

Designer rootstocks: the basis for precision management of apple orchards

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Abstract

Apple rootstocks affect many aspects of apple production including tree size, potential crop load, fruit set, fruit quality, tree anchorage and graft union strength, disease resistance, and total per hectare yield. Dwarfing rootstocks have revolutionized the apple industry, but up until a few years ago most commercial germplasm available was restricted to less than three genotypes (M.9, B.9, and M.26). While wide use of these rootstock provided a good paradigm-shift compared to unproductive non-dwarfing rootstocks, the 'one size fits all' implementation was riddled with inefficiencies. The Geneva® apple rootstock breeding program has been identifying apple rootstocks likely to match different applications allowing for precision matching with scion, soil and climate. Differences in growth habits and disease resistance of new apple cultivars require novel rootstock applications designed to match strengths and weaknesses of such cultivars in context of growing site. For example, scion cultivar NY-1 'SnapDragon®' is a weak growing cultivar with a tendency to over crop and produce small apples. M.9 was initially tested and proved to be inefficient providing slow growth and susceptibility to fire blight. Rootstocks G.935, G.969 and CG.5257 were chosen to grow this cultivar because of their increased vigor, disease resistance and in the case of CG.5257 influence on fruit size. Designer rootstocks are being developed to work under different soil pH conditions, nutrition management, water use and training systems. We envision providing apple growers with a group of highly efficient disease resistant rootstocks of varying vigor levels to allow matching of scion vigor, soil vigor and climate vigor with rootstock vigor to result in orchards that grow well enough to fill the space in only 2 seasons but then are highly efficient and manageable for the next 20 years. This type of customization has been proven to increase efficiency in the use of fertilizers as well as increase productivity of marketable apples per unit of land area and is being studied in the USDA NIFA Specialty Crop Project "AppleRoot2Fruit".

Keywords: dwarfing, fruit size, fruit quality, nutrient uptake, canopy development

INTRODUCTION

The implementation of dwarfing apple rootstocks around the world continues to significantly increase the output efficiency connected to yield and fruit quality in modern apple orchards. Most apple orchards planted nowadays are a testament of a transformation that has occurred in the past 60 years from seedling to dwarfing rootstocks which initially has utilized centuries old technology ('Malling' dwarfing 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 US). Choices of which rootstock to plant were simple when the availability of stocks and scion cultivars was limited to a few 'Malling 9' clones and some 'Budagovsky' rootstocks with the standard 'Golden', 'Red', 'Gala', 'Granny' scions. The apple scion cultivar portfolio available to apple growers is becoming increasingly diversified with new, high-value cultivars being released every year and more apple 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 cultivars to the strength of the rootstocks and vice versa. Optimal matching between

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scions and rootstocks requires empirical knowledge gained by testing multiple scions on multiple rootstocks in multiple environments. This is a work in progress for the Geneva® apple rootstock breeding program and has been accomplished for several rootstock scion combinations. For the combinations that have not been explored yet, it is possible to extrapolate performance based on similarities to tested scions and rootstocks.

Rootstocks are embedded in a complex environment where interactions with pH, soil particles, fungi, bacteria, insects, soil water status, scion cultivar, cover crops (and their competing roots) all play into their performance as foragers of nutrients (Fazio et al., 2012a, b). As an example, the scion cultivar's evapotranspiration potential can have a huge effect on the nutrients passively brought up to the leaves in the xylem (Fallahi 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 (Andziak 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 genetically determined nutrient profiles (Reig et al., 2018). It will likely be possible soon 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 number of resources.

Apple production is transitioning to more mechanized industrial applications that require the number of apples on each stem and the whole tree to be adjusted depending on the carrying capacity of stem and whole tree in order to achieve good fruit size, light penetration for fruit quality and spray efficiency. Apple rootstocks which can affect crop density, annual bearing capacity, wood production and partition of nutrients to fruit, need to be considered in the "precision management plan" for the modern apple orchard. Breeding apple rootstocks to match cultural and nutrient requirements of scion cultivars 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 desired result of such efforts is the production of a set of "designer" apple rootstocks that match the management needs for a set of growing conditions (scion cultivar, soil pH, irrigation, soil type, climate, etc.) to maximize the high-quality fruit production potential of apple orchards. 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. We discuss novel genetic and phenotypic diversity witnessed in results of multiple apple rootstock field trials in relation to the role of apple rootstocks in providing precision management options to apple growers worldwide.

MATERIALS AND METHODS

A field trial of lesser-known Geneva® rootstocks was established in 2013 in Geneva, NY with 'SnapDragon' as a scion cultivar. The purpose of the trial was to search for a mid-vigor productive rootstock for this low vigor cultivar. Trees were planted in early May 2013 on 16 different rootstocks spaced at 1×3.5 m. These trees had their fifth crop in 2018. Trees were both chemically and hand thinned to one fruit per cluster. Other examples of phenotypically diverse rootstock field trial data are taken from experiments described in several published works conducted between 2005 and 2018 (Table 1; Auvil et al., 2011; Fazio et al., 2018; Kviklys

et al., 2016; Lordan et al., 2017, 2018; Moran et al., 2018; Reig et al., 2018, 2019a, b; Tworowski et al., 2016; Wallis et al., 2017; Zhu et al., 2017). Additional published breeding population data from the Geneva® Apple Rootstock Breeding program was also utilized in exemplifying phenotypic diversity for novel selection traits like mineral nutrition (Fazio et al., 2015b). Data were analyzed and figures produced using SAS JMP Pro 14.

Table 1. Matching a designer apple rootstock to the characteristics of a scion cultivar requires some empirical testing where such rootstocks are trialed with multiple scion cultivars. 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 cultivar. Below, are some examples based on empirical data collected from multiple field trials.

	Fuji	Gala	Honeycrisp
Characteristics that could use improvement	Too much vigor Biennial Color	Fruit size Productivity Color/maturity Fire blight	Weak vigor Biennial Fruit disorders
Rootstocks that have shown to improve biennial bearing	G.935, G.214, CG.5257, G.41, CG.4004, CG.4011		G.935, B.10, G.814, G.41TC, G.202, CG.4003
Rootstocks that have shown to improve calcium in fruit	CG.5257, G.222, G.935, G.814, G.214, G.969		CG.4003, G.214, G.16, G.814, CG.6001, CG.6976
Rootstocks that have shown to influence fruit size	CG.5257, G.222, G.935, CG.4004, CG.3001	G.814	G.814, G.41, G.11, G.969
Rootstocks with improved productivity	G.11, G.41, G.214, G.935, G.4011, G.814	G.41, G.214, G.814, G.935, G.11, G.4004	G.890, G.41, G.935, G.814, G.969

RESULTS AND DISCUSSION

Designer apple rootstocks to match dwarfing and precocity parameters

The most frequently used pairing method between scion cultivars and rootstocks is based on matching the inherent vigor of the scion to the vigor of the rootstock and the training system. This practice adopted by some growers and nurseries is accomplished by determining a set spacing for a target training system, then matching the growth habit of the scion cultivar ('Fuji' = vigorous; 'Gala' = normal; 'Honeycrisp' = weak) to the average vigor potential of apple rootstocks (rootstocks ordered from more dwarfing to semi vigorous: M.27 < B.9 < G.41 < G.214 < G.202 < G.969 < G.210 < G.890 < B.118) with the understanding that there are certain scion rootstock interactions that may result in slightly different sizes (Autio et al., 2017a, b). Beyond this type of matching there are other factors that influence scion vigor: soil fertility, 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 $T = A_{\text{fertility}} + A_{\text{water}} + A_{\text{disease}} + A_{\text{system}} + S_{\text{vigor}} + R_{\text{dwarfing}}$ where $A_{\text{fertility}}$ 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 'Fuji' scion), R_{dwarfing} is the rootstock genetic potential for dwarfing the scion. Rootstocks are the conduit for water and nutrients to the scion and can have different sensitivity to diseases depending on their genetic composition, therefore the interactions with all these orchard elements can influence the final whole tree vigor and productivity. Another important characteristic that is related to vigor and productivity is the ability of a young tree to fill the allotted "orchard space" that captures sunlight and converts it to photosynthate and eventually fruit. Strategies to maximize vegetative growth include heavy fertilizer treatments but are also dependent on the genetic underpinnings of a rootstock to leverage those treatments and set fruiting wood in the early production phase of the

orchard. It can be noted in Figure 1 that for the weak growing cultivar ‘SnapDragon’ planted as a replicated rootstock trial in 2013 there is a significant difference in cumulative production per tree between the dwarfing rootstocks that had filled their space in the first two years (G.11, G.214, CG.4288, G.935, CG.4292, CG.4809) and the rootstocks that had struggled to build enough canopy after five seasons (CG.3902, M.9T337, M.26 and CG.5030). For example, the difference in cumulative production per tree between M.9T337 and G.11 was about 8 kg per tree for five years. That difference can amount to 20,000 kg ha⁻¹ (8 kg × 2,500 trees ha⁻¹) which turns into a significant opportunity cost to the grower for not filling the space. Similar results were observed with a ‘Honeycrisp’ rootstock trial when comparing B.9 rootstock and G.814 where the opportunity cost was approximately \$250,000 ha⁻¹ for the life of the orchard (Lordan et al., 2019). While we are able to model the main genetic factors for dwarfing and use them in breeding new designer apple rootstocks (Fazio et al., 2014; Knäbel et al., 2015), genetic variation for other rootstock traits will have an effect on tree size and productivity and will need to be considered in the breeding process.

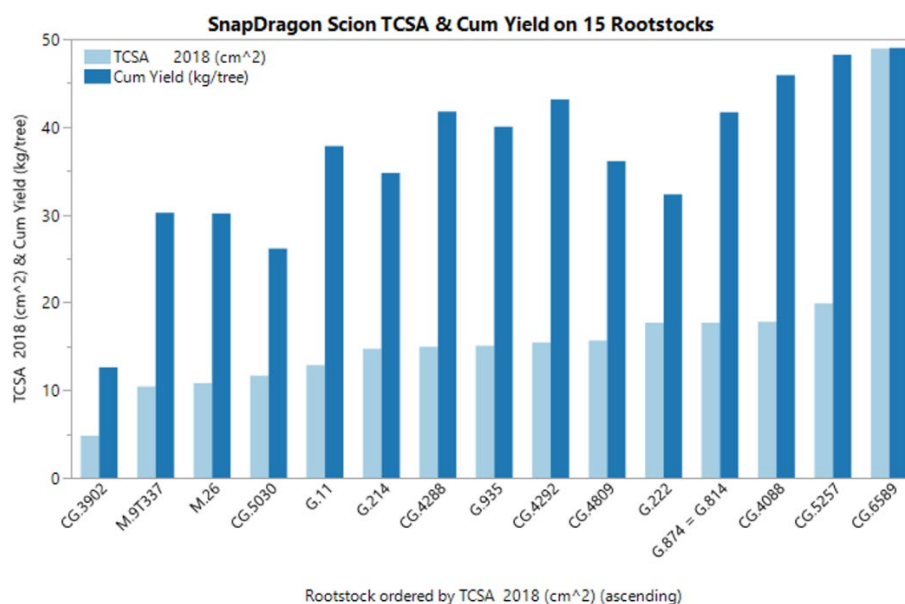


Figure 1. Trunk cross sectional area and cumulative apple production per tree of ‘SnapDragon’ cultivar on 15 different apple rootstocks after five harvest seasons. The choice of apple rootstock can have significant consequences on the profitability of an orchard as differences in cumulative production per hectare can be substantial.

Designer rootstocks to match fruit size and fruit quality parameters

Perhaps one of the most important fruit quality parameters that can be influenced by rootstock, crop load and growing conditions is fruit size (Reig et al., 2018). Fruit size has its own scion specific genetic determinants (Duan et al., 2017; Migicovsky et al., 2016) which can be altered by growing conditions (water, fertilizers) and crop load (Nielsen et al., 2016; Robinson and Lopez, 2012; Serra et al., 2016). Within the same growing parameters, apple rootstocks can also have a significant influence on fruit size. This is evident in Figures 2-4 where three separate experiments featuring three different cultivars (‘Fuji’, ‘SnapDragon’, and ‘Honeycrisp’) display on average significantly different fruit sizes over the cumulative history of the experiment (6-10 years) while maintaining a similar cumulative crop load (rootstocks in similar range for the x-axis). All those figures show the well-known negative correlation between mean fruit size and crop load; however, some rootstocks are able to maintain larger fruit size despite similar crop load and tree size. Perhaps, this can be another target for designer rootstocks when releasing a new apple cultivar by pairing the scion fruit size genetic potential with the potential rootstock sizing capacity.

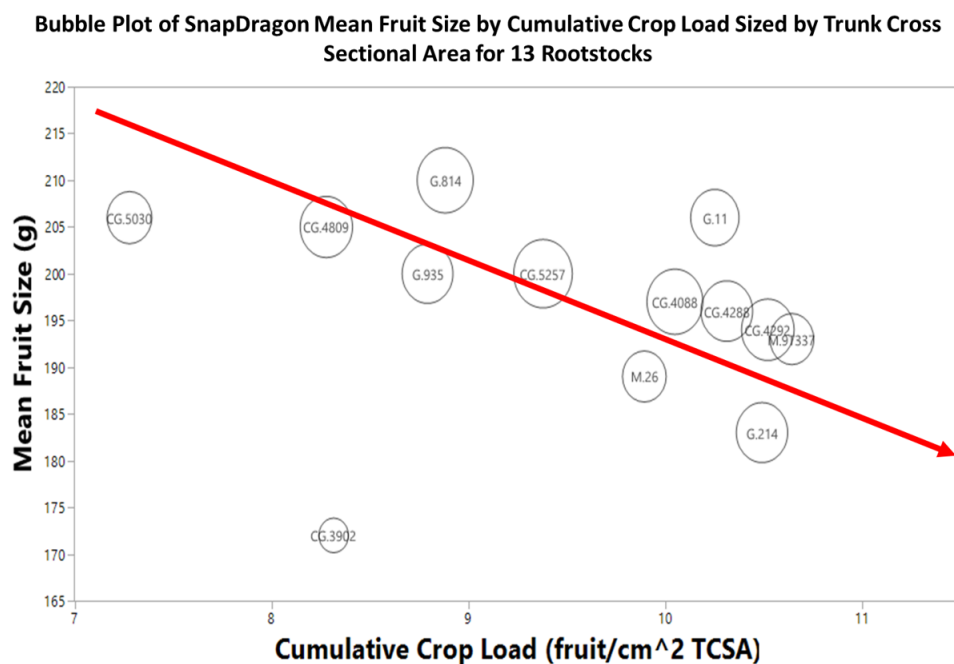


Figure 2. Bubble plot of ‘SnapDragon’ mean fruit size and cumulative crop load for five seasons where the bubble size represents tree vigor by rootstocks displayed as mean trunk cross sectional area. ‘SnapDragon’ may suffer from small fruit size and rootstocks like G.814 and G.11 seem to give a substantial size advantage.

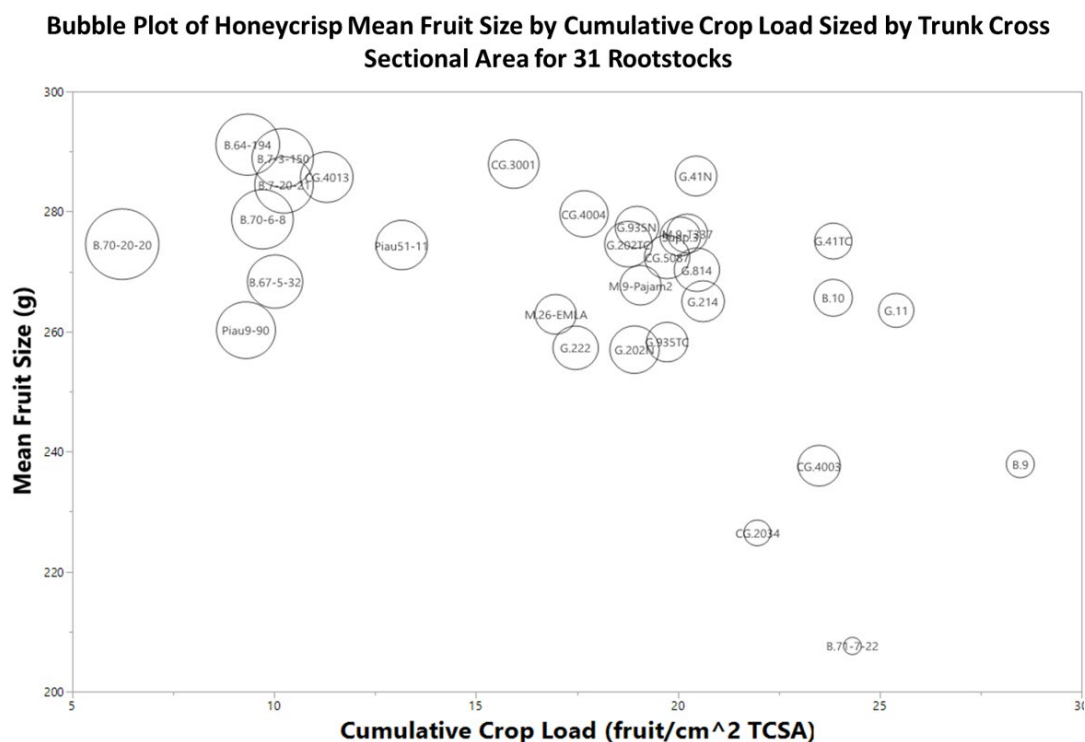


Figure 3. Bubble plot of ‘Honeycrisp’ mean fruit size and cumulative crop load for nine seasons where the bubble size represents tree vigor by rootstocks displayed as mean trunk cross sectional area. While B.9 seems to be more efficient with the highest cumulative crop load, it also produces much smaller fruit than other rootstocks like G.41TC, B.10 and G.11.

Bubble Plot of Fuji Mean Fruit Size by Cumulative Crop Load Sized by Trunk Cross Sectional Area for 48 Rootstocks

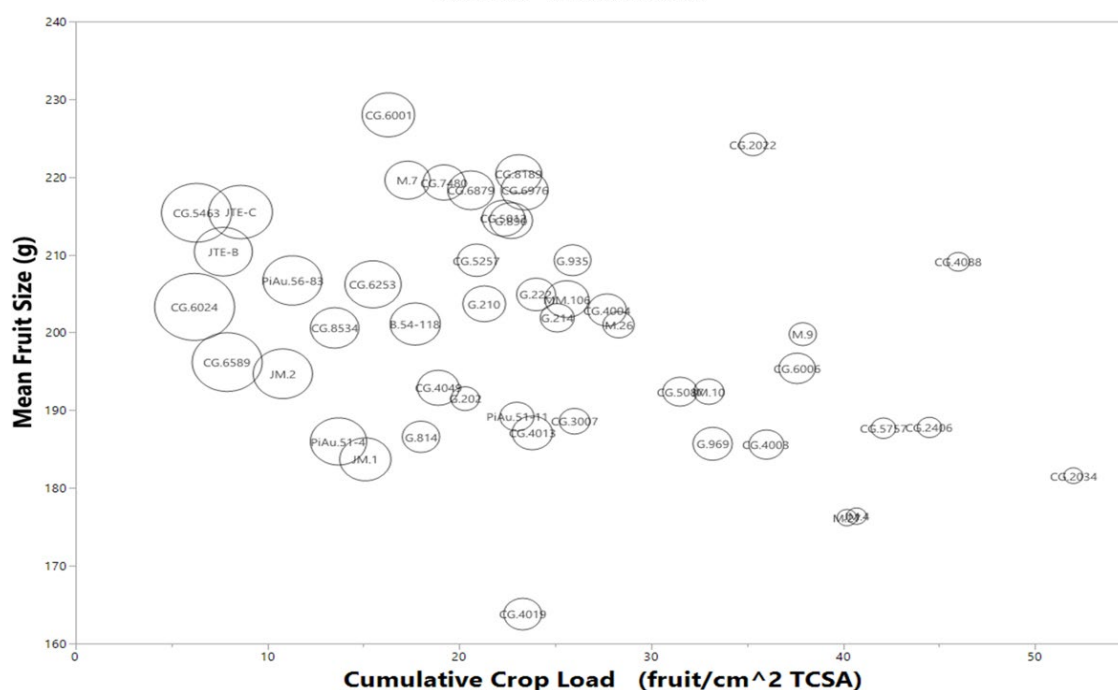


Figure 4. Bubble plot of ‘Fuji’ mean fruit size and cumulative crop load for ten seasons where the bubble size represents tree vigor by rootstocks displayed as mean trunk cross sectional area. The plot displays the phenotypic diversity that combines fruit size and yield efficiency of apple rootstocks. New genetic diversity beyond the ‘Malling’ and ‘Budagovsky’ apple rootstocks is the driver behind such wide phenotypic displays.

Designer rootstocks to match nutrient parameters

Root systems have important roles in tree fruit production as they forage for mineral nutrients and water necessary for fruit development and canopy growth (Nielsen 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. This was done with some knowledge of the inherent potential of a few traditional rootstocks to absorb more or less of a nutrient contained in the rhizosphere. However, most fertilizer recommendations were not tailored to a specific rootstock, creating the potential of making such applications less efficient (more or less than specifically needed by the rootstock-scion combination) and potentially wasteful. This is evident from recently developed data which shows (Figure 5) that in 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. Some apple scions are more sensitive than others to nutrient imbalances that cause fruit disorders like bitter pit (Buti et al., 2018; Jemrić et al., 2016; Krawitzky et al., 2016; Volz et al., 2006) where the K/Ca ratio has been shown to be associated with bitter pit (Valverdi et al., 2019). The influence of apple rootstocks on K/Ca ratio and associated incidence of bitter pit in ‘Honeycrisp’ apples was observed in a rootstock breeding population comprised of 150 different rootstocks (Figure 6). ‘Honeycrisp’ is well known to have deficiencies in calcium transport to the developing fruit (Kalcsits et al., 2017). Designer rootstocks able to overcome known nutritional deficits of apples can now be selected from a diverse group of apple rootstocks, perhaps facilitating improvements of overall fruit quality.

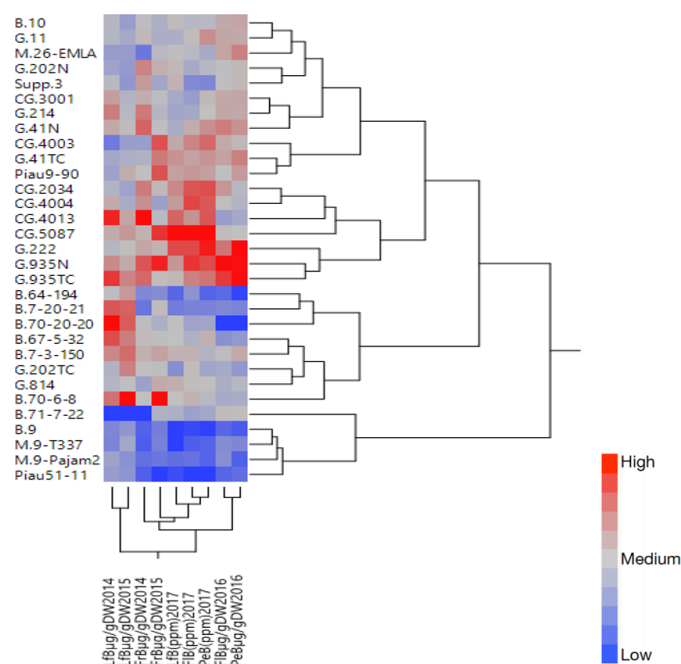


Figure 5. Results from field grown trees of 'Honeycrisp' show that boron concentration in leaves and fruit seems to be highly rootstock dependent as they are highly consistent through time (years). New recommendations on the application of boron should be made for newer rootstocks considering that M.9 and B.9 are among the poorest boron absorbers in the group. This information should also be combined with the specific scion nutrient requirements to make fertilizer use more efficient.

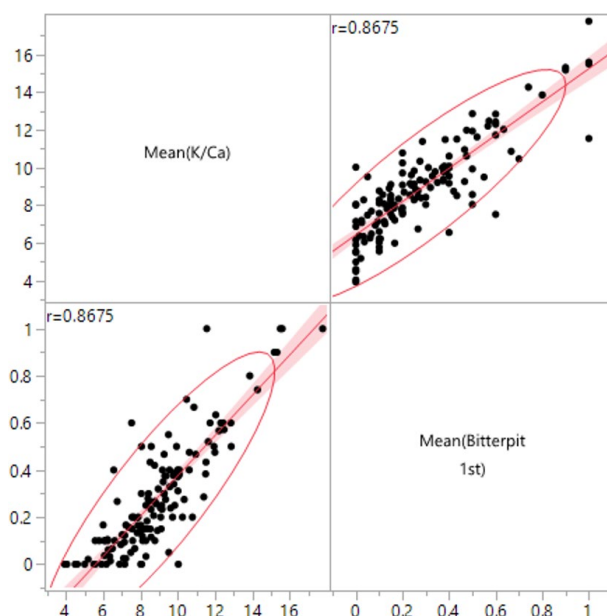


Figure 6. Correlation between mean K/Ca values of samples of 20 'Honeycrisp' apples for each of 150 apple rootstocks and the mean incidence of bitter pit in the apple samples where each apple that showed bitter pit was assigned a 1 and free of bitter pit was assigned a 0. There are several rootstocks in the "0" bitter pit range that may become future designer apple rootstocks for calcium challenged apple cultivars like 'Honeycrisp'.

Designer rootstocks to match disease and insect resistance parameters

Localized conditions which promote certain root disease pressures like replant disease, phytophthora root rot, scion and rootstock disease like fire blight (*Erwinia amylovora*) and insect proliferation (wooly apple aphid and dogwood stem borer) need to be accounted for when preparing to install a new apple orchard. The best way to avoid unnecessary treatments and where required to comply with organic management standards is to deploy genetic resistance to those pressures (Evans, 2013). Tolerance to the apple replant disease complex has been described in several apple rootstocks (Isutsa and Merwin, 2000; Nicola et al., 2018; St. Laurent et al., 2010) and proven in commercial orchards (Auvil et al., 2011). The availability of optimal, “fresh” orchard land is decreasing in certain areas of the world where apples (and pears) have been planted for centuries. In addition, the building of more permanent structures (trellis, irrigation, netting) for intensive apple orchards is becoming more prevalent to achieve higher packable yields of apples.

These trends make the employment of genetically resistant rootstocks more relevant as they can be used to replant in place aged or dead trees within these more permanent structures. Similarly, the deployment of rootstocks resistant to fire blight in areas where the pressure is relatively high provides a more precise way of protecting the investment into a new orchard (Wallis et al., 2017).

The removal of neonicotinoids from the arsenal of insecticides available to apple growers has increased the incidence of woolly apple aphids (WAA – *Eriosoma lanigerum*) in conventionally managed apple orchards. Apple rootstocks possessing resistance genes to WAA have been used in the past 70 years, with novel sources of resistance derived from *Malus × robusta* in the past 10 years (Bartish and Weeden, 1998; Bus et al., 2008; Sandanayaka et al., 2003). One of the best ways to manage this insect in temperate climates is to deploy a resistant rootstock which prevents the aphid from overwintering by feeding on the root system (Kelderer et al., 2016). The lack of burr knots in some novel apple rootstocks provide a level of protection to dogwood stem borer which sometimes uses the openings between these primordial aerial root initiations to gain their way into the stem, sometimes causing secondary infections by bacterial and fungal diseases that otherwise would be blocked by bark tissue (Ateyyat, 2006; Bergh and Leskey, 2003).

CONCLUSIONS

Novel genetic and phenotypic diversity in the portfolio of available apple rootstocks is creating new opportunities to precisely manage apple production and provide localized solutions to many of the challenges associated with apple production. Modern apple orchards require planning from the underground (rootstock) up as many of the parameters that are desired to be manipulated are affected by rootstocks. More modern methods of propagation including micro-propagation are key to the differentiation of the portfolio of available rootstocks and will be key to the precision management of apple orchards.

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Literature cited

- Andziak, J., and Tomala, K. (2004). Influence of rootstocks on mineral nutrition, fruit maturity and quality of ‘Jonagold’ apples. *Sodinink. Darzinink.* 23, 20–32.
- Ateyyat, M.A. (2006). Effect of three apple rootstocks on the population of the small red-belted clearwing borer, *Synanthedon myopaeformis*. *J. Insect Sci.* 6 (40), 1–5 <https://doi.org/10.1673/031.006.4001>. PubMed

- Autio, W., Robinson, T., Black, B., Blatt, S., Cochran, D., Cowgill, W., Hampson, C., Hoover, E., Lang, G., Miller, D., et al. (2017a). Budagovsky, Geneva, Pillnitz, and Malling apple rootstocks affect 'Honeycrisp' performance over the first five years of the 2010 NC-140 'Honeycrisp' apple rootstock trial. *J. Amer. Pomolog. Soc.* **71**, 149–166.
- Autio, W., Robinson, T., Black, B., Crassweller, R., Fallahi, E., Parker, M., Quezada, R.P., and Wolfe, D. (2017b). Budagovsky, Geneva, Pillnitz, and Malling apple rootstocks affect 'Fuji' performance over the first five years of the 2010 NC-140 'Fuji' apple rootstock trial. *J. Amer. Pomolog. Soc.* **71**, 167–182.
- Auvil, T.D., Schmidt, T.R., Hanrahan, I., Castillo, F., McFerson, J.R., and Fazio, G. (2011). Evaluation of dwarfing rootstocks in Washington apple replant sites. *Acta Hortic.* **903**, 265–271 <https://doi.org/10.17660/ActaHortic.2011.903.33>.
- Bartish, I.V., and Weeden, N.F. (1998). The use of interspecific crosses in *Malus* to map the genes of characters important for apple rootstock breeding. *Acta Hortic.* **484**, 319–324 <https://doi.org/10.17660/ActaHortic.1998.484.55>.
- Bergh, J.C., and Leskey, T.C. (2003). Biology, ecology, and management of dogwood borer in eastern apple orchards. *Can. Entomol.* **135** (5), 615–635 <https://doi.org/10.4039/n02-089>.
- Bus, V.G.M., Chagné, D., Bassett, H.C.M., Bowatte, D., Calenge, F., Celton, J.M., Durel, E., Malone, M.T., Patocchi, A., Ranatunga, A.C., et al. (2008). Genome mapping of three major resistance genes to woolly apple aphid (*Eriosoma lanigerum* Hausm.). *Tree Genet. Genomes* **4** (2), 223–236 <https://doi.org/10.1007/s11295-007-0103-3>.
- Buti, M., Sargent, D.J., Bianco, L., Magnago, P., Velasco, R., and Colgan, R.J. (2018). A study of gene expression changes at the Bp-2 locus associated with bitter pit symptom expression in apple (*Malus pumila*). *Mol. Breed.* **38** (7), 85 <https://doi.org/10.1007/s11032-018-0840-z>.
- Duan, N., Bai, Y., Sun, H., Wang, N., Ma, Y., Li, M., Wang, X., Jiao, C., Legall, N., Mao, L., et al. (2017). Genome re-sequencing reveals the history of apple and supports a two-stage model for fruit enlargement. *Nat. Commun.* **8** (1), 249 <https://doi.org/10.1038/s41467-017-00336-7>. PubMed
- Evans, K. (2013). The potential impacts of genetics, genomics and breeding on organic fruit production. *Acta Hortic.* **1001**, 155–160 <https://doi.org/10.17660/ActaHortic.2013.1001.16>.
- Fallahi, E., Fallahi, B., and Shafii, B. (2013). Water use, mineral nutrition, tree growth, yield, and fruit quality of 'Fuji' and 'Gala' apples under various irrigation systems and rootstocks. *Acta Hortic.* **984**, 57–68 <https://doi.org/10.17660/ActaHortic.2013.984.4>.
- Fazio, G., and Mazzola, M. (2004). Target traits for the development of marker assisted selection of apple rootstocks - prospects and benefits. *Acta Hortic.* **663**, 823–827 <https://doi.org/10.17660/ActaHortic.2004.663.149>.
- Fazio, G., Kviklys, D., Grusak, M.A., and Robinson, T.L. (2012a). Phenotypic diversity and QTL mapping of absorption and translocation of nutrients by apple rootstocks. *Asp. Appl. Biol.* **119**, 37–50.
- Fazio, G., Kviklys, D., Grusak, M.A., and Robinson, T.L. (2012b). Soil pH, soil type and replant disease affect growth and nutrient absorption in apple rootstocks. *N.Y. Fruit Q.* **20**, 22–28.
- Fazio, G., Wan, Y., Kviklys, D., Romero, L., Adams, R., Strickland, D., and Robinson, T. (2014). Dw2, a new dwarfing locus in apple rootstocks and its relationship to induction of early bearing in apple scions. *J. Am. Soc. Hortic. Sci.* **139** (2), 87–98 <https://doi.org/10.21273/JASHS.139.2.87>.
- Fazio, G., Chang, L., Grusak, M.A., and Robinson, T.L. (2015a). Apple rootstocks influence mineral nutrient concentration of leaves and fruit. *N.Y. Fruit Q.* **25**, 11–15.
- Fazio, G., Robinson, T.L., and Aldwinckle, H.S. (2015b). The Geneva apple rootstock breeding program. *Plant Breed.* **39**, 379–424.
- Fazio, G., Lordan, J., Francescatto, P., Cheng, L., Wallis, A., Grusak, M.A., and Robinson, T.L. (2018). 'Honeycrisp' apple fruit nutrient concentration affected by apple rootstocks. *Acta Hortic.* **1228**, 223–228 <https://doi.org/10.17660/ActaHortic.2018.1228.33>.
- Isutsa, D.K., and Merwin, I.A. (2000). *Malus* germplasm varies in resistance or tolerance to apple replant disease in a mixture of New York orchard soils. *HortScience* **35** (2), 262–268 <https://doi.org/10.21273/HORTSCI.35.2.262>.
- Jemrić, T., Fruk, I., Fruk, M., Radman, S., Sinkovič, L., and Fruk, G. (2016). Bitter pit in apples: pre- and postharvest factors: a review. *Span. J. Agric. Res.* **14** (4), e08R01 <https://doi.org/10.5424/sjar/2016144-8491>.
- Jivan, C., and Sala, F. (2014). Relationship between tree nutritional status and apple quality. *Hortic. Sci. (Prague)* **41** (1), 1–9 <https://doi.org/10.17221/152/2013-HORTSCI>.
- Kalcsits, L., van der Heijden, G., Reid, M., and Mullin, K. (2017). Calcium absorption during fruit development in 'Honeycrisp' apple measured using Ca-44 as a stable isotope tracer. *HortScience* **52** (12), 1804–1809 <https://doi.org/10.21273/HORTSCI12408-17>.
- Kelderer, M., Lardschneider, E., and Schütz, R. (2016). Efficacy evaluation of different methods for the control of

woolly apple aphid (*Eriosoma lanigerum* [Hausmann]) in organic apple growing. Paper presented at: Conference on Organic Fruits-Growing (Hohenheim, Germany: Fordergemeinschaft Ökologischer Obstbau e.V. (FOKO)).

Knäbel, M., Friend, A.P., Palmer, J.W., Diack, R., Wiedow, C., Alspach, P., Deng, C., Gardiner, S.E., Tustin, D.S., Schaffer, R., et al. (2015). Genetic control of pear rootstock-induced dwarfing and precocity is linked to a chromosomal region syntenic to the apple Dw1 loci. *BMC Plant Biol.* 15 (1), 230 <https://doi.org/10.1186/s12870-015-0620-4>. PubMed

Krawitzky, M., Orera, I., Lopez-Millan, A.F., Oria, R., and Val, J. (2016). Identification of bitter pit protein markers in *Malus domestica* using differential in-gel electrophoresis (DIGE) and LC-MS/MS. *Postharvest Biol. Technol.* 111, 224–239 <https://doi.org/10.1016/j.postharvbio.2015.09.006>.

Kviklys, D., Robinson, T.L., and Fazio, G. (2016). Apple rootstock evaluation for apple replant disease. *Acta Hortic.* 1130, 425–430 <https://doi.org/10.17660/ActaHortic.2016.1130.63>.

Lordan, J., Fazio, G., Francescatto, P., and Robinson, T. (2017). Effects of apple (*Malus x domestica*) rootstocks on scion performance and hormone concentration. *Sci. Hortic. (Amsterdam)* 225, 96–105 <https://doi.org/10.1016/j.scienta.2017.06.050>.

Lordan, J., Fazio, G., Francescatto, P., and Robinson, T.L. (2018). Effects of apple (*Malus x domestica*) rootstocks on vigor and yield response on ‘Honeycrisp’. *Acta Hortic.* 1228, 149–152 <https://doi.org/10.17660/ActaHortic.2018.1228.22>.

Lordan, J., Fazio, G., Francescatto, P., and Robinson, T.L. (2019). II. Horticultural performance of ‘Honeycrisp’ grown on a genetically diverse set of rootstocks under Western New York climatic conditions. *Sci. Hortic. (Amsterdam)* 257, 108686 <https://doi.org/10.1016/j.scienta.2019.108686>.

Migicovsky, Z., Gardner, K.M., Money, D., Sawler, J., Bloom, J.S., Moffett, P., Chao, C.T., Schwaninger, H., Fazio, G., Zhong, G.-Y., and Myles, S. (2016). Genome to phenome mapping in apple using historical data. *Plant Genome* 9 (2), <https://doi.org/10.3835/plantgenome2015.11.0113>. PubMed

Moran, R.E., Peterson, B.J., Fazio, G., and Cline, J. (2018). Genotypic variation in apple rootstock low temperature tolerance during spring and fall. *J. Am. Soc. Hortic. Sci.* 143 (5), 319–332 <https://doi.org/10.21273/JASHS04470-18>.

Neilsen, G., and Hampson, C. (2014). ‘Honeycrisp’ apple leaf and fruit nutrient concentration is affected by rootstock during establishment. *J. Am. Pomol. Soc.* 68, 178–189.

Neilsen, D., Neilsen, G., Guak, S., and Forge, T. (2016). Consequences of deficit irrigation and crop load reduction on plant water relations, yield, and quality of ‘Ambrosia’ apple. *HortScience* 51 (1), 98–106 <https://doi.org/10.21273/HORTSCI.51.1.98>.

Nicola, L., Insam, H., Pertot, I., and Stres, B. (2018). Reanalysis of microbiomes in soils affected by apple replant disease (ARD): old foes and novel suspects lead to the proposal of extended model of disease development. *Appl. Soil Ecol.* 129, 24–33 <https://doi.org/10.1016/j.apsoil.2018.04.010>.

Reig, G., Lordan, J., Fazio, G., Grusak, M.A., Hoying, S., Cheng, L.L., Francescatto, P., and Robinson, T. (2018). Horticultural performance and elemental nutrient concentrations on ‘Fuji’ grafted on apple rootstocks under New York State climatic conditions. *Sci. Hortic. (Amsterdam)* 227, 22–37 <https://doi.org/10.1016/j.scienta.2017.07.002>.

Reig, G., Lordan, J., Sazo, M.M., Hoying, S., Fargione, M., Reginato, G., Donahue, D.J., Francescatto, P., Fazio, G., and Robinson, T. (2019a). Long-term performance of ‘Gala’, ‘Fuji’ and ‘Honeycrisp’ apple trees grafted on Geneva (R) rootstocks and trained to four production systems under New York State climatic conditions. *Sci. Hortic. (Amsterdam)* 244, 277–293 <https://doi.org/10.1016/j.scienta.2018.09.025>.

Reig, G., Lordan, J., Sazo, M.M., Hoying, S.A., Fargione, M.J., Hernan Reginato, G., Donahue, D.J., Francescatto, P., Fazio, G., and Robinson, T.L. (2019b). Effect of tree type and rootstock on the long-term performance of ‘Gala’, ‘Fuji’ and ‘Honeycrisp’ apple trees trained to Tall Spindle under New York State climatic conditions. *Sci. Hortic. (Amsterdam)* 246, 506–517 <https://doi.org/10.1016/j.scienta.2018.11.029>.

Robinson, T., and Lopez, S. (2012). Crop load affects ‘Honeycrisp’ fruit quality more than nitrogen, potassium, or irrigation. *Acta Hortic.* 940, 529–537 <https://doi.org/10.17660/ActaHortic.2012.940.76>.

Sandanayaka, W.R.M., Bus, V.G.M., Connolly, P., and Newcomb, R. (2003). Characteristics associated with Woolly Apple Aphid *Eriosoma lanigerum*, resistance of three apple rootstocks. *Entomol. Exp. Appl.* 109 (1), 63–72 <https://doi.org/10.1046/j.1570-7458.2003.00095.x>.

Serra, S., Leisso, R., Giordani, L., Kalcsits, L., and Musacchi, S. (2016). Crop load influences fruit quality, nutritional balance, and return bloom in ‘Honeycrisp’ apple. *HortScience* 51 (3), 236–244 <https://doi.org/10.21273/HORTSCI.51.3.236>.

St. Laurent, A., Merwin, I.A., Fazio, G., Thies, J.E., and Brown, M.G. (2010). Rootstock genotype succession influences

apple replant disease and root-zone microbial community composition in an orchard soil. *Plant Soil* 337, 259–272 <https://doi.org/10.1007/s11104-010-0522-z>.

Tworowski, T., Fazio, G., and Glenn, D.M. (2016). Apple rootstock resistance to drought. *Sci. Hortic. (Amsterdam)* 204, 70–78 <https://doi.org/10.1016/j.scienta.2016.01.047>.

Valverdi, N.A., Cheng, L.L., and Kalcsits, L. (2019). Apple scion and rootstock contribute to nutrient uptake and partitioning under different belowground environments. *Agronomy (Basel)* 9 (8), 415 <https://doi.org/10.3390/agronomy9080415>.

Volz, R.K., Alspach, P.A., Fletcher, D.J., and Ferguson, I.B. (2006). Genetic variation in bitter pit and fruit calcium concentrations within a diverse apple germplasm collection. *Euphytica* 149 (1-2), 1–10 <https://doi.org/10.1007/s10681-005-9000-8>.

Wallis, A., Harshman, J.M., Butler, B., Price, D., Fazio, G., and Walsh, C. (2017). Performance of Geneva (R) apple rootstock selections with 'Brookfield Gala' and 'Cripps Pink' in a tall spindle system. *J. Am. Pomol. Soc.* 71, 137–148.

Zhu, Y., Mazzola, M., Fazio, G., Shao, J., Davis, R.E., Zhao, J., and Zhou, Z. (2017). Phenotypic characterization and transcriptomic analysis of apple root defense responses to apple replant soilborne pathogen *Pythium ultimum*. *Phytopathology* 107, 119.

