

Rutgers Cranberry Breeding Program

NICHOLI VORSA¹

Additional index words: cranberry breeding, genetics, disease resistance, molecular markers, mapping, QTLs

ABSTRACT

The American cranberry (*Vaccinium macrocarpon* Aiton) is an American fruit species native to northeastern US and southeastern Canada. The United States is a leader in cranberry production. Domesticated less than 200 years ago, breeding efforts did not start until 1929. The American cranberry is a long-lived woody perennial adapted to a temperate climate and well drained moist acidic soils. Cranberry reproduces both sexually and asexually, through stolons, which are used for clonal asexual propagation of cultivars. The flower is hermaphroditic, which needs to be pollinated, usually by hymenoptera pollinators for fruit set. Traits of economic importance include productivity, propagation vigor, disease resistance, fruit anthocyanins, brix, and increasingly fruit quality traits for sweetened-dried-cranberry products, e.g., fruit firmness and fruit size. Rutgers/NJAES has patented and released seven cultivars from a second breeding and selection cycle. The cultivars 'Crimson Queen' and 'Demoranville', selected and released for the juice market, were released for early season, high fruit color and improved productivity. 'Mullica Queen' is a mid-season cultivar with exceptional productivity. The cultivar 'Welker' is highly productive with precocious fruit bearing but is more predisposed to fruit rot, thus is recommended for growing regions with little to no fruit rot pressure, e.g. as in the oceanic climate of the Pacific Northwest. The 'Haines' cultivar is noted for high productivity, uniform color, firmness and has exhibited less fruit rot in variety trials than standard varieties, e.g., 'Stevens'. 'Vasanna', a full-sibling of 'Haines', has performed exceptionally well in 100 per cent peat soils of British Columbia. Quantitative trait loci (QTL) have been identified for productivity, berry size, total fruit anthocyanins measured as mg per 100 grams of fruit, fruit rot resistance and other traits. The fruit of American cranberry is recognized for human health benefits due to very high levels of the flavonoid classes, anthocyanins, proanthocyanidins, and flavonols, which result in a very high anti-oxidant status. Recent restrictions of traditional pesticides to control insect and disease pests have altered the ecology with former challenges, e.g., false-blossom, having a re-emergence. Genetic improvement of cranberry has been hampered by a long generation interval including three years from pollination to flower, and assessment of yield requiring 6-8 years after field planting, with typically limited field acreage for breeding.

Taxonomy

Vaccinium macrocarpon Aiton (Ericaceae) is a self-fertile diploid ($2n=2=24$) member of the *Ericaceae* (Heath family) genus *Vaccinium* section *Oxycoccus* (Hill) Koch meaning 'sour berry'. Vander Kloet (1983) treatment of the section recognized only one other species, *V. oxycoccus* L., the small-fruited cranberry. The two species are differentiated on predominantly size-related morphological characters, including leaf length, leaf shape, pedicel bract length, and pedicel bract shape. Both taxa are sympatric and syntopic over much of the distribution of *V. macrocarpon*. Although diploids exist in both taxa, *V. oxycoccus* also occurs at tetraploid and hexaploid levels (Vander Kloet 1983). The taxa

are reproductively isolated by differences in flowering phenology, with *V. oxycoccus* flowering earlier than *V. macrocarpon*, and also by ploidy difference in some cases. *V. macrocarpon* has been considered the more primitive of the two (Camp 1944). However, Mahy et al. (2000) found diploid *V. oxycoccus* to have significantly higher genetic diversity than *V. macrocarpon*, suggesting *V. oxycoccus* as being the more primitive form. *V. oxycoccus* by *V. macrocarpon* hybrids are fertile (Vorsa and Polashock, 2005).

Endemic to temperate eastern North America, the large cranberry's natural distribution spans from Newfoundland, throughout the Great Lakes region to Minnesota, and south along the Appalachian Mountains to

¹ Blueberry and Cranberry Research and Extension Center, Rutgers University Chatsworth, New Jersey, USA

North Carolina and Tennessee. However, the east coast distribution largely ending in south New Jersey. It is restricted to acidic soils (< 5.5 pH) and peat of open bogs, swamps, wet shores and headlands (Vander Kloet 1983) and stream banks. Native stands are typically near bodies of water, lakes, streams and rivers, or wetlands with high water levels during winter dormancy. Native stands typically have high water tables with high levels of organic matter, which are typically found in bogs, marshes and swamps.

American cranberry is an evergreen woody perennial, having a trailing stoloniferous vine. Flowers are typically borne on indeterminate ascending vertical stems referred to colloquially as 'uprights', which arise from stolons, referred to as 'runners'. Inflorescence buds, having 5-7 florets, are formed in late summer and early fall mostly at the apex of the vertical stems, uprights, with upward facing adaxial leaf surfaces. For the subsequent year's crop, in regions having moderate to severe winter freezes, e.g., Wisconsin, New Jersey and Massachusetts, inflorescence buds and leaf tissues are typically protected with a 'winter flood', that can span from December to April. Spring growth typically initiates in mid to late April, with flowering initiating in mid to late June and terminating by mid-July. For fruit set, cranberry requires insect pollination which occurs with mostly hymenopteran (bees) insects. Growers typically provide honey-bee colonies to enhance pollination. The requirement of an acidic media or soil (maximum pH 5.5) limits the American cranberry's adaptation. Having a fine root system lacking root hairs, best suited soils are sands, loamy sands, and organic soils consisting of coarse peat or muck. Cranberry, being a temperate woody perennial, for normal growth and flowering in spring, requires a minimum of 800-1000 hours of winter-chilling (~ 0 – 10 °C) to fulfill winter dormancy requirement. Flowers are 4-merous, perfect, having 8 anthers with an inferior four-locule ovary (> 20 ovules). Flowers are protandrous, pollen

shed before the style becoming receptive, with the style 6-7mm in length at anthesis inside the anther whorl, then elongating to 8-10mm, extending 2-3mm beyond the anther whorl 2-3 days post anthesis. The stigma appears most receptive 3-5 days after anthesis, producing an exudate. Characteristic of *Ericaceae* species, pollen is shed as a tetrad with the four pollen grains of a meiotic event held in a tetrahedral formation. All four pollen grains of the tetrad are potentially viable. Anthers of one cranberry flower shed over 7000 pollen tetrads (Cane et al. 1996). Typically, one to three fruit are set per upright, but up to five are common in many recently released, e.g., Haines, cultivars. Although species within the Vaccinoideae, e.g., utilize animal seed dispersal, cranberry is typically found around bodies of water. Cranberry's fruit chemistry strongly suggests cranberry evolved for water seed dispersal. Cranberry fruit has relatively low sugar content (5-7%), high acid content (2-3%), high proanthocyanidin content, benzoic acid (0.1%) in the epicuticular wax (Cunningham et al, 2003), and large locular chambers, allowing the fruit to readily float.

Commercial cultivars are highly self-fertile and do not require, nor appear to benefit from cross-pollination, for seed set nor fruit set (Sarracino and Vorsa 1991). Thus, the productivity in small plots carries over in large planting as in commercial settings. In the northern hemisphere the majority of fruit development occurs during Aug. with seed maturation occurring Sept. Early maturing varieties, e.g., 'Ben Lear', 'HyRed', 'Crimson Queen' typically begin to ripen early Sept., and later maturing varieties, e.g., 'Stevens', in Oct.

Domestication of the American Cranberry

The American cranberry (*Vaccinium macrocarpon* Aiton) is one of the few fruit crop species that is native to North America. The major production of cranberry is in the United States and Canada. Other production areas are Chile, New Zealand and Europe.

Today cranberries are cultivated in the Pacific Northwest in the states of Oregon and Washington, the Midwest in Wisconsin and Michigan and in the northeastern states of New Jersey, Massachusetts and Maine. In 2017, United States production was 905 million pounds, valued at \$257 million. Wisconsin is the principal cranberry producing state with more than half of the nation's cranberry production followed by Massachusetts, New Jersey, Oregon and Washington (<http://www.agmrc.org/agmrc/commodity/fruits/cranberries/>).

Cranberry has received considerable attention due to the 'antioxidant' status and benefits to human health (Pappas and Schaich, 2009, Shabrova et al. 2011). The American cranberry was thought to relieve scurvy during trans-Atlantic voyages from the New World back to Europe, and by American Indians as a wound dressing and a treatment for blood poisoning (Eck 1990). What has received much attention is the use of cranberry to relieve symptoms of dysuria, or urinary tract infections. Cranberry's unique fruit chemistry appears to be the result of evolution away from animal seed dispersal, as is the case in blueberry, another major *Vaccinium* fruit crop species, but towards water dispersal.

The domestication and culture of cranberry was initiated about the 1820's in Massachusetts (Stevens et al. 1957). The first propagation of a 'variety', named 'Early Black', reportedly was done by Nathaniel Robbins where the first vines were selected from a 'swamp' in Harwich Massachusetts about 1852, from which the first commercial planting was established in 1857 in Massachusetts (Chandler and Demoranville 1958). During the 1880's and early 1900's over 132 varieties were named from indigenous selections from Massachusetts, New Jersey, Wisconsin, and Michigan (Dana 1983; Eck 1990). Criteria for selection was likely season of harvest, fruit color, berry size, and productivity. Of the many varieties selected from native populations "the Big Four", 'Early Black', 'Howes', 'McFarlin' and 'Searles',

became the principal cultivars planted during the early and mid-20th century. 'Early Black', 'Howes' (East Dennis, MA about 1843) and 'McFarlin' (South Carver in 1874) were selections from Massachusetts and 'Searles' (Walker, WI in 1894) was a selection from Wisconsin (Eck 1990).

Like most crop species, cranberry has both insect and disease threats which can cause severe economic losses. Fruit rot is the most serious disease problem facing cranberry production, particularly in New Jersey and Massachusetts (Oudemans et al. 1998; Johnson-Cicalese et al. 2009).

Breeding of the American Cranberry

The first breeding and selection cycle was initiated in 1929 by the United States Department of Agriculture (USDA) and the New Jersey and Massachusetts Agricultural Experiment Stations in response to a devastating disease, 'false blossom', caused by a phytoplasma (Chandler et al. 1947) belonging to the subgroup of 16SrIII-V phytoplasmas (Lee et al., 2014). Being the disease was most severe in New Jersey, the first breeding populations were field planted in 1.5 x 1.5 m plots in 1934 at J.J. White Inc., at Whitesbog, Pemberton, NJ. Breeding populations from additional crosses were planted in 1937 and 1943. The breeding program's objective was stated as "...the aim of originating varieties that would show resistance to the spread of false-blossom disease and that would produce large crops of superior fruit". From 30 crosses made between 18 native selections at total of 8,692 seedlings were evaluated at Whitesbog. The majority of the parents were selections from Massachusetts native stands. Other cultivars used for crossing were native selections from Michigan, 'Prolific', and Wisconsin, 'Searles' and 'Potter'. Of the 30 crosses 'McFarlin' was a parent in 16 crosses, likely because of the larger fruit size.

Selection of progeny from the 1934 planting was initiated in 1938 and carried out over three years through 1940. Of the over 8,000 seedling plots, 1,800 plots that produced at

least a ‘pint’ (approx. 100 g) for two to three consecutive years were further evaluated. The berries were hand-harvested and placed into storage for 2-3 months. The selection criteria included average yield, percent sound berries post-storage and ‘general appearance’. Since only the seedlings producing a minimum quantity of fruit were evaluated, there likely was indirect selection for establishment (stolon) vigor, precocious fruiting, upright production, fruit set, and fruit size. From the Whitesbog planting, 40 selections were initially selected for further testing. In 1945 an additional 182 seedlings were selected for further testing. The selections were further evaluated in a ‘second test’ in New Jersey, Massachusetts and Wisconsin. From this first breeding and selection cycle, six named varieties were released. The cultivars initially released in 1950 from the 40 ‘numbered’ selections were ‘Stevens’, ‘Beckwith’, and ‘Wilcox’. Subsequently ‘Pilgrim’, ‘Bergman’, and ‘Franklin’ were released in 1961 (Dana 1983). A second round of selections were made and identified by a ‘two-letter code’, e.g. CN, DF5, AR, etc. that were not officially named except for BE4 and ‘Crowley’. BE4 was subsequently named ‘Willapa Red’ by K. Patten of the Washington State University Cranberry Research Station, Long Beach, WA (Vorsa, 2010). This early USDA/NJAES breeding program only carried out a single breeding cycle.

Cranberry production is currently based on few cultivars, and many farmers still grow native selections made as early as the 1800s (Dana 1983; Eck 1990; Table 1). Of the named varieties, ‘Stevens’ and to a lesser degree ‘Pilgrim’, are currently the most widely planted cultivars. Both of these cultivars have ‘McFarlin’, the larger fruited of the native varieties, as a parent which most likely contributed to a larger fruit size. ‘Ben Lear’ a native selection from Wisconsin before 1901 is still commercially grown today (Dana, 1983). Following the initial breeding efforts, further cranberry genetic improvement through breeding was largely delayed

until the 1970’s when a private program in Wisconsin initiated hybridization of native varieties. Dr. D. Boone, from the University of Wisconsin-Madison, initiated the selection of seedlings from open-pollinated cultivars. Currently, there are two active public breeding programs, one at Rutgers University and one at University of Wisconsin-Madison, USDA-ARS, and there is an additional grower operated breeding program, Valley Corporation, in Tomah, Wisconsin. Since 2003, these programs have released new cultivars from a second cranberry breeding cycle (Table 1). The recently released cranberry cultivars are: ‘HyRed’ and ‘Sundance’ (Wisconsin); ‘Demoranville’, ‘Crimson Queen’, ‘Mullica Queen’, ‘Scarlet Knight’, ‘Haines’, ‘Welker’ and ‘Vasanna’ (Rutgers); ‘GH1’, ‘GH2’, GH3, and ‘BG’ and others (Valley Corporation); and ‘Willapa Red’ (renamed from BE4) by K. Patten (Washington State) (Vorsa 2010, 2012). Many of these cultivars were generated by crossing first-generation hybrids and elite wild selections and resulted in improved fruit quality (mainly fruit anthocyanin content, i.e., total fruit anthocyanin (Tacy) measured in mg/100 g of fruit, and fruit size) and increased productivity. A recent survey found that new cultivars like ‘Mullica Queen’ (released in 2007) are becoming increasingly more popular among growers, demonstrating the value of breeding efforts in cranberry aiming to improving fruit quality characteristics (Gallardo et al. 2018).

Current Rutgers Breeding Program

The objectives of the cranberry breeding program have changed through the years. The development of more recent cranberry products, e.g., sweetend-dried-cranberries (SDCs), have directed the parameters of the berry that are most suitable for the product. For sauces and juice products, individual berry characteristics, e.g., berry size and homogeneity of color were less important. When sauce was the primary product pectin content and gelling quality, was measured. In the advent of juices, in 1950’s, Tacy and

Table 1. The major cranberry cultivars and new hybrids in production today (in part from Vorsa and Zalapa, 2019).

Variety*	Source*	Release/Selection Year
<i>Native Standards:</i>		
‘Early Black’ ^{1,2}	Native Selection, MA	1835
‘Howes’ ^{1,2}	Native Selection, MA	1843
‘McFarlin’ ^{1,2}	Native Selection, MA	1874
‘Searles’ ^{1,2}	Native Selection, WI	1893
‘Potter’s Favorite’ ¹	Native Selection, WI	1895
‘Prolific’ ¹	Native Selection, MI	1900
‘Ben Lear’ ^{1,2}	Native Selection, WI	1901
‘LeMunyon’ ^{1,2}	Native Selection, NJ	1960
<i>First Breeding Cycle Hybrid</i>		
‘Franklin’ ^{1,2}	‘Early Black’ x ‘Howes’	1930
‘Stevens’ ^{1,2}	‘McFarlin’ x ‘Potter’	1950
‘Beckwith’ ^{1,2}	‘McFarlin’ x ‘Early Black’	1950
‘Wilcox’ ^{1,2}	‘Howes’ x ‘Searles’	1950
‘Bergman’ ^{1,2}	‘Early Black’ x ‘Searles’	1961
‘Crowley’ ^{1,2}	‘McFarlin’ x ‘Prolific’	1961
‘Pilgrim’ ^{1,2}	‘Prolific’ x ‘McFarlin’	1961
‘No.35’**	‘Howes’ x ‘Searles’	N/A
<i>Newer Released Varieties:</i>		
‘GH1’ ³	‘Earl Rezin Native’ x ‘Searles’	1994
‘GH2’ ³	‘Earl Rezin Native’ x ‘Searles’	1996
‘HyRed’ ^{3,5}	‘Stevens’ x ‘Ben Lear’	2003
‘GH3’ ³	‘Earl Rezin Native’ x ‘Searles’	2004
‘Demoranville’ ³	‘Franklin’ x ‘Ben Lear’	2006
‘Crimson Queen’ ³	‘Stevens’ x ‘Ben Lear’	2006
‘Mullica Queen’ ³	#35 x ‘LeMunyon’	2007
‘Willapa Red’ ³	‘Aviator’ x ‘McFarlin’	2009
‘Scarlet Knight’ ⁴	Stevens x (Franklin x Ben Lear)	2010
‘Sundance’ ⁶	‘Stevens’ x ‘Ben Lear’	2011
‘BG’ ⁴	‘Beckwith’ x ‘GH1’	2011
‘Haines’ ⁷	‘Crimson Queen’ x ‘#35’	2017
‘Welker’ ⁸	#35’ x (Franklin x Ben Lear)	2017
‘Vasanna’	‘Crimson Queen’ x ‘#35’	2020

Cultivar descriptors from Dana (1983)¹, Eck (1990)², Vorsa (2010³, 2012⁴), McCown and Zeldin. 2003⁵ Zeldin and McCown (2014)⁶. Vorsa and Johnson (2017a), Vorsa and Johnson (2017b)⁸. ** Not formally released nor named, but commercially in a few locales grown, selection #35 from USDA breeding program (Chandler et al. 1947).

brix, was held to a premium. For SDCs homogeneity of berry parameters (minimum fruit size 7.1 mm, with preferably size >13 mm, color uniformity, and firmness) are requirements. Yield and fruit rot resistance are traits obviously still relevant today from a grower’s perspective.

The Rutgers’ cranberry breeding program was initiated in 1985. The first objective was to assemble a germplasm collection of cultivars from domesticated plantings, Wisconsin, Massachusetts, Washington State, Brit-

ish Columbia and New Jersey, and varieties from native sites from Delaware to northeastern Canada out west to Minnesota. Over 600 accessions were collected and maintained in field plots. Because of the nature of cranberry, having both asexual (stolon’s) and sexual reproduction, it became apparent that most of the germplasm plots, from pollen stainability analysis, were genetically heterogeneous. Subsequently, plots were established from single vines ensuring genetic homogeneity within plots. The first set of

crosses were made in 1988, representing intercrosses, among the first generation hybrids USDA-AES program (cvs. Stevens, Pilgrim, Wilcox, and Franklin) along with ‘Ben Lear’ in a diallel. Seedling plots (>2,300) were grown out in a cooperating grower’s field (W. Haines) and a replicate subset of 800 seedlings were grown at Dubay, Wisconsin with the breeding program being supported by Ocean Spray Cranberries, Inc. From these initial 1988 crosses 55 hybrids were further tested in a replicated trial at City Point, Wisconsin and at the Marucci Center. Two varieties were released in 2006 from these selections that exhibited improved yields (over the cv. Stevens also in the trial) and higher fruit, Tacy. Content for the juice market. These were ‘Crimson Queen®’ from a ‘Stevens’ x ‘Ben Lear’ cross and ‘Demoranville®’ from a ‘Franklin’ x ‘Ben Lear’ cross.

Since cranberry has limited vegetative variation and much overlap of fruit characteristics, varietal discrimination was problematic, we also embarked in early 1990’s, on using DNA technology available at the time, to discriminate varieties from one another using Randomly Amplified Polymorphic DNAs (RAPDs) (Novy and Vorsa, 1995; Novy et al., 1995, 1996), followed by Sequenced Characterized Amplified Regions (SCARs) (Polashock and Vorsa, 2002). Currently, microsatellites (SSRs) and genotyping-by-sequencing (GBS) using single nucleotide polymorphisms (SNPs) are also employed. DNA markers enabled unambiguous varietal identification and discrimination of varieties in the germplasm collection. DNA technology also identified that many commercial beds and many variety plantings were composed of off-types mixtures and that ‘off-types’ were generally poor fruit producers and vegetatively vigorous likely infiltrating plantings through stoloniferous growth and resources likely being diverted to vegetative growth (Novy et al. 1996).

In the 1990s we also conducted a replicated 10-variety 10-year varietal trial, which included first generation hybrids from the first

breeding and selection cycle, e.g., ‘Stevens’ and ‘Pilgrim’. It was observed that #35, apparently a ‘Howes’ x ‘Searles’ hybrid selection from the previous breeding program, had smaller fruit but out-yielded both larger fruited varieties, (Davenport and N. Vorsa. 1999) ‘Stevens’ and ‘Pilgrim’. One reason this variety probably was not named along with ‘Stevens’ and ‘Pilgrim’ was because of its poor late color but fortunately it was maintained at the Rutgers Marucci Center. DNA fingerprinting identified three fingerprints in the #35 plots, and the most productive was chosen as the likely #35 from the previous breeding program and program and was used for subsequent breeding in the Rutgers program.

The variety, #35, was observed to be a superior parent in crosses, elevating yields in numerous crosses. I felt crossing #35 with larger fruited varieties, e.g., ‘Lemunyon’ would potentially lead to combining what I believed was the higher fruit set with larger fruit sized varieties. The ‘#35’ x ‘Lemunyon’ cross in 1997 gave particularly superior progeny from which CNJ97-105-4 was selected from over 100 seedlings, and fortuitously had the second best color in the population, was selected and patented as PP19,434 and trademarked as ‘Mullica Queen®’. ‘Mullica Queen’, released with minimal variety trials, has proven to be quite productive achieving yields in Wisconsin of over 700 barrels (bbl) per acre (one bbl=100 lbs, is the commonly used term in commercial cranberry production for yield), whereas, the average yield for the state is 230-240 bbl/ acre. ‘Mullica Queen’ has become a popular cultivar to renovate with, currently replacing about 4,000, acres or 10 per cent of the acreage of older varieties, and is being grown in Wisconsin, Massachusetts, British Columbia, New Foundland and Quebec. Besides ‘Crimson Queen’, ‘Demoranville’ and ‘Mullica Queen’, the program has patented and released four other cultivars: ‘Scarlet Knight®’, ‘Welker™’, ‘Haines™’ and ‘Vasanna™’. These cultivars have been in-

cluded in replicated field trials in Warrens, WI, Wisconsin Rapids, WI, Langlois, OR, and Delta, British Columbia besides at the Rutgers Marucci Center, Chatsworth, NJ. The cultivars 'Mullica Queen' and 'Haines', have achieved yields over 43 US tons/acre. 'Haines' having a uniform berry color and size is especially suitable for fresh fruit and SDCs as well as juices. Although 'Vasanna' has done well in all trials it has performed especially well in British Columbia's 'oceanic climate' in both coarse and degraded 100 percent peat soils.

Traits of interest in breeding

A recent survey to the industry identified breeding traits for priorities for genetic enhancement (Gallardo et al., 2018). For the cranberry grower, traits that are important include productivity, establishment vigor, and disease and insect resistance. With the specter of global warming heat stress and fruit rot, which is exacerbated with heat stress, are traits that might mitigate heat stress, e.g. epicuticular wax (bloom) on fruit, are being studied. Fruit traits of interest to processors are fruit shape and size (influences sorting and specific processing needs) and color, fruit shelf-life and firmness. Varietal resistance to false-blossom was considered to be based on the degree of "susceptibility to leafhopper feeding" (Chandler et al. 1947) and with the reemergence of the disease in Wisconsin, New Jersey and Massachusetts, resistance to false-blossom is relevant.

Fruit rot is a major challenge in New Jersey and Massachusetts and becoming more of an issue in Wisconsin. New Jersey climate subjects the cranberry to the most severe fruit rot pressure making New Jersey an ideal site to breed fruit rot resistant (FRR) cultivars which is a major objective of the Rutgers program. Cranberry fruit rot is caused by a complex of fungi from at least 12 genera (Oudemans et al. 1998) of which are largely considered necrotrophs (Tadych et al., 2012). The program identified four diverse sources of resistance in a screening (with reduced fungicide applica-

tions) of germplasm in New Jersey. Varieties identified as having resistance to fruit rot are 'Budd's Blues', 'Holliston', 'Cumberland' and a germplasm accession, 'US89-3' (Johnson et al. 2009), and we have established FFR is heritable (Johnson et al., 2015). These four FRR genotypes have been crossed with productive genetic backgrounds, to introgress and pyramid the FRR genes to enhance FRR in productive cultivars. We are identifying quantitative trait loci (QTL) (Darverdin et al. 2017, Georgi et al. 20012, 2013) and developing markers, e.g. KASP, for marker assisted selection facilitating breeding.

Cranberry has unique fruit chemistry, high in flavonoids and PACs and acids and low in sugars (Cunningham et al. 2003) likely because it's evolution for seed dispersal was away from animal dispersal towards water dispersal. Cranberry is also criticized for the 'added-sugar' that most cranberry products, e.g., sweetened-dried-cranberry and juice drinks, have. Palatability of fruit is a function of sugar to acid ratio. Whereas most fruits have a titratable acidity (TA) of $TA \approx 0.5$ and sugar content 10 percent or more, cranberry typically has a $TA > 2.3$, requiring much added-sugar to balance the acidity. Cranberry is also a unique fruit in having less fructose (2-4%) than glucose ($\approx 5\%$) (Cunningham et al. 2003). Genetic variation for fructose content only ranges 1 to 3% (unpublished data). Genetic variation for fructose content is minimal in our germplasm. However, we have identified two major loci, a *CITA* locus on chromosome LG1 with a *cita* allele when homozygous. *cita/cita*, reduces citric acid level in the fruit by about 90 percent (Fong et al. 2000). Unfortunately, malic acid is negatively correlated with citric acid in populations with this allele mitigating the TA level. The other locus we termed *MALA* on chromosome LG4 when homozygous recessive for the *mala* allele, *mala/mala*, reduces malic acid as well as citric and quinic acid content, and the genotype has a $TA \approx 0.5$ (Fong et al., 2021). Unfortunately, the recessive genotype is associated with a dwarf type phenotype

making commercialization questionable.

Cranberry is recognized for having one of highest anti-oxidant contents due to high levels of proanthocyanidins (PACs), flavonol glycosides, hydroxycinnamic acids and anthocyanins. Genetics of the flavonoids in cranberry and the genetics of American cranberry including heritability of traits, molecular markers, initial next-generation sequencing for marker development, single-sequence-repeats (SSR) marker development, SSR genetic diversity studies, nuclear and organelle genome assembly, linkage mapping and single-nucleotide-polymorphisms (SNP) markers and marker –trait association studies are reviewed in Vorsa and Zalapa (2019).

Acknowledgments

Support for this work was provided in part from Ocean Spray Cranberries, Inc.; New Jersey Cranberry and Blueberry Research Council; Cranberry Institute. Research findings presented were funded in part by project no. 5090-21220-004-00-D, USDA-SCRI under Grant 2008-51180-04878, and USDA-NIFA-AFRI Competitive Grant USDANI-FA-2013-67013-21107.

Literature Cited

Camp, W. H. 1944 A preliminary consideration of the biosystematy of *Oxycoccus*. Bulletin of the Torrey Botanical Club 71: 426–437.

Cane, J.H., D. Schiffhauer, and L.J. Kervin. 1996. Polination, foraging, and nesting ecology of the leaf-cutting bee *Megachile* (*Delomegachile*) addenda (Hymenoptera: Megachilidae) on cranberry beds. Ann. Entomol. Soc. Am. 89: 361–367.

Chandler, F. and I. Demoranville. 1958. Cranberry varieties of North America. Bulletin 5. Mass. Ag. Exp. Stat. Bull.

Chandler, F., R. Wilcox, H. Bain, H. Bergman, and H. Dermen. 1947. Cranberry breeding investigations of the U.S. Dept. of Agriculture. Cranberries 12:6-9.

Cunningham, D.G., S.A. Vannozzi, R. Turk, R. Rodriguez, E. O’Shea, and K. Brilliant. 2003. Cranberry phytochemicals and their health benefits. In Nutraceutical Beverages: Chemistry, Nutrition, and Health Effects; Shahidi, F., Weerasinghe, D. K., Eds.; ACS Symposium Series 871; ACS: Washington DC; pp 35–51.

Dana, M.N. 1983. Cranberry cultivar list. *Fruit Var. J.* 37:88–95.

Davenport, R.J. and N. Vorsa. 1999. Cultivar fruiting and vegetative response to nitrogen fertilizer in cranberry. *J. Amer. Soc. Hort. Sci.* 124:90-93.

Daverdin, G., J. Johnson-Cicalese, J.E. Zalapa, N. Vorsa, and J. Polashock. 2017. Mapping and identification of fruit rot resistance QTL in American in American cranberry using GBS. *Mol. Breed.* 37:38.

Eck, P. 1990. The American cranberry. Rutgers University Press, New Brunswick, NJ.

Fong, S.K., Kawash, J., Wang, Y., Johnson-Cicalese, J., Polashock, J., and Vorsa, N. 2020. A low citric acid trait in cranberry: genetics and molecular mapping of a locus impacting fruit acidity. *Tree Genet. Genomes* 16:42 <https://doi.org/10.1007/s11295-020-01432-4>

Gallardo, R.K., Q. Zhang, P. Klingthong, J. Polashock, C. Rodriguez-Soana, N. Vorsa, R. Harbut, A. Atucha, J. Zalapa, M. Iorizzo. 2018. Breeding Trait Priorities of the cranberry Industry in the United States and Canada. *HortScience* 53:1467–1474.

Georgi, L.L., R.H. Herai, R. Vidal, M.F. Carazzolle, G.G. Pereira, J. Polashock, and N. Vorsa. 2012. Cranberry microsatellite marker development from assembled next-generation genomic sequence. *Mol. Breed.* 30:227–237.

Georgi, L., J. Johnson Cicalese, J. Honig, S.P. Das, V.D. Rajah, D. Bhattacharya, N. Bassil, L.J. Rowland, J. Polashock, and N. Vorsa. 2013. The first genetic map of the American cranberry: Exploration of synteny conservation and quantitative trait loci. *Theor. Appl. Genet.* 126:673–692.

Johnson-Cicalese, J., N. Vorsa, and J. Polashock. 2009. Breeding for fruit rot resistance in *Vaccinium macrocarpon*. *Acta Hortic.* 810:191–198.

Johnson-Cicalese, J., J.J. Polashock, J. Honig, J. Vaciunas, D.L. Ward, and N. Vorsa. 2015. Heritability of fruit rot resistance in American cranberry. *J Am Soc Hortic Sci.* 140(3):233–242.

Lee, I.M., J. Polashock, K. Bottner-Parker, P. Bagadia, C. Rodriguez-Saona, and R. Davis. 2014. New subgroup 16SrIII-Y phytoplasmas associated with false-blossom diseased cranberry (*Vaccinium macrocarpon*) plants and with known and potential insect vectors in New Jersey. *Eur. Plant Path.* 139: 399–406. <https://doi.org/10.1007/s10658-014-0396-7>

Mahy, G., L.P. Bruederle, B. Connors, M. Van Hofwegen, and N. Vorsa. 2000. Allozyme evidence for genetic autoploidy and high genetic diversity in tetraploid cranberry, *Vaccinium oxycoccos* (Eriocaceae). *Am J Bot.* 87, 1882–1889.

McCown, B.H., and EL Zeldin. 2003. HyRed and early, high fruit color cranberry hybrid. *HortScience* 38:304-30.

Novy, R.G., C. Kokak, J. Goffreda, and N. Vorsa. 1994. RAPDs identify varietal misclassification and regional divergence in cranberry [*Vaccinium macrocarpon* (Ait) Pursh]. *Theor. Appl. Genet.* 88:1004-1010.

Novy, R.G. and Vorsa, N. 1996. Evidence for RAPD heteroduplex formation in cranberry: Implications for pedigree and genetic relatedness studies and a source of co-dominant RAPD markers. *Theor. Appl. Genet.* 92, 840-849.

Novy, R.G., Patten, K., and Vorsa, N. 1996. Identifying genotypic heterogeneity in the 'McFarlin' cranberry: A randomly-amplified polymorphic DNA (RAPD) and phenotypic analysis. *J. Amer. Soc. Hort. Sci.* 121:210-215.

Oudemans, P., F. Caruso, and A. Stretch. 1998. Cranberry fruit rot in the Northeast: a complex disease. *Plant Dis.* 82:1176-1184.

Pappas, E. and K.M. Schaich. 2009. Phytochemicals of cranberries and cranberry products: characterization, potential health effects, and processing stability. *Crit. Rev. Food Sci. Nutr.* 49: 741-781.

Polashock, J.J. and N. Vorsa. 2002. Development of SCAR markers for DNA fingerprinting and germplasm analysis of American cranberry. *J. Amer. Soc. Hort. Sci.* 127:677-684.

Sarracino, J.M. and N. Vorsa. 1991. Self and cross fertility in cranberry. *Euphytica* 58: 129-136.

Shabrova, V., Tarnopolsky, O., Singh, A.P., Plutzky J., Vorsa N., and L. Quadro. 2011. Insights into the molecular mechanisms of the anti-atherogenic actions of flavonoids in normal and obese mice. *PLoS ONE* 6. e24634. doi:10.1371/journal.pone.0024634.

Tadych M., M.S. Bergen, J. Johnson-Cicalese, J. Polashock, N. Vorsa, and J.F. White Jr. 2012. Endophytic and pathogenic fungi of developing cranberry ovaries from flower to mature fruit: diversity and succession. *Fungal Diversity* DOI 10.1007/s13225-012-0160-2

Vander Kloet, S. 1983. The taxonomy of *Vaccinium* section *Oxycoleus*. *Rhodora* 85:1-43.

Vorsa, N., J. Polashock, D. Cunningham, and R. Rodriguez. 2003. Genetic inferences and breeding and implications from analysis of cranberry germplasm anthocyanin profiles. *J. Amer. Soc. Hort. Sci.* 128:691-697.

Vorsa, N. 2010. Cranberry, p. 728. In: J.R. Clark and C.E. Finn (eds.). *Register of new fruit and nut cultivars, List 45*. HortScience 45:716-756

Vorsa, N. 2012. Cranberry. In: *Register of New Fruit and Nut Cultivars List 46*. Eds: J. R. Clark and C. E. Finn. HortSci 47: 536-562.

Vorsa, N. and Zalapa, J. 2019. Domestication, genetics, and genomics of the American cranberry. In: I. Goldman (ed.). *Plant Breeding Reviews*. <https://doi.org/10.1002/9781119616801.ch8nut> cultivars, List 46. HortSci. 47:536-562.

Vorsa, N., Johnson-Cicalese. 2017a. Cranberry Plant Named 'CNJ99-9-96', US PP **27,657**.

Vorsa, N., Johnson-Cicalese. 2017b. Cranberry Plant Named 'CNJ99-52-15', US PP **27,709**.

Vorsa, N. and J. Polashock. 2005. Alteration of anthocyanin glycosylation in cranberry through interspecific hybridization. *J. Amer. Soc. Hort. Sci.* 130:711-715.

Zeldin E.L. and McCown B.H. 2014 Cranberry Plant Named 'WI92-A-X15', US PP 25,066.

About The Cover:

Mullica Queen® (U.S. patent: US PP19,434 issued November 11, 2008) was released by the New Jersey Agricultural Experiment Station and the USDA. It is an early flowering cranberry cultivar with a tendency to produce multiple flower buds with high fruit set, resulting in high yield potential. Vines are vigorous and establish rapidly. Fruits have medium anthocyanin content. 'Mullica Queen' has a unique genetic background unrelated to most of the commonly grown cultivars. *Photo by Nicholi Vorsa.*