Breeding Apple Rootstocks to Match Cultural and Nutrient Requirements of Scion Varieties

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In the U.S., there are approximately 7,500 apple producers who collectively grow 240 million bushels of apples on average each year, on 322 thousand total acres of land. The farm-gate revenue, or wholesale value, of the U.S. apple crop annually is close to $4 billion, with a predicted additional $14 billion in related downstream economic activity each year (U.S. Apple Statistics). What is the impact of apple rootstocks on the bottom line of orchard growers? Well, let’s think of this question another way: what would our orchards look like if there were no dwarfing, precocious apple rootstocks? A similar question can be asked about all other apple rootstock qualities that are not quite well known, perhaps taken for granted, but which have significantly transformed our fruit industry and ushered in wealth, security and productivity.

Some of us experienced the 30-foot apple trees and the long ladders that needed to be hand-carried to harvest these trees — and some remember the injuries suffered by contemporaries when the ladders failed or people slipped. Most apple orchards planted nowadays are a testament to a transformation that has occurred in the past 60 years, from seedling to dwarfing rootstocks, which initially utilized centuries-old technology (some Malling dwarving rootstocks have been around for centuries), culminating in the almost total adoption of dwarfing and precocious rootstocks (94% of the 18–30 million apple trees planted each year in the U.S.). Choices of which rootstock to plant were fairly simple when the availability of stocks and scion varieties was limited to a few Malling and Budagovsky rootstocks and the standard Golden, Red, Gala, and Granny scions. The scion variety portfolio available to apple growers is becoming increasingly diversified, with new, high-value varieties being released, and rootstocks are following suit with more specialized characteristics beyond dwarfing. Bigger gains in productivity will be obtained when we are able to match the weaknesses of scion varieties to the strength of the rootstocks and vice versa. Optimal matching between scions and rootstocks requires empirical knowledge gained by testing multiple scions on multiple rootstocks in multiple environments — not an easy thing to do, but for several rootstock scion combinations, it has been accomplished. For the combinations that have not been explored yet, it is possible to extrapolate performance based on similarities to tested scions and rootstocks.

Breeding apple rootstocks to match cultural and nutrient requirements of scion varieties is a relatively new endeavor in the Geneva® apple rootstock breeding program. Apple rootstock breeding is a long-term process that has mostly focused on yields, disease resistance and efficiencies gained by tree architecture modification like dwarfing of grafted scions (Fazio et al. 2015b). In recent years, we have been able to understand more about the interaction between scions and rootstocks and have begun to leverage the interactions to identify scion-specific traits such as higher calcium rootstocks for calcium-deficient scions (Honeycrisp). The implementation of new selection traits in a plant breeding program requires knowledge related to the complexity, heritability and reliability of the selection process for the new trait (Fazio and Mazzola 2004). The complexity of a trait depends on the number of segregating factors and the importance (size) of their contribution. From there, we can estimate what these traits are worth to apple growers and the industry at large. This article will focus on three sets of traits that may be used to match rootstocks to varieties (dwarfing, nutrition, and resistance to fire blight) and estimate the impact they may have on the industry.

Breeding to match dwarfing and precocity needs

The most frequently used match-making between scion varieties and rootstocks is based on matching the inherent vigor of the scion to the vigor of the rootstock and the training system. Some growers and nurseries have accomplished this by choosing a set spacing for a target training system, then matching the growth habit of the scion variety (Fuji = vigorous; Gala = normal; Honeycrisp = weak) to the vigor potential of apple rootstocks (rootstocks ordered from more dwarfing to semi vigorous: B.9 < G.41 < G.214 < G.202 < G.969 < G.210 < G.890 < B.118).
this type of matching, there are other factors that influence scion vigor: soil fertility and water availability, soilborne diseases, and scion genetics. Therefore, if we imagine the final tree size product “T” is the size of a grafted scion (S) on a rootstock (R) in orchard A, then the size of such tree at maturity would be represented by the equation 


where \( A[fertility] \) is the fertility of orchard A soil, \( A[water] \) is the availability of water in orchard A, \( A[disease] \) is the presence of diseases that decrease the vigor of the scion, \( A[system] \) is the orchard system used, \( S[vigor] \) is the inherent vigor of the scion (e.g., a Honeycrisp scion is less vigorous than a Mutsu scion), \( R[dwarfing] \) is the rootstock genetic potential for dwarfing the scion. Since the rootstock is the conduit for water and nutrients and can be susceptible or resistant to diseases, the genetic composition of such a rootstock has been shown to interact with all such variables. While the main genetic factors for dwarfing have been described and used in breeding (Pilcher et al. 2008; Fazio et al. 2014), genetic variation for other root traits within apple rootstocks will have an effect on tree size and productivity. Fortunately, the main dwarfing genetic factors can be selected in the progeny by genetic fingerprinting and combined (Figure 1) to achieve, for the most part, levels that match the needs of target scion/training system combinations. Breeding for such genetic factors to match scion types is routine in the Geneva® breeding program.

**Impact of dwarfing apple rootstocks on the U.S. industry**

While it may seem a daunting task to quantify the economic impact that dwarfing rootstocks have had on U.S. apple production, it was possible using simple and blunt economic tools available in the form of the USDA-ERS (Economic Research Service) apple production databases to plot (Figure 2) the average productivity of apple orchards (metric tons/hectare) from 1982, when approximately 45% of apple trees being planted were on dwarfing rootstocks, to 2007 (the last date for which there are complete statistics on rootstocks), when approximately 92% of apple trees planted were on dwarfing rootstocks. We then made some assumptions regarding the effect of improved cultural practices, fertilizers, irrigation, pesticides, etc., and estimated conservatively that the average reported productivity increased by about 20% (from 15 ton/ha to 25 ton/ha) in that time period — of course, very good orchardists are pushing the limit of rootstock technologies and training systems to more than 100 ton/ha. Sticking to the conservative increased value of 20% and applying it to the farm gate value estimate of the 2007 apple crop ($2.6 billion), the increase in productivity due to dwarfing apple rootstocks was worth conservatively about $500 million dollars a year. The difference between a dwarfing and a non-dwarfing apple rootstock is caused by changes of 2–3 genes (out of approximately 35,000 predicted genes) in the genome of apple. The power of rootstock genes is illustrated in this example: 2–3 genes = more than $500 million extra in value to the primary fruit industry. This estimate does not take into account the cost savings in labor, pesticides, accidents, etc., that new orchard systems based on dwarfing rootstocks produce each year.

**Breeding to match nutrient needs**

Root systems have important roles in tree fruit production, in foraging for mineral nutrients and water necessary for fruit development and canopy growth (Neilsen and Hampson 2014). Traditionally, nutrient deficiencies found in soils of fruit orchards have been addressed with the addition of different formulations of fertilizers delivered by multiple means (Fallahi et al. 1984; George et al. 2002). This was done with some knowledge of the inherent potential of a few traditional rootstocks to absorb more or...
less of a particular nutrient contained in the rhizosphere (Chun et al. 2002). However, most fertilizer recommendations were not tailored to a specific rootstock, creating the potential for making such applications less efficient (more or less than what is specifically needed by the rootstock-scion combination) and potentially wasteful. This is evident from recently developed data that shows (Figure 3) that, in the case of boron, rootstocks have a major influence on the uptake and delivery of that nutrient consistently over years. The lowest boron absorbers were M.9 (clones) and B.9, which means that if growers keep using old nutrient recommendations for boron developed for the “poor” rootstocks on newer rootstocks like G.935, G.222, G.41, and similar “rich” rootstocks, they are probably wasting money and causing unnecessary nutrient imbalances in the orchard.

Rootstocks are embedded in a complex environment where interactions with pH, soil particles, fungi, bacteria, insects, soil water status, scion variety, and cover crops (and their competing roots) all play into their performance as foragers of nutrients (Kang et al. 2011; Fazio et al. 2012). As an example, the scion variety’s evapotranspiration potential can have a huge effect on the nutrients passively brought up to the leaves in the xylem (Falahi et al. 2013). Conversely, the roots’ ability to exude citrates in the rhizosphere can influence the pH-dependent availability of iron (Fe) and other micronutrients (M’Sehli et al. 2008; Valentinuzzi et al. 2015). The ability of root systems to associate with specific bacterial, fungal and mycorrhizal colonies sometimes enhances the reach and intensity of absorbance of macro- and micronutrients, allowing some plants to thrive in otherwise hostile environments (Heikham et al. 2012; Chu et al. 2013). All these interactions have genetic components in the rootstock, meaning that there are specific genes and associated alleles that affect the outcome of such interactions to the point that their effect can be detected in genetic experiments with segregating populations (Fazio et al. 2013). Fruit size and quality have been shown to be highly influenced by transpiration (Lordan et al. 2017), nutrient status (Jivan and Sala 2014), and subsequently by apple rootstocks (Andziaik and Tomala 2004), where a good portion of the variability may be explained by the rootstock potential to absorb and translocate nutrients to the scion, which implies that selection of a particular rootstock may be used to match nutrient weaknesses or requirements of fruit (Fazio et al. 2015a). Recently, data obtained from a diverse set of rootstock field experiments featuring 35 or more genetically different apple rootstocks have indicated the possibility to select for particular genetically determined nutrient profiles (Reig et al. 2018). It will likely be possible in the near future to match the nutrient requirements of the scions and the shortcomings of the soil substrate to the strengths of the rootstocks. Generating rootstock-tailored nutrition recommendations that may save the application of nutrients like potassium, boron, and phosphorous may save growers and the environment a significant amount of resources. It is hard to estimate a dollar amount for these rootstock-related nutrient efficiencies because the science is so young – we (the Geneva® apple rootstock breeding program) are the first ones to investigate this in the world, and it will take some time for more precise figures and recommendations, and at the same time to think about what one less boron application will save you each year...

Breeding to match disease resistance needs: fire blight

Another example of the need to match scion weaknesses to the strengths of apple rootstocks deals with resistance to fire blight. There was a time when a lot of Red and Golden Delicious apple trees were in the ground – two varieties that tolerate infections by fire blight – and that time is gone, as very susceptible varieties (Gala, Cripps Pink, Mutsu and similar)
have replaced them. Conservative estimates of average yearly losses due to this insidious bacterial disease range from $5–25 million in the U.S. alone, where single epidemics like the Michigan 2000 event cost the industry between $45M and $100M (Aćimović et al. 2015). Some readers have experienced firsthand how much fire blight susceptibility costs, where newly planted orchards on M.9 or M.26 have been decimated by the rootstock phase of fire blight. These costs are becoming more substantial as new susceptible (but market desirable) scion varieties are planted. We have had many field trials to test resistance of Geneva® rootstocks, but one that stands out was planted in a grower orchard in UT, with Gala trees on Geneva® rootstocks randomly dispersed in an orchard of Gala on M.26 and M.9 apple rootstocks (Figure 4). Within 2 years, fire blight had ravaged 40–50% of trees on susceptible rootstocks, while virtually all the trees on resistant rootstocks were still standing. Research showed that the genetic difference between resistant apple rootstocks such as G.41 (immune to fire blight) and M.9 (or M.26) was due to 4–6 DNA regions (genes). We found that fire blight-resistant rootstocks change the gene expression pattern of the grafted scion, perhaps reducing the incidence of the disease in the orchard (Jensen et al. 2012). When deployed in a series of new fire blight-resistant apple rootstocks, these 4–6 DNA regions have demonstrated the potential to save our apple industry millions of dollars every year. It makes sense then that, if the industry needs to plant a particular scion variety that is very susceptible to fire blight in a growing region that is known to have high infection risks, rootstocks are chosen that are tolerant or resistant to fire blight, as we have demonstrated that, even in a severe fire blight event affecting the scion, the affected material can be pruned off and new scaffolds reconstituted – a much more desirable scenario than the death of the rootstock (and the tree).

Table 1. Matching a rootstock to the characteristics of a scion variety requires some empirical testing where such rootstocks are trialed with multiple scion varieties. Some matches (weak rootstocks to vigorous scion to obtain balanced trees) are already being made in the industry, but more opportunities exist where mineral nutrients, growth type, and bearing type may be matched with rootstocks that improve the performance of the scion variety. Above are some examples based on empirical data collected from multiple field trials.

<table>
<thead>
<tr>
<th>Characteristics that could use improvement</th>
<th>FUJI</th>
<th>GALA</th>
<th>HONEYCRISP</th>
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<tbody>
<tr>
<td>Rootstocks that have shown to improve Biennial Bearing</td>
<td>G.935, G.214, CG.5257, G.41, CG.4004, CG.4011</td>
<td>Fruit Size, Productivity Color/Maturity, Fire blight</td>
<td>G.935, B.10, G.814, G.41TC, G.202, CG.4003</td>
</tr>
<tr>
<td>Rootstocks that have shown to improve Calcium in fruit</td>
<td>CG.5257, G.222, G.935, G.814, G.214</td>
<td></td>
<td>CG.4003, G.214, G.16, G.814, CG.6001, CG.6976</td>
</tr>
<tr>
<td>Rootstocks that have shown to influence Fruit Size</td>
<td>CG.5257, G.222, G.935, CG.4004, CG.3001</td>
<td></td>
<td>G.814</td>
</tr>
</tbody>
</table>
Figure 5. Another opportunity to match insect resistance to scions that are very susceptible to woolly apple aphids: resistant rootstocks like G.41 do not allow overwintering of these aphids in the roots and prevent the pest from taking hold in the orchard.

Conclusions

While we have made significant progress with dwarfing, fire blight and other unique traits of Geneva® rootstocks, we are still in the early stages of being able to breed apple rootstocks to match mineral nutrient modulation in scions. Projects are under way to shed more light on apple rootstock functions related to mineral nutrient physiology and genetics. These projects leverage high-throughput genotyping and more uniform growing conditions like aeroponics that allow better detection of minor effect genes and the painting of a more defined landscape for mineral nutrient traits. How long did it take to develop the series of fire blight-resistant Geneva® apple rootstocks? Just about 40 years. We are seeing an impact in the millions of dollars to the industry as production of Geneva® rootstocks is slated to reach 15 million trees planted each year within five years. We continue to learn about the quirks that each of our released rootstocks has, and hope to increase the value of the impact that new apple rootstock technologies have in the industry.

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