Journal of the American Pomological Society 77(3): 176-185 2023

Anthocyanin Profiles of Two Subtropical *Vaccinium* Species and 'O'Neal' Southern Highbush Blueberry

Todd W. Anderson[1], Robert W. Durst[2], Scott W. Leonard[2], Kim E. Hummer[3], Claire Luby[4], and Nahla V. Bassil[5]

Keywords: *Vaccinium myrtoides* (Blume), *Vaccinium floribundum* (Kunth), genetics, germplasm

Abstract

Vaccinium L., a globally distributed genus, encompasses economically and nutritionally valuable species such as blueberry (*V. corymbosum* L. and its hybrids), cranberry (*V. macrocarpon* A.), bilberry (*V. myrtillus* L.), and lingonberry (*V. vitis-idea* L.). There has been a robust growth of blueberry cultivation in the tropical and subtropical regions of the world, such as Central and South America, the Southern United States, Australia, and the Mediterranean. This growth has been enabled by the integration of various wild species such as northern lowbush blueberry *V. angustifolium* (Aiton), evergreen blueberry *V. darrowii* (Camp), and rabbiteye blueberry *V. virgatum* (Aiton) into highbush blueberry breeding programs. Still, numerous under-studied wild *Vaccinium* species have untapped potential for breeding use and local cultivation in diverse climates. The harvest of wild *Vaccinium* fruit has long contributed to the nutrition of local communities throughout Southeast Asia and the Americas. Our objective was to conduct preliminary investigations into the fruit qualities and anthocyanin profiles of two such under-studied species, *V. myrtoides* (Blume) and *V. floribundum* (Kunth), and compare their characteristics to that of the southern highbush blueberry cultivar 'O'Neal' (*V. corymbosum* hybrid). Over the spring and summer of 2021, we determined fruit size, percent soluble solids, pH, total anthocyanin concentration, and anthocyanin aglycons profiles. The fruit was sourced from the US Department of Agriculture (USDA), National Clonal Germplasm Repository (NCGR) in Corvallis, Oregon. The wild species' fruit size, soluble solids, and pH were not significantly different from those of 'O'Neal.' The total anthocyanin levels for *V. floribundum* (87.4 mg anthocyanin/100 g frozen fruit) and *V. myrtoides* (80.4 mg/100 g frozen fruit) were significantly higher than those for 'O'Neal' (32 mg/100 g frozen fruit). Anthocyanin profiles were also unique to each species. *V. myrtoides* had the most complex profile with eight anthocyanin peaks; *V. floribundum* had four peaks 'O'Neal' had three. One of the most prominent anthocyanins in blueberries, petunidin-3- galactoside, occurred in 'O'Neal' and *V. myrtoides* but was absent from *V. floribundum*. Del-3-arabinoside was present in both *V. myrtoides* and *V. floribundum* yet absent in 'O'Neal'. The unique anthocyanin profiles of the two wild species could have value in diversifying the anthocyanins available in cultivated blueberries and deserve further investigation.

The global demand for blueberry fruit exceeds the current supply and is projected to keep increasing for the foreseeable future (Rabobank, 2019). Cultivated northern highbush blueberry (NHB, *V. corymbosum* L. hybrid) and southern highbush blueberry (SHB, *Vaccinium corymbosum* L. hybrid) dominate the international market. The harvesting of managed stands of northern lowbush blueberry species, predominately (*V. angustifolium* (Aiton)) from Canada and the United States also contributes to the total harvest, with temperate regions of North America historically having the largest blueberry production (FAOSTAT, 2020).

Growing beyond the historical confines of blueberry production, breeding programs have enabled expansion into warmer climates. During the past 100 years, plant breeders at the USDA and elsewhere combined elite

[1] Department of Horticulture, Oregon State University, Corvallis, Oregon, 97331
[2] Linus Pauling Institute, Oregon State University, Corvallis, Oregon, 97331
[3] USDA ARS (Agricultural Research Service) National Clonal Germplasm Repository, 33447 Peoria Road, Corvallis, Oregon 97333
[4] USDA ARS Horticultural Crop Production and Genetic Improvement Research Unit, Corvallis, Oregon 97333 todd.anderson@Oregonstate.edu

NHB clones with southern distributed North American species developing SHB cultivars having low or no chilling for subtropical and tropical production (Patel, 1993). The low chill traits in SHB came from a wild species from Florida, (*V. darrowii* (Camp)), and have enabled improved adaptation to subtropical conditions (Draper and Hancock, 2003). In 1987, 'O'Neal,' a cultivar with a 400h chilling requirement, was introduced by North Carolina Agricultural Experiment Station in collaboration with the USDA (Ballington et al., 1990). This SHB blueberry was successfully produced in Florida, North Carolina, and South Carolina (Ballington et al., 1990) and in many subtropical regions worldwide (Ehlenfeldt et al., 1995). Due to the innovation of low and no-chill highbush blueberries, subtropical growing regions, particularly in Peru and Mexico, have skyrocketed in production over the past decade (FAOSTAT, 2020). However, significant disease pressure, low fruit quality, and aversion to tropical mineral soils continue to present challenges for the blueberry industry in tropical and subtropical climates (Stringer et al., 2008).

Predating the modern domestication and cultivation of domestic blueberries in subtropical and tropical regions, indigenous and local peoples of these regions have gathered numerous wild blueberry species from native stands (Santamaria et al., 2012; Chua-Barcelo, 2014). The Filipino "ayusep" (*V. myrtoides* (Blume)) and the Ecuadorian "mortiño" (*V. floribundum* (Kunth)) are essential sources of income and nutrition in specific highland communities (Ortiz et al., 2013). Value-added products of these species are in high demand and are culturally significant in these regions (Chua-Barcelo, 2014). Parallel to the rise in popularity of domestic blueberries, the demand for wild fruit has been increasing, straining wild populations (Taco-Ugsha., 2020). Over-harvesting these native stands now impacts wild populations in some of the most biodiverse ecosystems on earth (Mirghani et al., 2019). Understanding the physical and chemical traits of subtropical and tropical blueberries can help plant breeders and researchers better understand germplasm that has the potential to diversify the genetics of domesticated blueberries or develop new crops for these regions. Improved knowledge of wild *Vaccinium* can help diversify crops grown for local incomes and expand the cultivated range for domestic blueberries and related crops.

Physical fruit traits such as diameter and weight and fruit chemistry traits such as soluble solids, pH, and anthocyanin amount and profiles are valuable for plant breeders and further research. Berry size is essential in breeding for different markets (Saftner et al., 2008). For fresh markets, larger berry sizes are valued. Smaller sizes are preferred in North America for processed-focused markets (Saftner et al., 2008). Hence, understanding if wild accessions have a comparable size to other processed or domesticated blueberries is vital for accessing their potential applications as domesticated crops. Percent soluble solids are used to measure soluble solute concentration to approximate sugar concentration. Generally, higher sugar concentration in fruit is considered more desirable (Ferrão et al., 2020). Complex pH, phenolic, and physiological trait interactions create the flavor and sensory profile of the berries, with soluble solids being an essential factor (Barcello et al., 2015). Early SHB cultivars, such as 'O'Neal,' tend to have fruit that scores lower for flavor characteristics, such as soluble solids, than NHB selections (Hancock, 2004). Subtropical germplasm with higher soluble solids may have future uses in improving SHB adaptability without compromising the breeding gains in fruit quality.

For this reason, comparing these wild species to established interspecific SHB would be most beneficial because SHB is grown in the tropics and subtropics. Acidity influences the taste perception of blueberries, particularly the perception of the sugar-acid ratio (Ferrão et al., 2020). Anthocyanins are pigments and phytochemicals perceived as reds, blues, purples, and blacks. These pigments

Table 1. USDA plant information (PI) number, Latitude, Longitude, elevation, origin, and year collected by the USDA, National Clonal Germplasm Repository, Corvallis, Oregon, for the study accessions.

Plant name	PI number	Latitude Longitude Elevation	Origin	Year Collected
V. myrtoides	PI 666881	16.6230 120.8990 2922 m	Mt. Pulag, Luzon, Philippines	1992
V. floribundum	PI 554930	-0.2167 -78.3333 2764 m	Otavalo, Ecuador	1989
'O'Neal'	PI 554944	Cultivar	North Carolina, AES, and USDA	1987 (release)

contribute to the nutritional benefits of blueberries (Mirghani et al., 2019). The diversity of phytochemicals in *Vaccinium* species is poorly understood (Mengist et al., 2020). Environmental conditions influence anthocyanin quantities (Barcello et al., 2015). Different *Vaccinium* species are known to have vastly different anthocyanin profiles (Esquivel-Alvarado et al., 2019). However, environmental conditions are not expected to influence the presence of anthocyanin aglycons (forms of anthocyanin based on R-group location and configuration) in the profile, so we can expect our results to represent the presence of aglycons within the profile (Vilela et al., 2016).

Determining fruit physical and chemical traits for *V. myrtoides* and *V. floribundum* compared with established SHB cultivars such as 'O'Neal' helps document the nutritional composition of these berries for human consumption. Barcelo et al. (2015) measured the total flavonoid and phenolic concentration in mg GAE (gallic acid equivalent) per 100 grams of *V. myrtoides* fresh weight. They had the highest polyphenol concentration of the measured native fruit products. Since the direct comparison of both *V. myrtoides* and *V. floribundum* to domestic SHB in fruit traits has not been made, it is difficult to ascertain the differences and potential value of those species in blueberry breeding and research. Vasco et al. (2009) measured the phenolic concentration and anthocyanin profile of *V. floribundum*. Using *V. myrtillus* as a standard, they identified delphinidin-3-galactoside, cyanidin-3-galactoside, delphinidin-3-arabinoside, cyanidin-3-glucoside, and cyanidin-3-arabinoside, as present in ripe fruit purchased from local markets in Ecuador. We aimed to determine fruit traits and anthocyanin profiles for *V. floribundum* and *V. myrtoides,* in contrast to the established SHB cultivar 'O'Neal'.

Materials and Methods

Fruit Quality Evaluation. The fruit of each species was obtained from a single genotype representative clonal accession growing at the USDA ARS, NCGR in Corvallis, Oregon (Table 1). The harvest was dispersed from March to July 2021 for *V. myrtoides* and *V. floribundum*, with berries collected weekly. Ripe 'O'Neal' berries were harvested weekly from April through July 2021. Upon collection, fifty fruits were split into ten samples of five berries from each species. Each of the five berries in the 10 samples from each genotype was subsequently evaluated for fruit diameter, weight, percent soluble solids, and pH. The diameter (mm) was estimated with digital cal-

ipers at the fruit's equator, halfway between the calyx and the abscission scar. Weight (g) was also measured. Fruits were then crushed to expel juice in separate samples of five fruit. Percent soluble solids were then measured for the juice with an Atago portable refractometer (ATAGO, Saitama, Japan). The pH was also measured with a benchtop pH meter (Corning pH meter 240, Texas City, Texas) using the juice of subsamples of the fruit.

Anthocyanin Analysis. A sample of ripe fruit from each of the three accessions was gathered over the fruiting period to obtain approximately 15 grams per genotype. After the weekly harvest, the fruit was immediately stored in a -80° freezer to prevent post-harvest cold storage degradation in anthocyanins (Yan et al., 2023) and aggregated until approximately fifteen grams of fruit (which varied in number between genotypes) were obtained for each accession. The aggregated fruit samples were then divided into six samples for each accession for chromatographic analysis with high-performance liquid chromatography (HPLC) at the Linus Pauling Institute (Corvallis, Oregon). These samples were juiced without heat treatment from thawed samples and centrifuged to separate debris. The chromatographic analysis was conducted on an HPLC (Agilent) 1090 equipped with a built-in diode array detector (DAD) or added refractive index (RI) detector (1047) and processed on Chemstation software (Agilent Technologies, Santa Clara, CA, USA). Spectrophotometer assays were performed on a Beckman DU-640 spectrophotometer (Beckman-Coulter, Brea, CA, USA). HPLC-grade methanol was the reagent used (Durst et al., 2001). Cranberry (*V. macrocarpon* (Aiton)) anthocyanin profiles were previously characterized by the Linus Pauling Institute (Durst et al., 2001), and the peaks from cranberry were used to approximate the anthocyanins in the other samples.

Data Analysis. Berry diameter, weight, soluble solids, pH data, and total anthocyanin data were analyzed using ANOVA through R studio using the Multcomp package (RStudio version, 4.1.1). Normality was tested using a q-plot distribution. A Tukey HSD was used to determine the significant difference in the means. The protocol used at Linus Pauling for cultivated and wild *Vaccinium* anthocyanin analysis uses cranberry as a standard. This protocol was previously used in analyzing the anthocyanins in other wild *Vaccinium* species from the NCGR (Hummer et al., 2013). Using the same standard allows comparison of our subject *Vaccinium* HPLC chromatograms to previous profiles. Retention times were used to identify anthocyanin components of *V. myrtoides*, *V. floribundum,* and 'O'Neal.'

Results and Discussion

Fruit Diameter and Weight. For these representative repository accessions, we found that the average berry diameter and berry weight for *V. myrtoides* were significantly lower than those of either *V. floribundum* or 'O'Neal' (Table 2). An approximate difference of 2.05 mm for diameter and 0.24 grams for fruit weight existed between the means of *V. floribundum* and *V. myrtoides*. There was no significant difference in size or diameter between *V. floribundum* and the SHB cultivar 'O'Neal.' *V. myrtoides* size was smaller than both 'O'Neal' and *V. floribundum*; the latter was comparable in size to that reported for commercially processed fruit such as *V. angustifolium*, known as northern lowbush blueberry, and *V. ovatum* or evergreen huckleberry (Mirghani et al., 2019). This preliminary exploration into basic fruit traits is essential to assess the potential for improvement and domestication of these wild species.

Percent Soluble Solids. Of the representative repository accessions, *V. myrtoides* had the highest soluble solids (Table 2). The mean soluble solids of *V. floribundum* and 'O'Neal' were similar. So, in terms of percent soluble solids, wild *V. floribundum* is comparable to the commercial cultivar 'O'Neal. However, *V. myrtoides* could contribute higher percent

Table 2. Diameter, weight, soluble solids, and pH means of five berries in 10 samples measured for each of the three accessions: *Vaccinium myrtoides*, *V. floribundum,* and 'O'Neal.' The total anthocyanins (mg/100g) are from six samples of the three accessions measured with HPLC.

Accession	Diam. (mm)	Fruit Wt. (g)	Sol. Solids (%)	pH	Total Anthocyanin (mg/100g)
V. myrtoides	5.83 a [z]	0.15 a	17.34 a	2.97 a	80.40 a
V. floribundum	7.88 b	0.39 b	11.09 b	3.02b	87.50 a
'O'Neal'	7.88 b	0.38 b	12.22 b	3.87b	32.40 b

[z] Means within columns followed by common letters do not differ at the 5% significance level by Tukey's HSD. The critical SE for the diameter is 0.487, with Tukey HSD value being 0.487, for the weight SE is 0.051 and Tukey HSD 0.078 value; for soluble solids, SE is 3.41 and Tukey HSD value being 5.25; for pH, SE is 0.189, and Tukey HSD is 0.29 and for total anthocyanin the SE is 14.106, and the Tukey HSD is 26.39.

soluble solids if introgressed into the cultivated SHB cultivars exemplified by 'O'Neal' in this study.

pH. Of the representative repository accessions, *V. myrtoides* and *V. floribundum* berries had lower pH than 'O'Neal' (Table 2). 'O'Neal' had the highest pH, *V. myrtoides* had the lowest pH, and *V. floribundum* was intermediate (Table 2). The lower acidity in these two wild species may result in more complex sugar-acid taste profiles that may not match what is expected for the fresh market in the current international market. In contrast, more acidic fruit is favorable in some processing markets (Vilela et al., 2016).

Anthocyanin Quantification and Profiles. 'O'Neal had the lowest anthocyanin concentration, *V. floribundum,* and *V. myrtoides* had comparable concentrations of total anthocyanins (Table 2). However, the standard error for total anthocyanins suggests that a follow-up study with larger sample populations than possible for this study may be needed to rank the measured species. The anthocyanin profiles for each species were different and unique to each species (Figures 1-3). *V. myrtoides* had delphinidin-3-galactoside, delphinidin-3-glucoside, cyanidin-3-galactoside, cyanidin-3-glucoside, cyanidin-3-arabinoside, petunidin-3-galactoside, petunidin-3-glucoside, and petunidin-3-arabinoside. The peak that overlapped with delphinidin-3-galactoside (Fig. 1) was unknown or unidentifiable. The overlapping peak shows the presence of another anthocyanin compound, which may only be identified with a different standard. All the anthocyanins in 'O'Neal' and *V. floribundum* were present in *V. myrtoides*. However, cyanidin-3-arabinoside was only detected in *V. myrtoides*. *V. floribundum* had delphinidin-3-galactoside, cyanidin-3-glucoside, delphinidin-3-arabinoside, cyanidin-3-glucoside, cyanidin-3-arabinoside, delphinidin-3-arabinoside, cyanidin-3-glucoside, and cyanidin-3-arabinoside (Fig. 2). A peak also overlapped with delphinidin-3-glucoside, so both were labeled as "E?", which corresponds with the internal labeling system of the Linus Pauling Institute. The peak could not be confidently identified. Most likely, this is the same anthocyanin found in *V. myrtoides*. 'O'Neal only had petunidin-3-galactoside, petunidin-3-glucoside, petunidin-3-arabinoside, and an unclear peak in its profile which is likely machine noise (Fig. 3). This profile of 'O'Neal' is different from profiles reported in other studies in which peonidin was identified (Chai et al., 2021). The absence of peonidin in the 'O'Neal' sample we used could have resulted from differences in

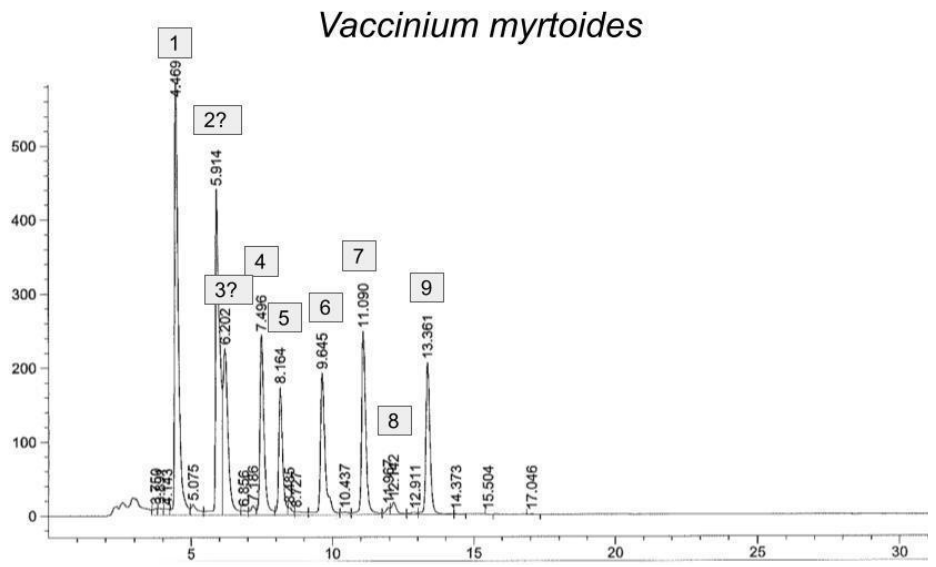

Fig. 1. Example HPLC chromatograph of PI 5554930 (*V. myrtoides*) output. Peak retention time and refraction are comparative and vary from response times. "1" at 4.469 minutes is delphinidin-3-galactoside, one "2?" at 5.914 minutes is delphinium-3-glucoside, and"3?" at 6.202 is unknown, the "?" emphasizes we cannot confirm which is which. "4" at 7.496 is cyanidin-3-galactoside, "5" at 8.164 is cyanidin-3-glucoside, "6" at 9.645 is cyanidin-3-arabinoside, "7"at 11.090 is petunidin-3-galactoside, "8" at 12.142 is petunidin-3-glucoside, and "9" at 13.361 is petunidin-3-arabinoside.

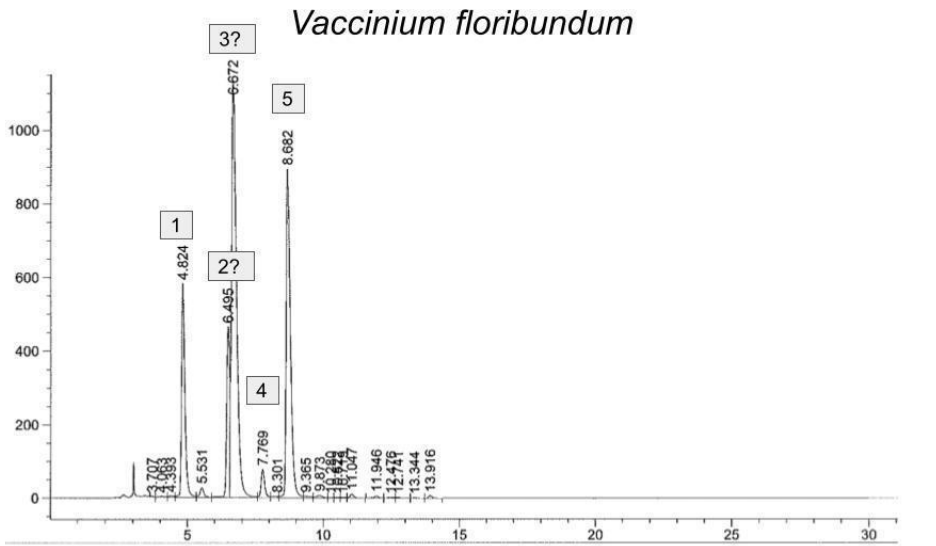

Fig. 2. Example HPLC chromatograph of PI 5554930 (*V. floribundum*) output. Peak retention time and refraction are comparative and vary from response times. "1" at 4.824 minutes is delphinidin-3-galactoside, one "2?" at 6.495 minutes is delphinium-3-glucoside, the "3?" at 6.672 minutes is unknown, but since they cannot be parsed, the "?" emphasizes we cannot confirm which is which. "4" at 7.769 minutes is cyanidin-3-galactoside, and "5" at 8.682 minutes is cyanidin-3-glucoside.

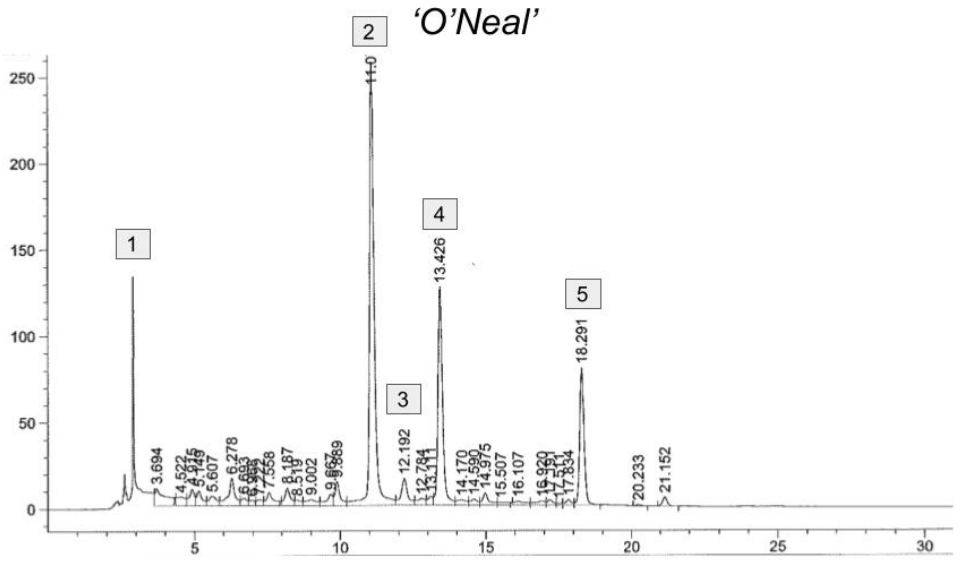

Fig. 3. Example HPLC chromatograph of 'O'Neal' output. Peak retention time and refraction are comparative and vary from response times. "1" at 3.00 minutes was in the initial peak or noise, "2" at 11.00 minutes is petunidin-3-galactoside, "3" at 12.192 minutes is petunidin-3-glucoside, and "4" at 13.426 minutes is petunidin-3-arabinoside; the final "5" at 18.291 minutes peak is unknown.

'O'Neal' genotypes used (Grace et al., 2019), possible differences in growing conditions, and/or small sample size and needs further investigation.

The Linus Pauling protocol uses cultivated cranberry (*V. macrocarpon*) as a standard anthocyanin profile reference for *Vaccinium* fruit analysis, as was previously described in *V. reticulatum* and *V. calycinum* (Hummer et al., 2013). Using the same reference allows the comparison of anthocyanin profiles across species and was therefore selected for this study. In comparison, cranberry did not have as many identifiable peaks as the profiles of our two wild species. Vasco et al. (2009) used *V. myrtillus* as a standard to analyze the profile of *V. floribundum*. Our results for the *V. floribundum* profile support the anthocyanin species described by Vasco et al. (2009), except for the 'E?' unidentified peak detected only in this study.

A follow-up project is needed to determine the identity of the unknown peaks we observed. Our results suggest that *V. myrtillus*, instead of cranberry, would be an improved standard as a basis for the anthocyanin profile analysis of these and other subtropical and wild *Vaccinium* species. Further research should examine fruit characteristics and anthocyanin profiles of other blueberry wild relatives in this diverse genus.

Conclusion

Fruits of *V. myrtoides* and *V. floribundum* are in demand in their native regions. A higher anthocyanin concentration was present in both species compared to 'O'Neal. *V. myrtoides* had more anthocyanin compounds than the other observed accessions, suggesting that the fruit of these wild species could help diversify anthocyanins available in domesticated blueberries. Since *V. floribundum* is comparable to O'Neal in percent soluble solids, pH, berry diameter, and weight, a broader exploration of cultivation for the fresh market may be warranted because the fruit is already considered acceptable according to these explored metrics. While we identified most of

Table 3. Comparison of detected anthocyanins in our study using NCGR plants, reported presence for *V. myrtillus* and *V. floribundum* in Vasco et al. 2009, and the cranberry standard at the Linus Pauling Institute. Abbreviations used with D being delphinidin, C being cyanidin, Pt being petunidin, Pd being peonidin, and M being malvidin. Gal is galactoside, Glu is glucoside and Arab is arabinoside.

Anthocyanin	D-3-Gal	D-3-Glu	C-3-Gal	D-3-Arab	C-3-Glu	Pt-3-Gal	C-3-Arab	Pt-3-Glu	Pd-3-Gal	Pt-3-Arab	Pd-3-Glu	(D-aglycon)	M-3-Gal	Pd-3-Arab	M-3-Glu	M-3-Arab	(C-aglycon)
Vaccinium myrtillus (Vasco et al. 2009)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓	✓
Vaccinium floribundum (Vasco et al. 2009)	✓		✓	✓	✓	✓	✓					✓					✓
Vaccinium floribundum (NCGR)	✓		✓	✓	✓		✓										
Vaccinium myrtoides (NCGR)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓							
O'Neal (NCGR)				✓		✓		✓		✓							
Cranberry (Linus Pauling)			✓		✓		✓	✓		✓							

the anthocyanins present, there is an anthocyanin peak in the profiles of *V. myrtoides* and *V. floribundum* that we could not identify. *V. myrtillus* may be a more appropriate standard to determine anthocyanin profiles of wild germplasm. Research into culturally relevant wild species can aid the expansion of blueberries and locally adapted related crops. Improved selections of these species could provide opportunities within their traditional communities. The differences in anthocyanin concentration and composition, which is higher in the wild species, may have future applications in diversifying these traits in cultivated blueberries.

Acknowledgments

We would like to acknowledge the staff of the NCGR for maintaining the living gene bank of accessions and CRIS 2072-21000-049-00D and the Oregon Blueberry Commission for financial support. We also appreciate the use, help, and support of the Linus Pauling Institute, Oregon State University, and Corvallis facilities.

References Cited

Ballington JR, Mainland CM, Duke SD, Draper AD, Galletta GJ. 1990. O'Neal' southern highbush blueberry. HortScience. 25(6):711-712. https://doi.org/10.21273/HORTSCI.25.6.711

Barcelo R, Basilio A, Calsiyao ID, Mabesa CB, Palconete RM, Tobias JA. 2015. Antioxidant property and total polyphenol and flavonoid content of selected fruits and fruit wines. PeJARD. 5:57-64. http://pejard.slu.edu.ph/vol.5/2015.12.17.pdf

Chua-Barcelo RT. 2014. Ethno–botanical survey of edible wild fruits in Benguet, Cordillera administrative region, the Philippines. Asian Pacific J Trop Biomed. 4:525-538. https://www.sciencedirect.com/

science/article/pii/S2221169115303221

Chai Z, Herrera-Balandrano D D, Yu H, Beta T, Zeng Q, Zhang X, Tian L, Niu L, Huang W. 2021. A comparative analysis on the anthocyanin composition of 74 blueberry cultivars from China. J Food Composition and Anal. 102:104051. https://doi.org/10.1016/j.jfca.2021.104051

Darnell RL, Williamson JG. 1997. Feasibility of blueberry production in warm climates. Acta Hort. 446:251-256. DOI: 10.17660/Acta Hortic.1997.446.37.

Draper A, Hancock J. 2003. Florida 4B: native blueberry with exceptional breeding value. J Amer Pomol Soc. *57*(4), 138.

Durst RW,Wrolstad RE. 2001. Separation and characterization of anthocyanins by HPLC. Current Protocols in Food Anal Chem. 00: F1.3.1-F1.3.13. https://doi.org/10.1002/0471142913.faf0103s00

Ehlenfeldt MK, Draper AD, Clark JR. 1995. Performance of southern highbush blueberry cultivars released by the US Department of Agriculture and cooperating state agricultural experiment stations. HortTechnology. 5(2):127-130. https://journals.ashs.org/horttech/view/journals/horttech/5/2/article-p127.xml

Esquivel-Alvarado D, Muñoz-Arrieta R, Alfaro-Viquez E, Madrigal-Carballo S, Krueger CG, Reed JD. 2019. Composition of anthocyanins and proanthocyanidins in three tropical *Vaccinium* species from Costa Rica. J Agric Food Chem. 68(10):2872-2879. https://pubs.acs.org/doi/full/10.1021/acs.jafc.9b01451

Faostat. 2020. Value of Agricultural Production, Blueberries. https://www.fao.org/faostat/en/#data/QV. [accessed 30 Nov 2022]

Ferrão LF, Johnson TS, Benevenuto J, Edger PP, Colquhoun TA, Munoz PR. 2020. Genome-wide association of volatiles reveals candidate loci for blueberry flavor. New Phytol. 226(6):1725-1737. https://nph.onlinelibrary.wiley.com/doi/full/10.1111/nph.16459

Grace MH, Xiong J, Esposito D, Ehlenfeldt M, Lila MA. 2019. Simultaneous LC-MS quantification of anthocyanins and non-anthocyanin phenolics from blueberries with widely divergent profiles and biological activities. Food chem. 277:336-346. https://doi.org/10.1016/j.foodchem.2018.10.101

Hancock J. 2004. Northern highbush blueberry breeding. VIII International Symposium on *Vaccinium* Culture 715:37-40. https://doi.org/10.17660/ActaHortic.2006.715.2

Hummer KE, Bassil NV, Rodríquez Armenta HP, Olmstead JW. 2015. *Vaccinium* species ploidy assessment. Acta Hort. 1101:199-204 https://doi.org/10.17660/ActaHortic.2015.1101.30

Hummer K, Durst R, Zee F, Atnip A, Giusti MM. 2013. Phytochemicals in fruits of Hawaiian wild cranberry relatives. J Sci Food and Agric. 94(8):1530-1536. https://onlinelibrary.wiley.com/doi/full/10.1002/jsfa.6453

Mengist MF, Grace MH, Xiong J, Kay CD, Bassil N, Hummer K, Ferruzi MG, Lila MA, Iorizzo M. 2020. Diversity in metabolites and fruit quality traits in blueberry enables ploidy and species differentiation and establishes a strategy for future genetic studies. Front Plant Sci. 11:370. https://www.frontiersin.org/articles/10.3389/fpls.2020.00370/full

Mirghani MES, Daoud JI, Elnour AA. 2019. Wild Species of *Vaccinium* composition, nutritional value, and utilization, p 523-537. In: Mariod AA (ed). Wild Fruits: composition, nutritional value, and products. Springer Cham, New York, NY, USA. https://onlinelibrary.wiley.com/doi/full/10.1002/jsfa.6453

Ortiz J, Marín-Arroyo MR, Noriega-Domínguez MJ, Navarro, Arozarena I. 2013. Color, phenolics, and antioxidant activity of blackberry (*Rubus glaucus* Benth.), blueberry (*Vaccinium floribundum* Kunth.), and apple wines from Ecuador. J Food Sci. 78(7):985-993. https://ift.onlinelibrary.wiley.com/doi/full/10.1111/1750-3841.12148

Patel N, 1993. Blueberry culture in Australia. Acta Hort. (346):45-52. https://doi.org/10.17660/ActaHortic.1993.346.5

Rabobank. 2019. Newcomers reshaping the US fresh blueberry market: what to expect in 2019/20 and beyond. https://research.rabobank.com/far/en/sectors/fresh-produce/US_blueberry_market.html. [accessed 9 Mar 2023]

Saftner R, Polashock J, Ehlenfeldt M, Vineyard B. 2008. Instrumental and sensory quality characteristics of blueberry fruit from twelve cultivars. Postharvest Biol Technol. 49(1):19-26. https://www.sciencedirect.com/science/article/abs/pii/S0925521408000173

Santamaría PC, Coronel D, Verdugo K, Paredes MF, Yugsi E, Huachi L. 2012. Estudio etnobotánico del mortiño (*Vaccinium floribundum*) como alimento ancestral y potencial alimento funcional. LA GRANJA. Revista de Ciencias de la Vida. 16(2):5-13. https://www.redalyc.org/articulo.oa?id=476047400002

Stringer SJ, Draper AD, Spiers JM, Marshall DA. 2009. Potential new blueberry cultivars for the Gulf Coast region of the U.S. Acta Hort. 810:87-92 https://doi.org/10.17660/ActaHortic.2009.810.7

Taco-Ugsha MA, Santacruz CP, Espinoza-Montero PJ. 2020. Natural dyes from Martino (*Vaccinium floribundum*) as sensitizers in solar cells. Energies. 13(4):785. https://www.mdpi.com/1996-1073/13/4/785

Vasco C, Riihinen K, Ruales J, Kamal-Eldin A. 2009.

Chemical composition and phenolic compound profile of mortiño (*Vaccinium floribundum* Kunth). J Agric Food Chem. 57(18):8274-8281. https://pubs.acs.org/doi/full/10.1021/jf9013586

Vilela A, Gonçalves B, Ribeiro C, Fonseca AT, Correia S, Fernandes H, Ferreira S, Bacelar E, Silva AP. 2016. Study of textural, chemical, color and sensory properties of organic blueberries harvested in two distinct years: A chemometric approach. J Texture Stud. 47(3):199-207. https://onlinelibrary.wiley.com/doi/abs/10.1111/jtxs.12173

Yan Y, Pico J, Gerbrandt EM, Dossett M, Castellarin SD. 2023. Comprehensive anthocyanin and flavonol profiling and fruit surface color of 20 blueberry genotypes during postharvest storage. Postharvest Biol and Technol. 199. 112274. https://doi.org/10.1016/j.postharvbio.2023.112274