The Genetic Composition and Tetrasomic Inbreeding Coefficients of Highbush Blueberry Cultivars

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Abstract. Inbreeding coefficients were calculated for highbush blueberry (*Vaccinium corymbosum* L.) cultivars based on a tetrasomic inheritance model. This model yielded lower inbreeding coefficients than previous calculations based on a disomic tetraploid inheritance model. Recent trends in breeding have resulted in significant use of *V. darrowi* Camp as a source of low-chilling germplasm for use in the southern United States. There is also a trend toward increased inbreeding in several crosses from which recently released cultivars have been derived. Increased inbreeding coefficients do not represent a detrimental situation in blueberry per se.

Inbreeding depression is a well-recognized phenomenon in outcrossing species. The detrimental results of self-pollination and inbreeding are well documented in blueberries (Hellman and Moore, 1983; Krebs and Hancock, 1988, 1991; Lyrene, 1983; Morrow, 1943; Vander Kloet and Lyrene, 1987; White and Clark, 1932). It was this concern over the inbreeding levels that caused Hancock and Siefker (1982) to calculate the inbreeding coefficients of highbush cultivars that had been released up to that time, using a model based on the assumption of disomic inheritance. More recent studies (Krebs and Hancock, 1989), coupled with older evidence (Draper and Scott, 1971) have made it clear that the mode of inheritance in tetraploid blueberries is polysomic. My study re-examines the inbreeding coefficients of highbush blueberry cultivars using a tetrasomic model and updates the cultivar listings of Hancock and Siefker (1982). My tables essentially follow Hancock and Siefker's format to allow ready comparison of the changes and additions.

Materials and Methods

The pedigrees of 83 cultivars (79 highbush and four half-high) released by public agencies were collected from various sources. Percentage contributions from wild selections were calculated for each cultivar, and average contributions were calculated for each decade based on the years of hybridization. For cultivars that had an ancestor resulting from a cross between *Vaccinium ashei* Reade and a diploid species selection, I assumed that the hybrid

est levels of inbreeding result in severe inbreeding depression.

Results and Discussion

As noted by Hancock and Siefker (1982), three wild species selections ['Brooks', 'Sooy', and 'Rubel' (*V. corymbosum* L.)] have contributed the largest portion of the genes found in cultivars (at overall levels of 23.5%, 12.5%, and 28.6%, respectively) (Table 1). The contribution of these selections to more recently released cultivars has remained high (Table 2) and has tapered off slowly only in recent decades. These high levels are due mainly to limited resampling of wild germplasm, and even in cases using wild germplasm, further crossing to standard materials is required to recover acceptable horticultural types. *Vaccinium angustifolium* Aiton (lowbush) selections have consistently been responsible for ≈10% of the genes found in cultivated material. The contributors of these genes range from 'Russell' in the original breeding selections to 'North Sedgwick' and 'Michigan lowbush #1' in more recent cultivars and R2P4 (1/2 *V. corymbosum*, 1/2 *V. angustifolium*) in the Minnesota half-high breeding program. The proportion of *V. darrowi* germplasm has increased within cultivated materials, largely due to the efforts begun in the late 1960s and early 1970s to develop low-chill highbush cultivars for the southern areas of the United States. Although *V. darrowi* is present primarily in the southern materials, it also is represented in 'Legacy' and 'Sierra' and is present in several advanced U.S. Dept. of Agriculture/New Jersey selections currently being considered for release. *Vaccinium ashei*, *V. constablaei* Gray, and *V. tenellum* Ait. also have made contributions to the germplasm base in northern- and southern-adapted materials, and the genetic contribution of these materials and that of species such as *V. elliotii* Chap. and *V. palidum* Ait. will probably increase slightly in the future. Virtually all highbush and half-high cultivars are in *V. corymbosum* cytoplasm. The exceptions are 'Bluetta' with *V. angustifolium* ('North Sedgwick') cytoplasm, 'Cape Fear' and 'Sierra' with *V. darrowi* ('Fla 4B') cytoplasm, and 'Flordablue' with unspecified *V. darrowi* cytoplasm.

A significant trend in highbush blueberry breeding has been the consistent increase in average inbreeding coefficients over the decades, rising from 0.0017 in the earliest material to 0.0106 in the 1971-80 decade and to 0.0281 for 'Sierra', the only cultivar hybridized in the 1980s (Table 3). Although Hancock and Siefker (1982) suggested that increases in inbreeding coefficients had leveled off in the 1961-70 decade, later cultivar releases in that decade and the subsequent decade increased the average inbreeding coefficient value (Table 4). 'Duke', one of the most successful and productive early cultivars released recently, also has the highest inbreeding coefficient at 0.0568 (Table 3). A brief examination of cultivars with high inbreeding coefficients and the source of their inbreeding follows:

was pentaploid with three chromosome sets from *V. ashei* and two from the species (Draper, personal communication), and relative contributions from the two species were proportioned accordingly. Inbreeding coefficients were calculated using an adaptation of Wright's (1922) pedigree method, adapted by potato researchers (Loiselle et al., 1989; Mendoza and Haynes, 1973) as follows:

$$F_x = 1/6 (F_y + F_z + 4 R_{yz})$$

where F_x is the inbreeding coefficient of the genotypes of the full-sib family and represents the probability that any pair of alleles at one locus are identical by descent; F_y and F_z are the inbreeding coefficients of the parents. R_{yz} is derived by the following formula:

$$R_{yz} = \sum \{ (1/4)^{n_1 + n_2 + 1} [1 + 3F_a] \}$$

where R_{yz} is the relationship coefficient between the parents obtained by the summation of the preceding formula over the paths of relationship for all common ancestors (F_a). The terms "n1" and "n2" are the number of generations separating parents Y and Z from the common ancestor. Unknown parents within any pedigree were assumed to have an inbreeding coefficient of $F = 0$. Mendoza and Haynes (1973) summarize the essential difference between polysomic tetraploid inbreeding coefficients and diploid inbreeding coefficients saying, "...the inbreeding coefficient of a tetraploid individual is not only a function of the degree of coancestry of its parents, but also of the inbreeding coefficient of each parent. If the parents are non-inbred and non-related, F will be 0 for both ends of ploidy [diploids and tetraploids]. If the parents are inbred, but not related, F for the diploid [progeny] is still 0, but for the tetraploid [progeny] will be greater than 0 with a maximum of 1/3." Thus, although the rate of inbreeding is less severe in tetraploids, it is potentially more cumulative. Typically, in polysomic polyploids, only mod-

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Table 1. Genetic contributions (percent) of various wild selections to blueberry (*Vaccinium corymbosum*) cultivars released between 1982 and 1994.

Cultivar	Brooks	Chatsworth	Crabbe 4	Grover	Sooy	Rubel	Russell	Other
Avonblue ^{z,y}	16.4	1.6		3.1	14.1	20.3	0.8	Harding, 6.3; <i>V. ashei</i> , 7.5; <i>V. darrowi</i> , 5.0; unknown, 25
Bladen ^z	16.4	9.4	12.5	3.5	9.4	23	3.9	<i>V. ashei</i> , 1.9; <i>V. darrowi</i> , 3.1; <i>V. tenellum</i> , 1.3; unknown, 15.6
Bluegold	15.7			6.3	14.1	18.7	1.6	Ashworth, 25; Michigan lowbush #1, 12.5; unknown, 6.25
Blue Ridge	17.2	3.1		4.7	10.9	23.4	3.1	Michigan lowbush #1, 12.5; <i>V. darrowi</i> , 25
Bounty	25.8	7.8	12.5	1.6	14.1	28.1	3.9	Harding, 6.25
Cape Fear	17.2	3.1		4.7	10.9	23.4	3.1	Michigan lowbush #1, 12.5; <i>V. darrowi</i> , 25
Chandler	25			3.1	25	37.5	3.1	Harding, 6.3
Cooper	20.3	7.8		3.1	10.9	28.1	4.7	<i>V. darrowi</i> , 25
Duke	25.8	10.9		6.3	17.2	35.9	3.9	
Flordablue ^z	1.6				1.6	4.7	1.6	Carter, 3.1; <i>V. ashei</i> , 15; <i>V. darrowi</i> , 25; unknown, 50
Georgiagem	16.4	1.6		6.3	11	23.4	3.9	Ashworth, 12.5; <i>V. darrowi</i> , 25
Gulfcoast	20.3	7.8		3.1	10.9	28.1	4.7	<i>V. darrowi</i> , 25
Legacy	18.8	6.3		9.4	10.9	28.1	1.6	<i>V. darrowi</i> , 25
Marimba								Unknown, 100
Misty ^z	16	2.4		3.5	12.5	20.7	1.2	Harding, 3.2; <i>V. ashei</i> , 5.6; <i>V. darrowi</i> , 5.6; <i>V. tenellum</i> , 1.3; unknown 28.1
Nelson	25			3.1	25	38	3.1	Harding, 6.25
Northblue	13.3	1.6		4.7	10.2	18.8	1.6	Ashworth, 25; Michigan lowbush #1, 25
Northcountry	7	1.6		1.6	3.9	9.4	1.6	Ashworth, 25; <i>V. corymbosum</i> , 25; <i>V. angustifolium</i> , 25
Northland	18.8			6.3	18.8	18.8		Michigan lowbush #1, 25; unknown, 12.5
Northsky	7	1.6		1.6	3.9	9.4	1.6	Ashworth, 25; <i>V. corymbosum</i> , 25; <i>V. angustifolium</i> , 25
O'Neal ^z	19.9	8.6	12.5	0.8	7.1	21.9	4.3	North Sedgwick, 6.3; <i>V. ashei</i> , 3.7; <i>V. darrowi</i> , 2.5; unknown (MI/USDA ^a), 12.5
Reveille ^z	16.4	9.4	12.5	3.5	9.4	23	3.9	<i>V. ashei</i> , 1.9; <i>V. darrowi</i> , 3.1; <i>V. tenellum</i> , 1.3; unknown, 15.6
Sharpblue (E30) ^{z,w}	12.5			2.3	10.9	16.4	1.6	Hildebrand, 12.5; <i>V. ashei</i> , 15; <i>V. darrowi</i> , 28.8
Sharpblue (E55) ^{z,w}	12.1			2.3	10.9	15.6	1.2	Harding, 1.6; Hildebrand, 12.5; <i>V. ashei</i> , 15; <i>V. darrowi</i> , 28.8
Sierra ^z	14.1	3.1		3.1	8.6	18.8	2.4	<i>V. ashei</i> , 15; <i>V. constablaei</i> , 15; <i>V. darrowi</i> , 20
St. Cloud	13.3	1.6		4.7	10.2	18.8	1.6	Ashworth, 25; Michigan lowbush #1, 25
Sunrise	25	7.8		1.6	12.5	32.8	4.7	Carter, 3.1; North Sedgwick, 12.5
Toro	25.1	18.8			12.5	37.5	6.3	
Average								
1908, 1994	23.5	5.8	2.6	4.9	12.5	28.6	5.5	

^zCultivars with presumed 5x ancestors resulting from crosses with *V. ashei*.^y'Avonblue' was released in 1977. The germplasm contribution calculated here differs from that of Hancock and Siefker (1982).^aMI/USDA = Michigan/U.S. Dept. of Agriculture.^wEstimates for 'Sharpblue' are based on alternative possible pedigrees, involving E30 and E55.

'Redskin' and 'Catawba'—F₂ segregants for pink-albino skin color out of the cross 'Brooks' x 'Russell'.

'Lateblue'—A cross of two genetically similar cultivars, 'Herbert' and 'Coville' (reciprocals). 'Stanley' and 'Atlantic' are common grandparents.

'Flordablue'—A cross of two sibling selections.

'Toro'—'Stanley' occurs as two of the four possible grandparents.

'Duke'—'Earliblue' occurs as a grandparent and great-grandparent. 'Stanley' occurs twice as a grandparent and twice as a great-great-grandparent. 'Jersey', 'Pioneer', and 394Y are also common ancestors.

'Sunrise'—The second most inbred cultivar. 'Earliblue' occurs three times as a great-grandparent. 'Stanley' occurs three times as a great-great-grandparent and once as a great-great-great-grandparent. 'North Sedgwick' lowbush, 'Coville', and 'Weymouth' are also common ancestors.

'Georgiagem'—'Bluecrop' occurs twice as a grandparent, and 'Stanley' occurs twice as a great-great-grandparent.

'Sierra'—One parent is a self of US 79, a pentaploid *V. darrowi* x (*V. ashei* x *V. constablaei*) clone.

The coefficients of inbreeding, especially those of 'Duke' (0.0568) and 'Sunrise' (0.0385), are significant considering the severe effects of inbreeding depression encountered on selfing older cultivars (Hellman and

Table 2. Mean percentage of wild blueberry (*Vaccinium* sp.) selections found in cultivars resulting from hybridizations in three decades.

Wild selection	Mean percentage in decade		
	1961–70	1971–80	1981–90
Ashworth	6.3	0.0	0.0
Brooks	17.2	18.7	14.1
Chatsworth	4.1	6.3	3.1
Carter	0.0	0.3	0.0
Crabbe 4	2.3	2.8	0.0
Grover	3.1	4.4	3.1
Harding	1.8	0.0	0.0
Hildebrand	0.8	0.0	0.0
Michigan lowbush #1	3.9	2.8	0.0
North Sedgwick	0.4	1.4	0.0
Sooy	12.2	10.8	8.6
Rubel	22.9	25.9	18.8
Russell	2.7	3.7	2.4
<i>V. angustifolium</i>			
(clone unspecified)	3.1	0.0	0.0
<i>V. ashei</i>	4.5	1.8	15.0
<i>V. constablaei</i>	0.0	0.0	15.0
<i>V. darrowi</i>	4.0	17.4	20.0
<i>V. tenellum</i>	0.1	0.3	0.0
Unknown	10.7	0.7	0.0
No. cultivars	13	12	1

Moore, 1983; Morrow, 1943; White and Clark, 1932). By comparison, selfing and sib-mating tetraploid parents (with F = 0) results in inbreeding coefficients of 0.1667 and 0.0208, respectively.

Several important conclusions can be drawn from these results:

- 1) Crosses resulting in high inbreeding coefficients are not necessarily detrimental, especially if the inbreeding is indirect

and not the result of selfing.

- 2) Having one parent that is the product of selfing may not be detrimental if the cross itself has sufficient diversity (i.e., 'Sierra').

- 3) Inbreeding can accumulate genes of horticultural value and may decrease levels of lethal or sublethal genes. This seems to be the case with 'Duke', which is high yielding, early, and self-fruitful.

4) Inbreeding coefficients calculated for tetraploids are less meaningful than those for diploids. Pollen of tetraploids has more opportunities to transmit homozygosity because it is 2x; however, this transmission of homozygosity may be limited by the advantage heterozygous gametes have in pollen tube growth. This advantage has been demonstrated in potato (*Solanum tuberosum* L.), where the heterozygous 2n pollen formed by first-division restitution mechanisms grows more vigorously than that formed by second-division restitution mechanisms (Simon and Peloquin, 1976). If this competitive advantage is also the case in blueberry, it is likely that the true inbreeding levels are less than predicted values and much of the selection within breeding programs chooses these more heterozygous plants.

Inbreeding coefficients are probability statistics useful in predicting the performance of progeny families; but often, they are less useful when applied to individuals because the individual's precise genotype is generally unknown. Inbreeding coefficients, as applied to breeding populations, also may have only limited utility. Loiselle et al. (1989) found no correlations in potato between inbreeding coefficients and the proportion of progeny selected at various evaluation phases. Because potato is a tetraploid crop, it is subject to the same considerations listed previously for blueberry and, thus, may have factors counteracting much of its apparent inbreeding. It can be extrapolated that the higher inbreeding coefficients observed in blueberry cultivars from recent decades are of no detriment per se and that actual levels of inbreeding are limited by the nature of the breeding and selection process itself.

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Table 3. Tetrasomic inbreeding coefficients of blueberry cultivars released by public agencies.

Cultivar	Origin ^z	Source or decade of hybridization ^y	F
Adams	USDA	WHS	0
Brooks	USDA	WHS	0
Carter	USDA	WHS	0
Chatsworth	USDA	WHS	0
Dunfee	USDA	WHS	0
Grover	USDA	WHS	0
Harding	USDA	WHS	0
Rubel	USDA	WHS	0
Russell	USDA	WLS	0
Sam	USDA	WHS	0
Sooy	USDA	WHS	0
Taylor	Michigan AES	WHS	0
Cabot	USDA	1910	0
Catawba	USDA	1910	0.0208
Concord	USDA	1910	0
Greenfield	USDA	1910	0
Jersey	USDA	1910	0
June	USDA	1910	0
Katherine	USDA	1910	0
Pioneer	USDA	1910	0
Rancocas	USDA	1910	0
Redskin	USDA	1910	0.0208
Scammell	USDA	1910	0
Wareham	USDA	1910	0
Atlantic	USDA	1920	0
Burlington	USDA	1920	0
Coville	USDA/New Jersey AES	1920	0.0039
Dixi	USDA	1920	0.0039
Keweenaw	Michigan AES	1920	0
Pemberton	USDA	1920	0
Stanley	USDA	1920	0
Weymouth	USDA	1920	0.0026
Angola	USDA/North Carolina AES	1930	0.0013
Berkeley	USDA/New Jersey AES	1930	0.0039
Bluecrop	USDA/New Jersey AES	1930	0.0034
Blueray	USDA/New Jersey AES	1930	0.0034
Collins	USDA/New Jersey AES	1930	0.0039
Croatan	USDA/North Carolina AES	1930	0.0013
Herbert	USDA/New Jersey AES	1930	0.0039
Ivanhoe	USDA	1930	0.0028
Murphy	USDA/North Carolina AES	1930	0.0013
Wolcott	USDA/North Carolina AES	1930	0.0013
Bluehaven ^x	Michigan AES	1940	0.0014
Bluetta	USDA/New Jersey AES	1940	0.0034
Darrow	USDA/New Jersey AES	1940	0.0032
Earliblue	USDA/New Jersey AES	1940	0.0032
Elizabeth	NJBC ^w	1940	0.0033
Elliott	USDA	1940	0.0059
Harrison	USDA/North Carolina AES	1940	0.0023
Lateblue	USDA/New Jersey AES	1940	0.0224
Morrow	USDA/North Carolina AES	1940	0.0002
Northland	Michigan AES	1940	0.0014
Bluejay	Michigan AES	1950	0.0046
Meador	New Hampshire AES	1950	0.0016
Patriot	USDA/Maine AES	1950	0.0043
Spartan	USDA	1950	0.0016
Avonblue ^x	Florida AES	1960	0.0083
Bluechip	USDA/North Carolina AES	1960	0.0023
Bluegold	USDA/New Jersey AES	1960	0.0055
Bounty	USDA/North Carolina AES	1960	0.0052
Chandler	USDA	1960	0.0035
Flordablue	Florida AES	1960	0.0208
Nelson	USDA/New Jersey AES	1960	0.0029
Northblue	Minnesota AES	1960	0.0004
Northcountry	Minnesota AES	1960	3 × 10 ⁻⁵
Northsky	Minnesota AES	1960	3 × 10 ⁻⁵
Sharpblue	Florida AES	1960	0.0052 ^w
St. Cloud	Minnesota AES	1960	0.0004
Toro	USDA/New Jersey AES	1960	0.0118
Bladen	North Carolina AES	1970	0.0007
Blue Ridge	USDA/North Carolina AES	1970	0.0010
Cape Fear	USDA/North Carolina AES	1970	0.0010
Cooper	USDA	1970	0.0018
Duke	USDA/New Jersey AES	1970	0.0568

Continued on next page

Table 3. Continued.

Cultivar	Origin ^z	Source or decade of hybridization ^y	F
Georgiagem	USDA/Georgia AES	1970	0.0109
Gulfcoast	USDA	1970	0.0018
Legacy	USDA/New Jersey AES	1970	0.0016
Marimba ^v	Florida AES	1970	---
Misty	Florida AES	1970	0.0027
O'Neal	USDA/North Carolina AES	1970	0.0018
Reveille	North Carolina AES	1970	0.0007
Sunrise	USDA/New Jersey AES	1970	0.0385
Sierra	USDA/New Jersey AES	1980	0.0281

^zUSDA = U.S. Dept. of Agriculture; AES = Agricultural Expt. Station; NJBC = New Jersey Blueberry Council.

^yWHS = Wild highbush selection; WLS = wild lowbush (*V. angustifolium*) selection.

^xUnknown ancestor, F value taken as 0.

^wCoefficient value for either possible pedigree.

^vPedigree unknown.

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Table 4. Mean inbreeding coefficients of blueberry cultivars resulting from hybridizations in different decades.

Decade of hybridization	No. cultivars	Mean inbreeding coefficient
<1921	24	0.0017
1921–30	9	0.0013
1931–40	10	0.0026
1941–50	10	0.0047
1951–60	4	0.0030
1961–70	13	0.0045
1971–80	12	0.0099
1981–90	1	0.0281

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