an ancestor. In previous studies, 'Beckyblue' was ranked as relatively less hardy (LT_{50} = –16.9 °C, ranked 22 of 25), whereas 'Premier' was among the hardier selections (LT_{50} = –22.4 °C, ranked 5 of 25) (Ehlenfeldt et al., 2006).

Even among selections with larger *V. ashei* components, if this component derives from the proper parent, it can result in hardy germplasm (e.g., the 'Climax' × 'Little Giant' family that is 75% *V. ashei*). 'Climax' ranked only 15 of 25 (LT_{50} = –19.6 °C) in previous studies (Ehlenfeldt et al., 2006), but there is good reason to believe that the *V. ashei* component from 'Little Giant' was itself exceptionally hardy.

We conclude that derivatives of *V. ashei* with sufficient percentages of *V. constablaei* can produce selections as hardy as or hardier than 'Bluecrop'. Selections with 50% to 100% *V. constablaei* germplasm were extremely hardy, but hardiness, in general, decreased as the *V. constablaei* percentage decreased. In looking to create northern rabbiteye, a 25% *V. constablaei* constitution appears suitable if proper selection of parents occurs and if sufficient selection pressure for winterhardiness is exercised.

We are currently enacting several strategies to produce "northern rabbiteye." These include: 1) utilization of the knowledge of cold-hardiness of rabbiteye (coupled with knowledge of traits such as suckering, fruit size, vigor, disease resistance, and so on); 2) introgression of *V. constablaei* into *V. ashei* targeting useful combinations of 75% *V. ashei*:25% *V. constablaei* (50%:50% combinations usually have insufficient fruit size, fruit color, and plant stature); 3) improvement of native *V. constablaei* germplasm through introgression of *V. ashei* and subsequent backcrossing to produce 25%:75% breeding parents; and 4) recombination among hybrids with various germplasm combinations and percentages. We believe that recombination among hardy rabbiteye hybrids offers the potential of being able to select secondary hybrids adapted anywhere from the far southern United States to the far northern United States. The greatest challenges in ultimately using this germplasm are achieving still earlier ripening (if they are to be competitive with highbush blueberries) and developing adequate fruit size.

Table 2. LT_{50} values and germplasm composition for cultivars, selections, and families evaluated in 2004 to 2006.

		Germplasm composition (%)	
Germplasm or selection	LT_{50} (°C)[z]	*Vaccinium constablaei*	Other species[w]
Tifblue	–17.2 a	0	100 *ash*
US 1043	–17.3 a	25	50 *ash*, 18 *cor*, 5 *dar*, 2 *ang*
Delite	–20.3 ab	0	100 *ash*
Baldwin	–20.3 ab	0	100 *ash*
Climax	–20.5 ab	0	100 *ash*
Delite × Little Giant family	–20.9 ab	25	75 *ash*
US 1056	–24.4 bc	25	50 *ash*, 18 *cor*, 5 *dar*, 2 *ang*
US 1112	–25.8 bc	75	18 *cor*, 5 *dar*, 2 *ang*
Climax × Little Giant family	–26.0 bc	25	75 *ash*
Bluecrop	–26.1 bc	0[x]	100 *cor*
NC 86-40-2 × US 831 family	–27.2 bc	100	—
ARS 99-89	–28.4 c	50	50 *ash*
US 1080	<–28.0[y]	60	27 *cor*, 10 *ovt*, 2 *ang*, 1 other spp.
Little Giant	<–28.0	50	50 *ash*
NC 86-40-2 × NC 86-28-3 family	<–28.0	100	—

[z]Mean separation among genotypes within column; Šidák-adjusted to ensure $\alpha = 0.05$.
[y]Asterisks indicate clones/selections/families that had LT_{50} estimates that fell below the range of temperatures actually observed.
[x]Bluecrop was included as a northern highbush standard.
[w]*ash* = *Vaccinium ashei* Reade, *cor* = *V. corymbosum* L., *dar* = *V. darrowi* Camp, *ang* = *V. angustifolium* Ait., *ovt* = *V. ovatum* Pursh.

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