The genus Vaccinium contains a wide diversity of culturally and economically important berry crop species, including blueberry and cranberry. Consumer demand and scientific research in both have increased globally over the crops’ relatively short domestication history (~100 years). Consumer and industry demand for more fruit with improved quality and health related traits continues to grow.

New tools and resources are needed to develop superior cultivars that meet consumer preferences, and are more resilient to a changing environment. Over the years, there have been increasing accomplishments and goals across a wide variety of Vaccinium fruit crop research areas. But, more comparative studies in Vaccinium that include a wider diversity of wild and cultivated species are needed to meet those consumer and industry demands.

Breeding Priorities for Blueberry, Cranberry, and Related Crops

The main commercial Vaccinium crops are cranberry, lingonberry, and blueberries, which includes northern highbush blueberry, lowbush blueberry, and rabbiteye blueberry. Traditional blueberry and cranberry breeding methods are expensive and time-consuming, taking at least a decade to release new cultivars. Over the last thirty years, investments in blueberry breeding led to the development of new low-chill southern highbush cultivars and contributed to the massive expansion of the industry.
of production in many non-traditional areas worldwide. Other target breeding traits for blueberry improvement are:

- **Yield**
- **Fruit quality (size, color, firmness, flavor)**
- **Vegetative characteristics (vigor, disease resistance, plant architecture to facilitate harvest mechanization)**
- **Adaptation (cold hardiness, self-fruitfulness, soil pH tolerance).**

For cranberry, high but stable yields are a critical trait as many cultivars exhibit a biennial—every other year—bearing habit. Other priority traits for cranberry improvement are:

- **Fruit quality (color, firmness, uniform large size for the sweetened dried cranberry market)**
- **Disease and pest resistance**
- **Vegetative characteristics (vigor, adaptation including heat, cold tolerance)**

Breeding priorities across the North American blueberry and cranberry industries were assessed through a survey, conducted between 2016-2018, as part of a planning grant funded by USDA-NIFA, and served as a foundation to establish the Vaccinium Coordinated Agricultural Project (VacCAP).

**Genomic, Transcriptomic, and Metabolomic Resources for Vaccinium**

Blueberry cultivar development, while already seeing improvement, needs more publicly available genomic resources to meet increased consumer demand and preferences quicker. There has been significant development of marker-assisted breeding resources, but next-generation genomic, transcriptomic, and metabolomic resources are critical to guide the development of these markers.

The Genome Database for Vaccinium (GDV) — the crop community database for Vaccinium—provides access to integrated genomic, genetic, and breeding peer-reviewed published data, and analysis tools. The repository in GDV contains gene, genome, genetic map, marker, phenotype, publications, QTL, species, transcriptome, and trait data curated by the GDV team. Tools include a genetic map viewer, genome browser, synteny viewer, metabolite pathways browser, sequence retrieval, BLAST, and breeding information management system (BIMS). A suite of search tools provides intuitive querying of all major data types.

Additional Vaccinium genomic resources will soon be available through VacCAP. A cornerstone of VacCAP is developing a Vaccinium pangenome—a collection of genetic material present within a taxonomic group. Building a pangenome is necessary to identify and characterize all important genes in Vaccinium, and to develop markers to guide future breeding efforts.

Recent availability of high-quality reference genomes for Vaccinium and technological advances in RNA-sequencing have also advanced transcriptome profiling. Recent studies have focused on everything from the biosynthesis of metabolites with human health benefits to postharvest storage. Transcriptome and transcript expression data can also be found through GDV and future resources will be made available through VacCAP.

While databases for genome and transcriptome data are available, there is no comprehensive resource to access metabolic information specific to Vaccinium. However, several papers reporting metabolite composition of several Vaccinium species have been published. With the increasing use of metabolomic techniques, more studies on the metabolite composition of Vaccinium are expected. As depositing data in a metabolomics database like GDV, researchers can enhance our understanding of these compounds and their potential uses.
repository becomes a requirement for publishing, this will allow for more comprehensive metabolite resources to be available and easily accessible in the future. Species-specific differences could complicate data analysis for Vaccinium, so a source of Vaccinium metabolite data generated by a consortium of laboratories will be crucial for establishing metabolomics as a functional genetics tool.

Having publicly available comprehensive genomic, transcriptomic, metabolomic and proteomic datasets in addition to a community-based platform for connecting such data is essential to understanding how gene-metabolite networks determine specific traits. The recently established Paired Omics Data Platform is an initiative to help streamline access to paired genomic and metabolomic data from public databases and repositories.

**Genetics of Fruit Quality and Related Target Traits**

Fruit quality is subjective depending on your role in the production chain—a grower may value a different trait than a consumer. This discrepancy poses a challenge to modern blueberry and cranberry breeding programs, who now must balance the needs of all parties and release new cultivars that produce higher quality fruit without sacrificing the horticultural traits required by the industry. Researchers recently revised some blueberry quality standards established in the 1990’s and noticed that the rapid genetic progress has changed the standards for fruit quality.

Firmness has experienced the fastest breeding progress in blueberry. Firmness, an indicator of texture quality, is a desirable fruit quality trait for both growers and consumers. Firmness may reduce internal bruising during machine harvesting and delay postharvest decay. In a comprehensive review, Cappai et al. (2018) reported a large diversity in firmness between and within blueberry types and most importantly, a substantial improvement in modern cultivars compared to the first-released cultivars, indicative of intense breeding progress.

Blueberry fruit size is another trait that has experienced profound changes over time. A large variability among cultivars and wild species has been reported, and a significant association for firmness and size co-localized in both a QTL and genome-wide association (GWAS) study indicate good prospects for simultaneous selection for both traits. Sugar-acid balance is another trait of importance in blueberry flavor perception, as consumers prefer a sweeter berry, resulting in newer cultivars with reduced soluble solids/total titratable acidity ratios.

A recent consumer perception survey showed that consumers are most interested in fruit aspects related to flavor and human health attributes. A second group of metabolite traits have been explored at the breeding level, with the potential for flavor and nutritional improvements.

Besides the recent advances in blueberry and cranberry genetics, an understanding of the genetic mechanisms controlling various traits in blueberry and cranberry is still limited. Few QTLs have been validated across multiple studies and very few candidate genes have been identified. The increasing availability of genetic and genomic tools for Vaccinium crops will help fill in the gaps. Multiple genetic studies targeting several fruit characteristics such as harvest and postharvest studies to assess texture and storability, organic acids and metabolites are currently ongoing as part of VacCAP. Along with other projects, these efforts will establish a roadmap for a marker assisted breeding (MAB) strategy in Vaccinium crops.

**Molecular Markers and High-Throughput Genotyping Platforms**

Diverse tools and approaches have been used to guide breeding efforts in Vaccinium. Dominant markers were developed and used in blueberry and cranberry over the years. Simple sequence repeats (SSRs) were extensively used both to assess relatedness and genetic diversity, for cultivar identification, and linkage mapping. As Next Generation Sequencing (NGS) technologies were applied in Vaccinium, species-specific SSRs were developed and the era of high throughput genotyping and single nucleotide polymorphism (SNP) markers began in blueberry and cranberry.

There are two types of approaches to high throughput genotyping, targeted and non-targeted. Both approaches have been used in tetraploid cultivated blueberry (V. corymbosum), while only genotyping by sequencing (GBS), a non-targeted approach, has been used in cranberry.

GBS has been useful in both crops, used for the analysis of genetic diversity linkage mapping and QTL analysis. In cranberry, high-density linkage maps allowed the identification of many cranberry QTLs associated with traits like fruit shape and fruit color. However, GBS has limited application for polyploid Vaccinium such as highbush and rabbiteye blueberries as its sequencing read depth is often highly variable between loci and samples. Target capture's read depths are more consistent between samples and loci. This allows for more correctly estimated allele dosage which helps in identifying SNPs associated with traits like fruit quality and cold hardness. Target sequencing also has been used to genotype a diversity panel of 280 blueberry accessions and cultivars collected from the North Carolina State breeding program and National Clonal Germplasm Repository in Corvallis.

GBS and target capture require bioinformatics capability and reproducible workflows for data analysis. VacCAP’s goals to develop high-throughput genotyping platforms, improve of software, decrease sequencing costs, and create reproducible workflows are necessary in this endeavor. These will allow for faster MTA discovery, and enable genomic and marker-based selection that are all needed for the development of new superior cultivars.

**Genome-Assisted Breeding in Vaccinium**

Modern genomic tools have shown the potential to reshape
current blueberry and cranberry breeding programs by allowing for more efficient selection, faster cultivar development, and assists in maintaining a genetically diverse breeding population. Genomic-assisted breeding has been bolstered by advancements and declining costs in sequencing technologies along with new methods for genomic data manipulation.

Linkage maps help with the detection of major QTLs in association analyses. Genetic linkage maps in blueberry have become continually more saturated and higher resolution by including more markers and recombinant individuals, respectively. A high degree of collinearity between blueberry and cranberry genetic maps indicates the potential for QTL and marker transferability between species. The objective of QTL mapping analyses is to identify marker-trait associations based on the inheritance of markers within a family-based mapping population. Identifying the genomic regions controlling important horticultural and fruit quality traits are important for marker-assisted selection. The first QTL mapping study focused on understanding the underlying genetics of cold hardiness and chilling requirement related traits in blueberry. In the years since, consistent QTLs were identified for fruit quality and machine harvest-related traits.

GWAS is a genomic tool for the identification of genetic variants associated with important traits. GWAS takes advantage of the linkage disequilibrium from historic recombination events accumulated over generations in a diverse panel of genotypes. Thereby, it provides higher resolution for the QTL mapped, makes use of greater allele numbers, detects more frequent QTLs in the population, and multiple traits can be assessed. GWAS analyses have been recently performed in southern highbush blueberry for fruit quality and yield-related traits, including flavor-related volatile compounds.

QTL mapping and GWAS studies are paving the way for the use of molecular markers to select superior genotypes. Marker-assisted selection is not being fully integrated into any public Vaccinium breeding program so far, but once significant markers explaining a large proportion of trait variability are identified, it can be used to inform breeding and selection decisions. Genomic selection is being implemented in select public and private blueberry breeding programs.

Gene and Gene Editing for High Precision Breeding

Traditional breeding of Vaccinium crops is a time-consuming and labor-intensive process. However, recent advances in Vaccinium genomics and gene editing technologies could be used to target desirable horticultural traits within the genomes of Vaccinium species.

Genetic engineering relies on the presence of suitable target genes and new biotechnological tools such as efficient transformation protocols and effective gene manipulation. Genetic engineering would greatly speed the introduction of individual genes of interest for precision breeding of desirable characteristics among existing cultivars. Stable transformation of both blueberry and cranberry has been made possible with the development of efficient regeneration protocols. Genetic transformation of cranberry has, to date, resulted in the development of transgenic cranberry for herbicide resistance. Transgenic blueberries have been developed for herbicide resistance, freezing tolerance, early flowering, yield increase, and gene knock-out.

Great efforts have been made to improve blueberry and cranberry using genetic engineering; however, no genetically modified Vaccinium crops have been released for commercialization. Currently, a lack of research funds from government and industry sources has slowed the application of genetic engineering for improvement of Vaccinium crops and consumer acceptance is unclear.

Conclusion

Over the last few years, the first high-quality chromosome-scale assemblies for blueberry, cranberry, and bilberry have been published and provided an excellent set of resources for understanding the underlying genetics of important target traits in Vaccinium fruit. Creating pangenomes for each crop will be instrumental in quantifying and dissecting the diversity present in wild populations and various breeding programs. Developing new genotyping tools and technologies in phenotyping will help accelerate genetic discoveries and advance breeding efforts. New tools and resources will pave the way for developing new cultivars that meet consumer and industry preferences. Data infrastructure, storage and analyses, and efforts to conserve wild germplasm around the world are also important. Genetic and phenotypically diverse wild populations could improve the resilience of Vaccinium crops and various fruit quality traits, particularly important in mitigating production issues related to global climate change.
High-Density Linkage Map Construction and Identification of Loci Regulating Fruit Quality Traits in Blueberry

Blueberries have seen a rapid increase in consumer demand and production over the past 15 years. The North American blueberry industry and consumers are more selective of their fruit choice, with an increased focus on quality. Multiple studies in blueberry over the last decade reported that fruit quality (FQ) traits influence consumer preferences. As fruit quality traits play a significant role in consumer preferences, understanding what controls these qualities within the berry is important. Some cultivars already meet consumer preferences, but FQ traits vary greatly between them. The blueberries consumers pick up in grocery stores are a mix of multiple cultivars, often leading to an inconsistent eating experience for consumers and impacting future consumption.

Developing new cultivars that meet consumer preferences is critical for sustaining the growth of the blueberry market. For years, blueberry breeding has relied on phenotypic-based selection. But this process is pricey, can take anywhere from 10–20 years, and is somewhat inefficient, leaving breeders only able to select for a limited number of traits. With so much need to improve FQ traits, techniques like DNA or genomic-assisted breeding will be a necessity for the future of the industry in order to meeting consumer FQ preferences at a faster pace. Understanding the genetics that influences these traits is the first step to further develop DNA-assisted breeding.

The most common method to study the genetic mechanism and genes that control a phenotype like FQ traits, is called quantitative trait loci (QTL) mapping. Through this analysis, DNA markers representing the region of the genome are associated with a given phenotype and are named QTL. Due to limited availability of resources—like high-density linkage maps—needed for this type of study in blueberry, only a few QTL studies for FQ traits have been performed. VacCAP is working to close these gaps and to gain a better understanding of these economically important traits’ genetics, in order to improve future cultivars for consumer preferences.

The objectives of this study were to construct a high-density linkage map and to identify the underlying genetic basis of FQ traits in blueberry. The study also investigated the association between FQ traits and organic acids, sugars, and amino acids.

A total of 287 F1 individuals derived from a cross between two southern highbush blueberry cultivars, ‘Reveille’ and ‘Arlen’, were phenotyped over three years (2016–2018) for FQ traits. These traits include:

- size (FW)
- total soluble solid content (TSS), correlated with fruit sweetness
- itratable acidity (TA), correlated with fruit acidity

In addition, the study evaluated the correlation between FQ traits and the chemical composition of blueberry fruits in particular organic acids and sugars, which contribute to TA and TSS, respectively.

**High Density Linkage Map Construction**

High-density genetic maps are necessary for genetic/QTL mapping studies, and are useful for genomic-assisted breeding—providing critical information about the organization of the genome of the population being evaluated. Yet, due to high costs and limited tools, only two linkage maps are currently available for tetraploid blueberry. The linkage map constructed here integrated 17,438 DNA markers, that represent the largest set of markers (17,438) and F1 individuals (287) in blueberry. Also, the map covered all 96 parental homologous chromosomes.

**Genetics of Fruit Quality Traits and Association with Chemical Composition**

Eighteen QTLs loci for FW, TA, TSS and pH were identified, with ten of them detected in more than one year. A total of 25 metabolites peaks including seven sugars, five organic acids, and nine amino acids were detected and used for correlation analysis.

Citric acid and quinic acid were the most abundant organic acids in blueberry, respectively. Beta glucose followed by fructose were the most abundant sugars. Arabinose and maltose were the least abundant sugars in blueberry. The data also showed that arabinose is an important discriminant variable
in the sugar group. Among the annotated amino acids, arginine and 4-amino butyrate were the most abundant. Isoleucine and asparagine were the least abundant amino acids observed in blueberry.

Highlights of the QTL mapping and correlation analysis for each trait are summarized below.

**Total Soluble Solid Content (TSS)**
- Seven QTLs were identified
- Six of those QTLs, three mapped on chromosome 7 and three mapped on chromosome 10, were detected across three years
- QTLs explained phenotypic variance ranging from 7 to 28%
- Sugars molecules showed a positive correlation with TSS.

**Titratable Acidity (TA)**
- Seven QTLs were identified
- Six of those QTLs, three mapped on chromosome 3 and three mapped on chromosome 5, were detected across three years
- QTLs explained phenotypic variance ranging from 7 to 28%
- Organic acids, citric acid, and quinic acid were significantly and positively correlated with TA
- Citrate is an important variable to discriminate the genotypes and strongly associated with TA

**pH**
- Ten QTLs were identified
- Three of those QTLs, mapped on chromosome 3, were detected across three years and co-localized with that of TA
- QTLs explained phenotypic variance ranging from 8 to 13%

**Fruit Size (FW)**
- Thirteen QTLs were identified
- Three of those QTLs, mapped on chromosome 4, were detected across three years
- QTLs did not explain more than 10% of the phenotypic variance

Overall, stable QTLs—those detected across three years—were noted for all FQ traits. This indicates that the genetic regions underlying these QTLs affect the traits independently of the year or environment. Stable QTLs are the best candidates to design DNA assisted-breeding strategy.

The results also indicated that the QTLs for TA and pH mapped on chromosome 3 likely represent the same genetic locus and are explained by the accumulation of organic acids, in particular citric acid.

**Why Are These Traits Important?**

Consumers indicated flavor and sweetness as positive blueberry traits, with TSS as the most and TA as the least important characteristics associated with overall consumer preferences.

The balance between sugars and acids is a determinant factor for taste. For example, sweet berries don't inherently have high sugar content, but simply lower level of acids, resulting in a higher the sugar/organic acid ratio. In this study, strong correlation was observed between TA and pH, which are excellent predictors of blueberry sourness—a negative trait for consumers. The higher the acidity, the less they prefer the fruit. However, they did not show strong and consistent correlation with FW and TSS over the years, suggesting that the relationship between these traits was strongly environmentally dependent, which aligns with previous studies.

FW is an important as consumers prefer larger berries. This study highlighted that larger-sized berries have higher sugar concentrations than smaller-sized berries. This suggests selection for larger fruit could lead to selection for high sugar content and TSS—associated with sweetness, a positive consumer trait. However, FW was negatively correlated with multiple acids, and both phenotypic and genetic analysis suggests the trait is a complex genotype by environmental factors.

**The Future of Blueberry Breeding**

This study provides critical, first insight into the genetic inheritance of multiple, key FQ traits, developed a high-density linkage map with highest number of markers and individuals, and established the first assessment of the relationship between fruit quality traits and metabolites (sugars, organic acids, and amino acids).

The development of blueberry varieties that consistently meet consumer preferences is a high priority for the industry. Informed by the observations in this study, breeders can design a strategy to optimize their breeding programs, selecting for QTLs that meet the right balance between increase TSS and reduce TA, to bring the best cultivars to consumers. Complementary studies on FQ traits associated to consumer preference—including FW, TSS, TA and pH—are ongoing as part of the VacCAP project.
What is the project you’re working on for VacCAP about?

With Dr. R. Karina Gallardo, my study focuses mostly on evaluating the potential socioeconomic impact of improved blueberry and cranberry fruit quality on market demand. The first objective is to determine whether “added sugars” on the nutrition facts panel influences consumers’ preference for sugar-sweetened cranberry products under different nutrition-related information treatments. The second objective is to examine the consumers’ trade-off between reduced sugar content and gene-editing; and the third objective is to determine what stimulates the consumption of blueberries.

What is something you like or find most interesting about your work?

The most interesting part is to apply knowledge on performing the analyses and understand consumer’s behavior and it is a great opportunity to communicate and collaborate with excellent researchers.

What do you hope to do in the future after your work here?

I hope to continue working as a researcher to comprehend consumer behavior and to be a good contribution to the global food safety.

Anything else you would like to add?

I would like to thank Dr. Karina Gallardo for her guidance and mentorship during my study.
Breeder Spotlight: Jim Olmstead and Jessica Gilbert

In our Breeder Spotlight Series, we interview blueberry and cranberry breeders to learn more about their roles, challenges in their breeding programs, and have them highlight some of their favorite new cultivars. In this spotlight, we spoke to Jim Olmstead, Global Blueberry Breeding Director, and Jessica Gilbert, Molecular Blueberry Breeder, from Driscoll's, Inc.

Please describe your role in the cranberry industry.

Jim: We are part of the Blueberry Breeding team at Driscoll’s. Driscoll’s has been in the berry business for over one hundred years, but only began breeding blueberries in the 1990s. I have been the Global Blueberry Breeding Director for Driscoll’s for almost six years now. My role is to provide vision and leadership for the multiple blueberry breeding programs and trial locations for the R&D Business Unit. I direct a team of scientists with the sole focus on breeding and genetics.

Jessica: In 2015, Driscoll’s leadership made significant additional investment in developing molecular breeding techniques. Along with building state of the art molecular and chemistry labs, I was hired along with several new scientists that year. My role as the Molecular Blueberry Breeder works in close collaboration with our global blueberry breeding programs and molecular team to establish genomic resources, design trials to identify molecular markers for important traits, and implement strategies for genomic prediction.

Together, we are part of a team of 17 breeders and scientists in the US, Mexico, Peru, Morocco, Portugal, and the UK. We develop new blueberry cultivars that advance the mission at Driscoll’s worldwide – to continually delight Berry Consumers through alignment with our Customers and our Berry Growers.

Cultivar Highlight - Please tell us about some top cultivars you’re excited about and why you chose them.

There are three recent commercial releases from Driscoll’s that we’d like to highlight. They epitomize the opportunity we both saw when moving to Driscoll’s. They will grow in different areas but have the common thread of being highly differentiated in flavor, fruit size, and texture compared to the standard cultivars grown in those areas. Lucy is a high chill mid-to-late season cultivar that we are planting widely in the Pacific Northwest. We look to use its beautiful appearance and outstanding flavor to follow Draper in timing. Rosita and Raymi are two no chill cultivars that will be grown in Mexico and Peru, respectively. Both have outstanding flavor, size, and firmness.

What are some challenges in the breeding program?

We think the biggest challenge for the Driscoll’s breeding program is just how good the competition is. There are a lot of very strong breeding programs out there, releasing highly competitive cultivars into the marketplace. For a company that has built a business model around providing the best genetics to growers, this keeps us on our toes!

Where do you see the future of Vaccinium breeding going in the next 20 years?

We expect to see a continued move toward commoditization of blueberry production. If you look at the North American marketing curve for 2021, the windows where there used to be low points of production with higher prices have really begun to level out. There are no “easy wins” anymore – every new cultivar will have to be competitive from a yield and fruit quality standpoint. The marketplace is looking for flavor and fruit quality, so there is no margin for error there, but growers will need competitive yield and harvest efficiency to make future plantings viable. Differentiation will be the key to making new cultivars stand out, and we are excited to follow in the footsteps of our specialty Tropical and Rosé strawberries and raspberries. Expect to see some exciting new product differentiation from blueberries in grocery stores in the next several years!

In what way have you used resources from VacCAP to facilitate your work?

We made the decision early on to focus on the community-developed genotyping platform for our high throughput genotyping needs. From the start, we’ve participated and contributed to develop genotyping capacity. We have submitted hundreds of selections in our breeding programs for genotyping via the VacCAP-developed high density genotyping probe set. We expect to be able to use the genotypic data for continued marker discovery and parent prediction modeling.
Bilberry (Vaccinium myrtillus L.) is prized for its taste and health properties and has provided essential nutrition for Northern European indigenous populations. It contains high concentrations of phytonutrients, with perhaps the most important being the purple-coloured anthocyanins, found in both skin and flesh.

Unlike its cultivated relatives, bilberry remains largely undomesticated, with berry harvesting almost entirely from the wild. As such, it is ideal for genomic analysis, providing comparisons with the domesticated Vaccinium species.

The bilberry genome assembly sequenced by a team from Plant & Food Research and VacCAP researchers, builds on the genomic resources and knowledge of Vaccinium species, to help understand the genetics underpinning some of the quality attributes that breeding programs aspire to improve. The conservation of genome structure between bilberry and blueberry genomes means that comparative genome mapping can be applied to transfer knowledge about marker-trait association between these two species, as the loci involved in key characters are orthologous (genes in different species that evolved from a common ancestral gene by speciation).
Oregon State University Blueberry Field Day 2022

On July 20, 2022, Oregon State University hosted their Blueberry Field Day. The event was an opportunity for the community to learn about current blueberry research at OSU, as well as try the latest fruit selections from the USDA/OSU cooperative breeding program. Photos courtesy of Lisa Wasko DeVetter.

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