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Inbreeding Among Muscadine Cultivars

Haley N. Williams[1,2], Eric T. Stafne[1], and Patrick J. Conner[3]

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Abstract

Pedigrees were used to identify inbreeding among named muscadine (*Vitis rotundifolia* Michx., syn. *Muscadinia rotundifolia* (Michx.) Small) cultivars for the purpose of improving decision making by breeding programs. Public muscadine breeding programs in the United States operate in hopes to improve the quality of muscadine grapes and expand their consumption. Major quality goals of muscadine breeding programs are to achieve more productive, bigger berry, self-fertile cultivars with more sugar content. While the hybridization of bunch grape (*Vitis* sp.) and muscadine germplasm has the potential to reduce inbreeding, most current muscadine cultivars are based on a narrow genetic background. We examined 153 muscadine cultivars and selections to determine their parentage and then subjected the reported parentage of every cultivar to statistical analysis to identify inbreeding coefficients for each cultivar. This list was compiled by examining sources dating as far back as 1909. Inbreeding coefficients ranged from 0 to 0.369, higher than what was previously found in other studies. Inbreeding coefficients of 57 out of 153 cultivars were greater than 0, with 'Redgate', 'Tara', 'Scarlett', and 'African Queen' having the highest coefficients of inbreeding. Newer released cultivars showed higher inbreeding coefficients than older releases. While many cultivars with higher inbreeding coefficients have been commercially successful, breeders should be cautious of using germplasm with high levels of inbreeding when considering new crosses in a muscadine breeding program.

Muscadine grapes (*Vitis rotundifolia* Michx., syn. *Muscadinia rotundifolia* (Michx.) Small) native to the southeastern United States, were first reported by English colonists in 1584 when landing on Roanoke Island, North Carolina. This was the first U.S. native grape to be brought into cultivation, and due to the many vines growing along the Scuppernong River, a bronze-fruited variety was named 'Scuppernong' by Dr. Calvin Jones in 1810. Afterward, many more vines with desirable qualities were discovered in the southeast and named prior to the start of breeding programs in the late 1800s and early 1900s (Lane, 1997; Onokpise, 1988; Schwartz, 1976; Stuckey, 1919). These programs began in hopes to improve muscadine grapes by producing improved male vines and self-fertile cultivars, achieving greater yields, better berry adherence, higher sugar and lower acid content, thinner berry skin, and more uniform ripening, increasing fruit cluster size, and decreasing seed size (Dearing, 1917; Lane, 1997; Riaz et al., 2008; Schwartz, 1976; Stuckey, 1919).

Inbreeding is a consequence of continued crosses among similar individuals. The breeding of individuals that are closely related increases the uniformity among progenies (Lesley, 1957; Noiton and Alspach, 1996); however, inbreeding also increases the likelihood of passing along deleterious recessive genes, which could negatively affect the vigor, yield, and size of fruit (Dale et al., 1993; Fejer and Spangelo, 1974). Therefore, understanding the level of inbreeding within muscadine cultivars is important to reduce any negative attributes that could potentially build up.

One long term goal of breeding programs was to develop *Muscadinia* (muscadines) and *Euvitis* (bunch grapes; *Vitis vinifera* and oth-

[1] Mississippi State University, MAFES South Mississippi Branch Experiment Station, Coastal Research and Extension Center, 711 W. North St., Poplarville, MS 39470
[2] Corresponding author hnw111@msstate.edu
[3] University of Georgia-Tifton Campus, 2360 Rainwater Road, Tifton, GA 31793

er *Vitis* sp.) hybrids to combine the resistance and adaptability of *Muscadinia* with the fruit quality of *Euvitis* (Anderson, 2006; Bouquet, 1980; Conner, 2006; Dearing, 1917; Einset and Pratt, 1975; Goldy, 1987; Goldy et al., 1988; Lane, 1978, 1997; Mortensen, 1971; Munson, 1909; Olien, 1990; Olien and Hegwood, 1990; Olmo, 1986; Riaz et al., 2008; Schwartz, 1976). These hybrids would also increase the genetic diversity among cultivars and potentially decrease inbreeding; however, most of these efforts have not led to successful cultivar releases, with notable exceptions, such as 'Southern Home', 'RazzMatazz', and 'Oh My!' (Bloodworth, 2014; Mortensen et al., 1994).

While studies on coefficients of coancestry and inbreeding and molecular analysis have been done (Cao et al., 2020; Onokpise, 1988; Qu et al., 1996; Riaz et al., 2008), they have focused on a limited number of cultivars. The purpose of this study was to use published muscadine pedigrees to determine the level of inbreeding among a broader set of established muscadine cultivars.

Materials and Methods

Muscadine cultivars and parentage (Tables 1, 2) were sourced through publications dating from 1909 to 2020 (Anderson, 2006; Brooks and Olmo, 1997; Cao et al., 2020; Conner, 2006, 2009, 2013, 2014, 2020; Dearing, 1917, 1947; Fry, 1967; Goldy, 1987; Gray et al., 2009; Lane, 1997; Mortensen, 1971, 2001; Mortensen et al., 1994; Munson, 1909; Murphy et al., 1938; Onokpise, 1988; Qu et al., 1996; Riaz et al., 2008; Schwartz, 1976; Stafne et al., 2015; Stuckey, 1919). Where possible, cultivar names and parentage were also checked in the Vitis International Variety Catalogue (Maul et al., 2020).

The data analyzed are based on reported

Table 1. Muscadine cultivars that do not exhibit inbreeding based on examination of common parentage.

Cultivar	Female	Male	Year[z]	Cultivar	Female	Male	Year
Babson	Unknown	Unknown	Unknown	Fox	Unknown	Unknown	Unknown
Barret Mn-1	Unknown	Unknown	Unknown	Georgia Red	GA42-28	GA46-32	1977
Beula	Unknown	Unknown	1870	Hope	Unknown	Unknown	1917
Big Red	Unknown	Unknown	Unknown	Hopkins	Unknown	Unknown	1845
Black Beauty	Fry	GA12-12-1	1991	Howard	Scuppernong	Black Male	1929
Brown	Unknown	Unknown	Unknown	Hunt	Flowers	White Male	1919
Brownie	Sanmonta	Unknown	1933	Irene	Thomas	Black Male	1919
Burgaw	Thomas	V19R7B2	1946	James	Unknown	Unknown	1866
Carolina Belle	Unknown	Unknown	1880	Jeter	Unknown	Unknown	Unknown
Chowan	Creswell	Burgaw	1962	Jones Perfumed	Unknown	Unknown	Unknown
Clarke	Unknown	Unknown	1930	Kilgore	Labama	Unknown	1946
Clayton	Unknown	Unknown	Unknown	Labama	Unknown	Unknown	Unknown
Creek	Sanmonta	Unknown	1938	Lady James	Unknown	Unknown	1885
Creswell	Unknown	Unknown	1946	La Salle	Scuppernong	Post Oak	1891
Dallas	Unknown	Unknown	1953	Latham	Unknown	Unknown	1855
Darlene	GA5-11-3	Carlos	1988	Lucida	Irene	White Male	1933
Dawn	Scuppernong	Black Male	1938	Luola	Unknown	Unknown	1890
Dearing	Luola	Burgaw	1957	Magnolia	Scuppernong x (Thomas x Hope)	Topsail x Tarheel	1962
De Soto	Scuppernong	*V. munsoniana*	Unknown	Marsh	Unknown	Unknown	Unknown
Dixie Red	GA44-6	GA44-7	1976	Memory	Unknown	Unknown	1868
Dulcet	Irene	White Male	1934	Mish	Unknown	Unknown	1846
Duplin	Stanford	V10R15B4	1946	Morrison	Scuppernong	NCAF7082	1946
Early Fry	Sweet Jenny	Ison	1993	Nevermiss	Unknown	Unknown	1945
Eden	Unknown	Unknown	Unknown	New River	San Jacinto	Unknown	1946
Excel	Sugargate	Unknown	1983	New Smyrna	Unknown	Unknown	Unknown
Farrer	Sugargate	Unknown	1983	Noble	Thomas	Tarheel	1974
Flowers	Unknown	Unknown	1816	November	Scuppernong	Black Male	1920
Flowers Improved	Unknown	Unknown	1869				

Cultivar	Female	Male	Year
Oh My!	Unknown	Unknown	2014
Onslow	V22R5B4	Burgaw	1946
Orton	Latham	Burgaw	1946
Pam	GA5-11-3	Senoia	1988
Pamlico 1871	Unknown	Unknown	Unknown
Pee Dee	Unknown	Unknown	1859
Pender	Latham	V20R36B4	1946
Pink Hunt	Unknown	Unknown	Unknown
Qualitas	Thomas	Black Male	1920
RazzMatazz	JB94-38-7-44	JB98-13-1-10	2013
Rich	Unknown	Unknown	Unknown
Roanoke	Lucida	Topsail x Tarheel	1962
Sanalba	San Jacinto	Brilliant	1898
San Jacinto	Scuppernong	*V. aestivalis*	1891
Sanmelaska	San Jacinto	Brilliant	1898
Sanrubra	San Jacinto	Brilliant	1898
Scott	Unknown	Unknown	1930
Scott's Imperial	Unknown	Unknown	1930
Scuppernong	Unknown	Unknown	1810
Seedlin	Unknown	Unknown	Unknown
Sloe	Unknown	Unknown	Unknown
Smith	Unknown	Unknown	1890
Spalding	Flowers	White Male	1920
Stanford	San Jacinto	Unknown	1946
Stuckey	Scuppernong	Black Male	1920
Sugar	Unknown	Unknown	1870
Sugar Grape	Unknown	Unknown	Unknown
Sugar Pop	Fry	8_16_1	1988
Sweet Jenny	GA11-2-2	GA12-12-1	1986
Tarheel	Luola	V68R14B4	1946
Tenderpulp	Unknown	Unknown	1868
Tennessee Island	Unknown	Unknown	Unknown
Thomas	Unknown	Unknown	1845
Thornhill	Unknown	Unknown	Unknown
Topsail	Latham	Burgaw	1946
Trayshed	Unknown	Unknown	Unknown
Wallace	V26R5B4	Willard	1946
Watergate	GA2-3-1	GA19-6-1	1974
Welder	Dearing	Unknown	1972
Westbrook	Unknown	Unknown	Unknown
Woodard	Unknown	Unknown	Unknown

[z] Year = date of release or selection from the wild.

parentage of cultivars and not on recent reports using molecular fingerprinting techniques (Cao et al., 2020; Riaz et al., 2008) that contradict the reported parentage. While we understand that reported parentages may not always be correct, new reports may also be disputed or unconfirmed. Even though these new reports have determined that some reported pedigrees are incorrect, they cannot confirm the actual parentages. Cultivars with unknown parentage were assumed to be non-inbred. Wild muscadine grape vines are male or female, so we can assume cross-pollination took place when cultivars were selected from the wild. We assumed open-pollinated cultivars would have been cross-pollinated as well, since most came from female grapes. These assumptions lessen the level of possible inbreeding. To express the degree of inbreeding among cultivars, the parentage of cultivars was analyzed to determine the inbreeding coefficients of individual cultivars, which are obtained by a summation of coefficients for every line of descent by which parent cultivars are connected. The scale of inbreeding coefficients runs from 0 to 1 (Wright, 1922). Inbreeding coefficients were generated using the INBREED procedure in SAS (version 9.4; SAS Institute, Cary, NC). A constellation plot from inbreeding coefficients was created in JMP (version 12; SAS Institute, Cary, NC), based on Ward's minimum variance method, to visualize the coefficient relationships. Correlations were estimated by restricted maximum likelihood (REML) using the Multivariate procedure and correlation probability was tested by Pearson's correlation coefficient.

Results and Discussion

The inbreeding coefficients of individual cultivars range from 0 to 0.369 and are dependent on the amount of common ancestry of parents. There are 96 cultivars that appear to have no level of inbreeding (Table 1). The reason many of these have inbreeding coefficients of 0 is that most of their parentage is unknown. Examples of cultivars with unknown pedigree are: 'Black Beauty', 'Darlene', 'Early Fry', 'Pam', 'Sweet Jenny', and 'Watergate'. All of these cultivars were released and patented by Ison's Nursery in collaboration with retired University of Georgia (UGA) muscadine breeder, B.O. Fry, and have UGA selections in their pedigrees. Unfortunately, due to poor record keeping the pedigrees of these selections are unknown (P. Conner, UGA, personal communication 2021). However, these cultivars were developed using the same germplasm used in developing UGA-released cultivars and so likely have similar levels of inbreeding. The remaining cultivars in Table 1 represent either cultivars selected directly from the wild or their immediate progeny with likely low levels of inbreeding.

Of the 153 named cultivars, 57 have coefficients greater than 0 (Table 2), indicating some level of inbreeding. Onokpise (1988) indicated that inbreeding depression in muscadine was not yet a concern due to the low inbreeding coefficients found among 12 commonly grown cultivars, ranging from 0 to 0.06. Our results indicate that the inbreeding coefficients of these 12 cultivars are higher, likely due to our list being more comprehensive and including several subsequently released cultivars with elevated levels of inbreeding.

Of the cultivars exhibiting inbreeding depression, twenty-six percent (15) had inbreeding coefficients greater than or equal to 0.25. These cultivars, in order from lowest to highest, include 'Albemarle', 'Magoon', 'Floriana', 'Supreme', 'Higgins', 'Late Fry', 'Lane', 'Majesty', 'Paulk', 'Ruby Crisp', 'Hall', 'African Queen', 'Scarlett', 'Tara', and 'Redgate' (Table 2). All were released since 1955, with most being released since 1988 (Conner, 2006, 2009, 2013, 2014; Goldy, 1987; Lane, 1997; Onokpise, 1988; Schwartz, 1976; Stafne et al., 2015), indicating that inbreeding coefficients correlate with year of release (r=0.327, P=0.015) and that inbreeding is increasing with newer cultivars. Most of the inbred cultivars were self-fertile (40 out of 57), but the mean inbreeding coefficient did not differ between self-fertile and pistillate groups (data not shown).

In these more inbred cultivars, commonly used parents include: 'Supreme', 'Tara', 'Triumph', 'Burgaw', 'Fry', and 'Summit' (Table 2). Although, 'Burgaw' may not actually be a parent of 'Magoon', as was previously reported (Brooks and Olmo, 1997; Cao et al., 2020). Several of these commonly used parents are important fresh-market cultivars with large berry size and good flavor (Mortensen, 2001), so it makes sense for breeders to make crosses using what cultivars are more easily available and have desirable traits that lend themselves to creating useful progeny populations (Onokpise, 1988).

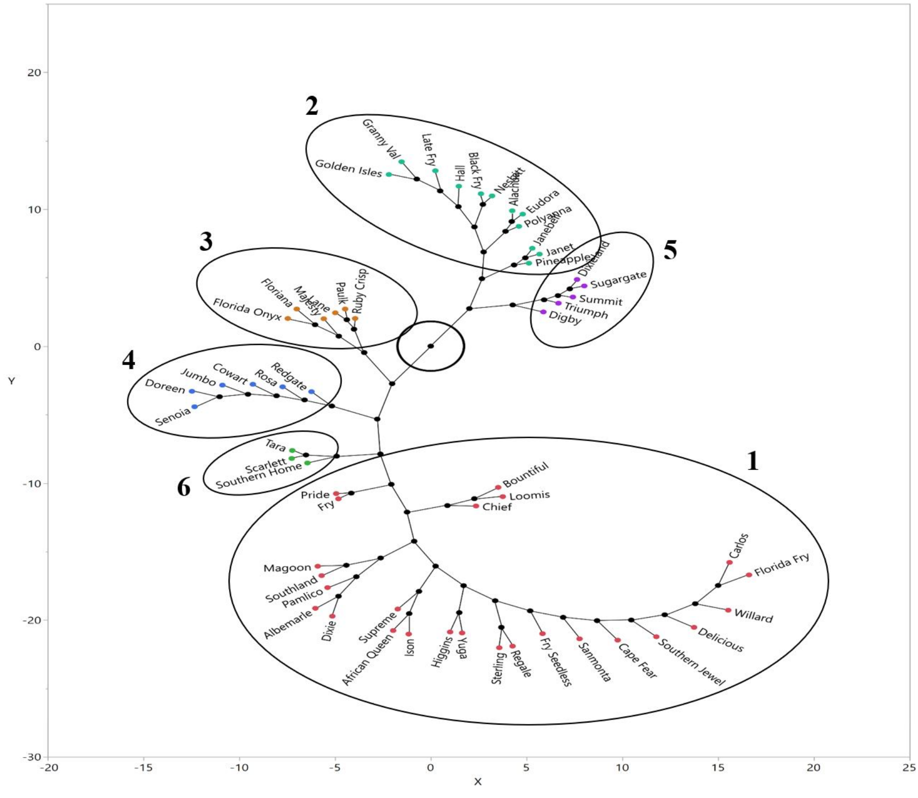
'Summit', 'Triumph', 'Dixieland', and 'Sugargate' are all full-sibs resulting from the same cross: 'Fry' x GA 29-49 (Conner, 2006, 2013, 2014). Crosses among these four full-sib cultivars resulted in high inbreeding coefficients for 'African Queen', 'Scarlett', and 'Tara' (Table 2). However, Cao et al. (2020) found that 'Triumph' may not actually be a parent of 'Scarlett', as was previously reported by Brooks and Olmo (1997).

'Redgate', which was selected from the cross 'Higgins' x GA 29-49, had the highest inbreeding coefficient of 0.369. GA 29-49 was selected from the cross 'Higgins' x GA 1, and thus appears on both sides of the 'Redgate' pedigree. 'Higgins', believed to be a source of large berry size and red bronze color, was used extensively in the UGA breeding program (Fry, 1967; Lane, 1997). It has an elevated inbreeding coefficient of 0.281, and further breeding with it led to a higher level of inbreeding in 'Redgate'. 'Redgate' is not considered a competitive cultivar (Mortensen, 2001). It has medium berry size, moderately uneven ripening, and heavy yields but poor fruit quality (Basiouny, 2001; Leong, 2001; Mortensen, 2001), which may or may not have relation to its elevated level of inbreeding.

The constellation plot consists of the 57 cultivars that appear to have some level of inbreeding and can be divided into six different groups (Fig. 1). Group 1 is the largest, made up of 25 cultivars, most of which originated either from the United States Department of Agriculture (USDA) or North Carolina State University. Group 2 consists of 12 cultivars, with over half originating from Georgia, especially from Ison's Nursery. Group 3 contains six cultivars, with three originating from UGA and three originating from Florida A&M University. Group 4 has six cultivars, with over half originating from Ison's Nursery and UGA. Group 5 has five cultivars, with four of five originating from UGA and one from Ison's Nursery. Group 6 consists of only three cultivars, with two originating from UGA and one from University of Florida (Stafne et al., 2015). Based on this analysis, it is evident that most inbred cultivars originated from only a few sources, and especially from Georgia, where a major goal of breeding has been to achieve large, high-quality fruit.

Despite the differences in chromosome number and little success in the past (Dearing, 1917; Goldy, 1987; Mortensen, 1971; Olien, 1990; Olien and Hegwood, 1990; Qu et al., 1996; Riaz et al., 2008; Stafne et

Figure 1. Constellation plot based on the 57 named muscadine cultivars with inbreeding coefficients greater than 0 (Table 2). The plot illustrates the similarity between the cultivars, with those most similar being closer together and with the same color point and group number. The axis scaling, orientation of points, and angles of the lines on the plot are arbitrary with no assigned unit.



al., 2015), some successful crosses between *Muscadinia* and *Euvitis* have been made. 'Sanmonta', a Munson hybrid, was reported to be a cross between *V. rotundifolia* and *Euvitis* (Schwartz, 1976). Others report that it was a cross between *V. rotundifolia* and *V. munsoniana* (another species within *Muscadinia*) (Lane, 1997; Stuckey, 1919). Later reports indicate 'Sanmonta' may only be *V. rotundifolia* (Schwartz, 1976). The first successful *Muscadinia* x *Euvitis* hybrid that was released was 'Southern Home' and comes from the cross 'Summit' x P. 9-15. It is resistant to several diseases and has an attractive leaf shape, but the berries and yields are small, making it better suited as an ornamental cultivar (Conner, 2006; Mortensen et al., 1994). It has a low inbreeding coefficient of 0.0137 (Table 2). Another recent hybrid was 'RazzMatazz', released in 2013 (Bloodworth, 2014; Stafne et al., 2015). It does not exhibit any level of inbreeding in our analysis (Table 1). 'Oh My!', also released by Bloodworth (2014), is reported to have *Euvitis* parentage; although, the names of the cultivars used to make this cross have not been released.

Conclusion

While the parentage of many muscadine cultivars is still unclear (Cao et al., 2020; Riaz et al., 2008), thirty-seven percent of the named cultivars examined exhibited some level of inbreeding. Even though Conner (2006) stated that muscadines appear to be tolerant of inbreeding, high levels of inbreeding within a crop species can lead to reduced vigor, yield, and fruit size (Dale et al., 1993; Fejer and Spangelo, 1974), and it is pos-

Table 2. Muscadine cultivars with inbreeding coefficients greater than 0, along with reported parents year of release.

Cultivar	Female	Male	F[z]	Year[y]	Cultivar	Female	Male	F	Year
Bountiful	Creek	Topsail seedling	0.0039	1967	Summit	Fry	GA29-49	0.135	1977
Loomis	Creek	USDA15	0.0039	1989	Triumph	Fry	GA29-49	0.135	1977
Chief	Creek	Topsail sibling	0.0078	1967	Sterling	NC50-55	Magnolia	0.141	1981
Carlos	Howard	NC11-173	0.0156	1971	Rosa	Higgins	Granny Val	0.145	1988
Southern Home	Summit	P9-15	0.0156	1994	Janebell	Fry	Senoia	0.146	1988
Dixie	Topsail	NC28-193	0.0410	1976	Janet	Fry	Senoia	0.146	1988
Golden Isles	Fry	GA19-6	0.0459	1987	Pineapple	Fry	Senoia	0.146	1988
Florida Fry	Triumph	AD3-42	0.0460	1987	Fry Seedless	Farrer	Redgate	0.160	1990
Fry	GA19-13	USDA19-11	0.0586	1971	Florida Onyx	Supreme	Black Beauty	0.173	2020
Pride	GA19-13	USDA19-11	0.0586	1972	Ison	Sugargate	Senoia	0.183	1986
Alachua	Fry	Southland	0.0596	1990	Black Fry	Fry	Cowart	0.186	1986
Eudora	Fry	Southland	0.0596	2007	Nesbitt	Fry	Cowart	0.186	1971
Polyanna	Fry	Southland	0.0596	1998	Digby	Jumbo	GA29-49	0.221	Unknown
Senoia	Higgins	Carlos	0.0615	Unknown	Albemarle	Topsail	Burgaw	0.250	1962
Regale	Hunt	Magnolia	0.0625	1982	Magoon	Thomas	Burgaw	0.250	1959
Southland	Thomas	Topsail seedling	0.0625	1967	Floriana	Supreme	Pineapple	0.265	2020
Willard	Stanford	V19R7B2	0.0625	1946	Supreme	Black Fry	Dixieland	0.269	1988
Yuga	Sanmonta	White Male	0.0625	1934	Higgins	Yuga	White Male	0.281	1955
Granny Val	Fry	Carlos	0.0635	1983	Late Fry	Fry	Granny Val	0.296	1993
Doreen	Higgins	Dixie	0.0747	1982	Lane	Supreme	Tara	0.303	2012
Pamlico	Lucida	Burgaw	0.0938	1962	Majesty	Supreme	Triumph	0.303	2009
Jumbo	Higgins	USDA19-11	0.111	1971	Paulk	Supreme	Tara	0.303	2017
Delicious	AA10-40	Polyanna	0.114	2009	Ruby Crisp	Supreme	Tara	0.303	2020
Southern Jewel	Granny Val	DB3-63	0.120	2009	Hall	Fry	Tara	0.332	2014
Cape Fear	Burgaw	V20R36B4	0.125	1946	African Queen	Sugargate	Dixieland	0.337	1988
Cowart	Higgins	GA28	0.125	1968	Scarlett	Summit	Triumph	0.337	1998
Sanmonta	San Jacinto	Herbemont	0.125	1898	Tara	Summit	Triumph	0.337	1993
Dixieland	Fry	GA29-49	0.135	1976	Redgate	Higgins	GA29-49	0.369	1974
Sugargate	Fry	GA29-49	0.135	1974					

[z] F = inbreeding coefficients for individual cultivars.
[y] Year = date of release or selection from the wild.

sible that these effects are now being seen in muscadines. With the increasing levels of inbreeding in newer cultivar releases, poor fruit quality seen in 'Redgate', and recent not yet reported findings of reduced vigor in other inbred cultivars, breeders should be careful if using cultivars with high inbreeding coefficients when developing new crosses. Breeders may instead consider incorporating more bunch grape or old, wild muscadine germplasm in new crossings to reduce inbreeding (Cao et al., 2020), but should be wary of linkage drag when using wild material. By actively avoiding inbreeding lines in muscadine breeding efforts today, muscadine cultivars with lower probability of wide-ranging defects can be achieved in the future.

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About the cover: Cocoa (*Theobroma cacao* L.) pod ready for harvest. Cacoa is an important economic crop. Archaeological evidence suggests the center of origin is in the upper amazon region of northwest South America where cacoa was used 5,300 years ago. In 2017 world production was 5.2 million tonnes and major cocoa bean producing countries include Côte d'lvoire, Ghana, and Ecuador. The cocoa bean is the main ingredient in chocolate and the global chocolate industry is worth more about $100 billion. Photo courtesy of Richard Campbell.