Apple Breeding, Genetics and Genomics

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Cornell's apple breeding program has released 65 apple varieties since its inception in the late 1890s. These varieties have contributed to the sustainability of our apple industry. However, what sets Cornell apple breeding apart from many other programs is the broad interdisciplinary team of researchers and extension personnel that provides expertise to our program. Plant pathologists, entomologists, physiologists, geneticists, food scientists, postharvest physiologists, anatomists and marketing experts are all willing to engage in collaborative projects, aid in screening of germplasm (plants/progenies, named varieties) and study unique recombinants (offspring) often found in the program. These unique offspring may hold the answer to common problems in apple production, they may offer new tree forms, enhanced quality, or a key to genetic resistance to diseases and disorders.

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Cornell's 'Cortland' apple turns 100 years old this year! This demonstrates the staying power of a variety released in 1915. 'Macoun', released in 1923, has found a new boost with MCP use for storage. More recent releases, NY 1 and NY 2 apples, patented in 2011 (Brown and Maloney 2011a, 2011b) and trademarked as 'SnapDragon'™ and 'RubyFrost'™, respectively, have been a great success story of a University (Cornell), partnering with an industry (NY Apple Growers, LLC., now Crunchtime Apple Growers). Please see the website at www.crunchtimeapplegrowers.com. These apples have tag lines: "Monster Crunch" for 'SnapDragon'™ and "Cool, crisp and craveable" for 'RubyFrost'™. The logos are attractive and the packaging draws consumers in. Growers have been active in conducting in-store demonstrations and providing fruit samples. Consumer reactions have been very positive. Pack-outs are excellent for these two new varieties. (Figures 1, 2).

Growers have been helped in harvest timing and storage decisions from the work of Chris Watkins and Jackie Nock, in cooperation with our program (Brown et al. 2012). Sequential harvest of these two apples, over a 5-week interval, followed by grower and research assessment of fruit from each harvest, helps to target optimum harvest timing and the best storage temperatures and conditions. These tests have been conducted yearly.

Rootstock recommendations for NY 1 and NY 2 have been aided by Cornell researchers, our experience with these cultivars, and feedback from growers. NY 1 is a weak scion, while NY 2 is a vigorous grower, so rootstock choice should be adjusted accordingly. The significant acreage of these two varieties has aided in rapid identification and analysis of any emerging production issues. A recent example is leaf coloration on NY 1. Samples are being collected and nutrient analyses run. Potassium deficiency may be the cause of this disorder, and Professor Lailiang Cheng in the Horticulture section at Cornell will be providing recommendations.

Figures 1 and 2. Fruits of NY 1 and NY 2, ready to be sold.

Variety Testing and Discussion of New Offerings

We test materials from many breeding programs and nursery offerings and report on their strengths and weaknesses, from data collected as part of our New York Apple Research and Development Grant. Additional information on varieties is available upon request. Examples of updates include an update on cultivars, brands and clubs (Brown and Maloney 2013, 2009) and scab resistant cultivars (Brown and Maloney 2008).

Apple scab ***(Venturia inaequalis)***. Scab-resistant varieties remain of interest, despite the challenges in finding varieties with both resistance to more than scab, and commercial quality (Brown and Maloney 2008). The erosion of the major gene, Vf,

used almost exclusively in many breeding programs, has made breeders accelerate the pyramiding or stacking of resistance genes. Disease resistance, including scab, is a priority of the Specialty Crops Research Initiative grant, RosBREED 2. Genes other than Vf are being investigated (such as from Malus baccata jackii and 'Antonovka') and molecular markers are being developed to allow pyramiding of genes in one variety. 'Honeycrisp' apple, known for good field resistance to scab, was found to have additional genes for resistance (Clark et al. 2004). These resistance genes are being studied in the RosBreed2 project, so that they can be identified and molecular makers can be developed for selection. There is an advanced selection from our program that is performing very well in the organic planting at the NYS Agricultural Experiment Station (A. Agnello, T. Robinson, K. Cox, NYSAES). A patent is being written for this selection to advance it to being named.

Fire blight *(Erwinia amylovora).* Breeding to enhance resistance to fire blight continues to be a focus worldwide. There are several different sources of fire blight resistance (Malus fusca, 'Evereste', Malus robusta 5), yet all need time to be incorporated into high quality commercial cultivars. Boggini et al. (2014) has applied a transgenic approach to improving resistance, but it still remains uncertain what consumer acceptability of transgenic apples will be.

The occurrence of streptomycin-resistant fire blight strains is another challenge, as is the control of fire blight in organic plantings. Our higher temperatures and increased frequency of hail events exacerbate this problem. Dr. Kerik Cox will be studying susceptibility of advanced selections from our breeding program to understand their resistance status at an early stage in the pipeline. This work was funded by the NY Apple Research and Development Program.

USDSA/ARS. Cornell's apple breeding program greatly benefits from collaboration with USDA/ARS scientists and access to the extensive collections maintained by this agency at Geneva. This resource and the need to assess the vulnerability of apple germplasm worldwide was the subject of a review by Volk et al. (2014).

There are many beneficial compounds in apple, but one in particular (phloridizin) has gained attention in the medical community, due to its potential role in regulation of glucose metabolism and diabetes. Ben Gutierrez, a graduate student of Susan's program in collaboration with Dr. Gan Yuan Zhong, USDA Research Leader at Geneva, is also an employee of the US Department of Agriculture/Agricultural Research Service (ARS). Ben's research focuses on characterizing many different Malus (apple) species and accessions/varieties for phloridizin content. This information will help in the breeding and understanding of important compounds in apple related to human health. Other research groups are also investigating apple antioxidants, yet we have the advantage of ready access to a rich collection of many different materials in the USDA and from within the breeding program.

Vitamin C. Improvement of vitamin C and the study of its inheritance has been a target of study at Geneva, in Belgium, and in other programs. Andrea Burke, a doctoral student at Cornell in Susan's program, quantified the vitamin C content at harvest and after storage for several advanced selections in the Cornell breeding program. Very simply, we crossed two high-vitamin C content apples and found that most offspring fell between the two parents, but several selections were even better than the parents (this is called transgressive segregation). This research shows that enhancing vitamin C content is a readily achievable goal, and that such progenies will aid our understanding of this vitamin. Davey (2006) found QTLs (quantitative trait loci) for vitamin C on linkage groups 6, 10 and 11, while Mellidou et al. (2012a, 2012b) identified linkage groups 10, 11.16, 17 as important to this study.

Cider apples. The new interest in cider apples is evident in the publication of new books, such as Jolicoeur's (2013) "The New Cider Maker's Handbook: A Comprehensive Guide for Craft Producers" and Beechum's (2013) "The Everything Hard Cider Book: All you need to know about making hard cider at home."

Cornell is forming a Program Work team (PWT) on hard cider to provide extension programming and research in this area. A cider meeting organized by Cornell Cooperative Extension had over 100 registered participants. A common refrain was that NYS was poised to become the "Napa Valley of hard cider", due to our industry, the new farm beverage laws, and the wealth of expertise at Cornell. The hiring of Dr. Gregory Peck, formerly at Virginia Tech., adds to our cider expertise. Greg will be in the Horticulture section of the School of Integrative Plant Sciences at Cornell. Greg has published on the economics of selling specialty apples (Farris et al. 2013). The establishment of Angry Orchard cider's research laboratory in Walden, NY, also adds to our cider resources, as does the work on cider at NYSAES.

Some of the traditional cider varieties, the bittersweets (low in acids and high in tannins, such as 'Dabinett', 'Yarlington Mill' and 'Tremlett's Bitter') and bittersharps ('Stokes Red', 'Porters Perfection') are needed in small amounts to produce a traditional hard cider (Merwin et al. 2015). These varieties are difficult to grow, many are extremely susceptible to fire blight, and they may have other production problems, such as premature fruit drop.

Two advanced selections are being tested for cider production, both at Cornell and with commercial ciderists. They are not crabapple or cider types, but in evaluating them, we felt they had sufficient flavors and characteristics to contribute to a good blended product. Initial results are promising. We will make crosses at Geneva with traditional bittersweets and bittersharps by selections having good resistance to fire blight, to produce regionally adapted cider varieties with fewer production problems, including disease susceptibility. We also have populations from a cross with Malus fusca, a native crabapple, that may hold potential for cider apples, due to its quality composition and its resistance to apple scab and fire blight. (Figure 3).

Fresh-cut. Many apple varieties brown extensively after cutting, and breeding for reduced flesh browning has been an objective of our program, coupled with a study of increasing vitamin C content. Several varieties from Cornell have excellent resistance to flesh browning, including 'Cortland', 'AutumnCrisp', and 'RubyFrost'™, which is an offspring of 'AutumnCrisp'. Other NY advanced selections have better resistance to browning than 'Cortland'. Doctoral studies by Andrea Burke and research funded by Federal Formula Funds (Hatch) identified several other selections that have excellent resistance to browning. In some cases, the resistance is due to low levels of the enzyme polyphenol oxidase (PPO), low levels of total phenolics, or a combination of the two. In some (but not all) selections, Vitamin C is correlated with reduced browning.

Morimoto et al. (2014) identified QTLs for fruit acidity and juice browning on LG 16, with high acidity cultivars/progeny showing less browning. The allele for high acidity was associated

Figures 3. Advanced selections being tested for hard cider.

with the allele for low juice browning. Sun et al. (2014) identified linkage groups 10, 15 and 17 as the areas associated with flesh browning after cutting.

'Arctic'® apples, which use anti-sense technologies to silent the browning reaction, have been approved for sale in the US, becoming the first transgenic apple approved in the US. The US-based company Intrexon acquired Okanagan Specialty Crops, the Canadian company that developed these varieties, paying $41 million. The news report is at http://www.arcticapples.com/.

Self-incompatibility (S) alleles. Understanding the incompatibility alleles (what varieties can cross-pollinate each other) is important in orchard design for pollination, yet it is especially important in making controlled crosses. The review of incompatibility by Orcheski and Brown (2012) provided information on the S alleles of many commercial varieties. Ben Orcheski, a doctoral student in the Brown lab, used molecular markers to determine that the S-alleles for NY 1 are S2S20, and the alleles for NY 2 are S9S20. Although they share an S-allele in common (Semi-compatible), test crosses and orchard performance indicates they are sufficiently cross-compatible.

RosBREED and RosBREED 2. These two cooperative projects (grants) provide large-scale coordination and characterization of traits across US apple breeding programs in NY, WA and MN (Evans et al. 2012). This allows us to leverage data across three different regions and maximizes our opportunity to tweak out effects of environment versus genetics. Such studies are identifying regions of the genome where traits are located, and are also helping to develop and test the use of molecular markers for selections of parents and/or progeny. Fruit texture (Schmidt et al. 2013), sugars, fresh fruit sensation and many other trials have been elucidated, and the information shared with breeders and other researchers. Many pedigree errors were revealed by the molecular markers, which has resolved some unexpected segregation in progenies. This research is greatly aiding genetic improvement and has fostered increased communications within the research community. Read the latest newsletter by visiting: http://www.rosbreed.org./

Future Challenges

Climate change is already increasing the occurrence of new exotic species, and we are seeing southern diseases in apples that were never previously reported in our region. Temperature extremes have resulted in the loss of crop in 2012 and hail in late summer of 2014. Extremely wet or dry conditions are impacting our choice of controls. Fruit surface disorders such as weather checking, fruit cracking, and cuticle disorders are increasing. The use of 'Honeycrisp' in breeding programs has resulted in increasing problems in progeny for both leaf spots and summer rots. Our breeding program is rating many more diseases and disorders than at any other time in its history. This echoes our need for multi-site testing to ensure that production challenges are identified and resolved. Breeding programs look to the future and try to anticipate the loss of certain chemicals or the potential for new diseases and pests. The future hiring of a person to work on the genetics and genomics of disease resistance in the Rosaceae will be a valuable addition to our core strengths in apple and other Rosaceous fruit crops. The future will be challenging, but we have many more tools and resources to meet these challenges. There will be future releases that will benefit both growers and consumers. There has never been a better time than now to be involved in apple breeding, genetics and genomics.

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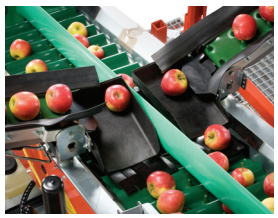

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