Imagine (Apple) Rootstocks

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Abstract

For centuries rootstocks were considered just a means to propagate delectable fruit. In the 20th century, they were used to dwarf plants, increase per hectare productivity, enable high density production systems, resist some very important diseases and insects and tolerate some abiotic stresses. As our understanding of root-shoot relationships increases, we are developing more opportunities to utilize the breeding efficiencies generated by separating root (rootstock) trait selection from scion trait selection to include traits that were not envisioned possible. Combined with the increased ability to dissect traits into their DNA components (and derived gene expression), we can imagine being able to use rootstocks to modulate more than the "traditional" traits. For example, we have recently discovered that apple rootstocks can modulate the scion's gene expression, hormone flux, nutrient concentration, and metabolite production and concentration. We may be able to leverage rootstocks to plant orchards that have increased fruit quality, have reduced fruit storage disorders, are more mechanization compatible, or deliver therapeutic molecules to scions to resist more disease pressures. With increasing diversity in the development of new scion varieties, it will become more important to precisely match rootstock and scion genotype with the climate, soil, and management system to optimize orchard productivity and efficiency; hence the term "designer rootstock" is meant to describe a unique rootstock that is compatible with a specific scion, soil, climate and management parameters which enable higher efficiencies in the production of high-quality fruit and nuts. This evolution can be imagined and achieved for many tree crops that currently lack a designer rootstock component leading to enormous benefits from such systems. The development and application of rootstock systems with novel traits are poised to provide the world with more diverse, affordable, environmentally sustainable horticultural tree crops.

Keywords: rootstock modulated trait, nutrient uptake, gene expression, rootstock breeding, yield components, fruit quality.

INTRODUCTION

Within the context of an increasing world population, decreasing land resources, and increasing production burdens, our orchard cropping systems will be under increasing pressure to do more with less. In that framework, what will rootstocks technologies look like in the future, and what will they be able to contribute to the benefit of humanity? Will novel rootstock technologies match and exceed the advances gained by the broader application of rootstocks and rootstock breeding to fruit and vegetable crops in the past few decades? The answer to these questions will depend on our ability to leverage the unique opportunities that rootstocks provide us in various specialty crop systems. One of these opportunities is largely due to the ability to decouple root-specific trait selection from scion specific traits (divide and conquer strategy), thus reducing the complexity of genetic combinations needed to make gains from selection, as witnessed by the increased research on grafting in the latter years (Belmonte-Ureña et al., 2020).

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A great example is found in apple rootstocks, where, resistance to fire blight was derived from small-fruited, sour, tannic wild apple species that are not well suited for developing new fresh apple varieties because it would require multiple generations of introgression steps to select for both fire blight resistance and high fruit quality (Aldwinckle and Lamb, 1978; Gardner et al., 1980). Whereas the development of resistant apple rootstocks took only one generation (Cummins et al., 1983; Fazio et al., 2015). The two simplified genetic systems are joined by grafting: a practice that started thousands of years ago and has evolved from just serving propagation needs to purposefully change the dynamics of grafted scions to increase productivity and efficiencies (Janick, 2005; Mudge et al., 2009).

Changes in rootstocks technologies will be obtained through the art and science of conventional breeding and other forms of genetic manipulation (such as gene editing), many of which have not yet been developed. To "imagine" what rootstocks technologies may look like in the future, we should look at the past to understand how their use has evolved and how recent advancements have enabled increased knowledge of rootstock functions. A quick look at evidence from the distant past shows that grafting on seedling rootstocks has been around for millennia and used mainly to facilitate asexual propagation of desired scions. In apples, a transition to clonal rootstocks (same variety propagated by rooted suckers, layers, or cuttings) is supported by some historical evidence and seems associated with Alexander the Great, who sent dwarf 'Paradise' apples to the garden of Aristotle (5th-4th century BCE) (Janick, 1989; Mudge et al., 2009) where it is possible that it was used as a rootstock to propagate other apples. It seems like naturally occurring rooted suckers, also called layers, might have been used as stocks to receive bud grafts of scions. The art and science of grafting fruit trees were experimented and reported on by Greek, Roman, Middle-Eastern, and Eastern (China) cultures, where fruit fanciers tried all sorts of combinations to see what would work (quince and pear, apple and pear, apple and medlar, etc.). There is evidence that this type of experimentation occurred through the middle ages and into the age of Illuminism as fruit researchers argued why certain combinations would work while others could not, bringing up outlandish practices like witchcraft and less outlandish theories where the root system was thought to filter the lifeblood of a plant and that the resulting lifeblood could support the scion depending on kinship (Mudge et al., 2009). It is likely that populations of clonal rootstocks and genetically identical seed stocks (as they occur in some drupaceous species) were propagated and exchanged between monasteries, fruit fanciers, and later among tree nurseries that were operating in the past 500 years. Ease of rooting, dwarfing, and induction of early bearing (inverse of juvenility) were some of the more important reasons why clonal rootstocks were desired (Hatton, 1920). For apple rootstocks, this process resulted in a cluster of misidentified, admixed groups of rootstocks that were sold under similar names but performed very differently and lacked uniformity with regards to dwarfing and early bearing. By the late 1800s, as formal agricultural research was being established, scientists at the East Malling Research station decided to put an end to the confusion and conducted detailed studies on apple propagation material that had been collected throughout Western Europe, resulting in the first comprehensive description of homogeneous clonally propagated apple rootstocks (Hatton, 1917; Hatton, 1919). This description included important descriptors such as flowering timing, type, growth habit, rooting, graft-ability, and level of vigor induction which were essential for apple nurseries and the industry to grow. Formal genetic crosses were made between these cultivars, resulting in more well-known apple rootstocks like 'M.26', 'M.27', 'MM.106', and 'MM.111' (Preston, 1966). While the idea of using dwarfed trees in backyard plantings, royal outdoor and indoor gardens and other small gardens had been practiced for hundreds of years, the transition to planting dwarfing clonal rootstocks in large scale orchards settings began to be implemented in the second half of the 20th century likely spurred by the research results from East Malling (Costa et al., 1997). The majority of orchard owners were very hard to convince that smaller trees, planted at a higher density, would be more productive than the very large trees common in apple orchards throughout the world. It took some keen experimenters, entrepreneurial apple growers, and entire industries to demonstrate the efficiencies and productivity gained by the conversion (Sansavini et al., 1981; Wertheim, 1981; Sansavini and Bonomo, 1986; Palmer et al., 1989). Similar to apple, the effect of clonal quince rootstocks had also been known since the 1700' but did not gain traction until much later. Spurred by similar developments in dwarfing rootstocks other crops like cherries, peaches, and avocados followed suit in the quest for high-density production in the late 20th century and early 21st century (Robinson et al., 2008; Reighard et al., 2020). The discovery and application of dwarfing and early bearing rootstocks in apple catalyzed the industrialization of apple production and increased productivity of the U.S. industry by approximately 2 billion dollars per year (Robinson et al., 2007; Robinson, 2008; Fazio et al., 2019). Industrialization hinges on system uniformity, where certain management practices are able to be standardized throughout the system and generate repeatable outcomes. For example, tree height: if every tree in a row had a different height, managing pruning, picking, and spraying would become very time-consuming, and time = money and efficiency. Similar issues are faced when trees begin bearing on different timelines (Robinson et al., 2016). Rootstocks that control height (vigor) and when the trees come to bearing have enabled mass production and increased fruit availability to the consumer. Various training systems adapted to rootstock dwarfing and bearing potential and local production capacity have been developed by scientists and growers alike and have proven to increase profitability while maintaining or increasing the availability of higher quality fruit to the consumer (Tustin et al., 2016). Imagine now if the same technological advances could be transferred to crops like coffee, cacao, or mango, which are plagued by non-uniform tree productivity, maturity, and disease sensitivity that novel rootstock applications could address. Similar gains could also be achieved in nut production (macadamia, walnut, pecan), where most systems are late bearing, and shaving off 3-10 years from the juvenile non-bearing period would cause dramatic increases in efficiency. After the results of the first formal apple, rootstock crosses were evident with 'M.26' and 'M.27', several breeding programs were organized throughout the world with the goal to customize the dwarfing and early bearing effect to the needs of different countries/environments (Marini and Fazio, 2018). Therefore, through breeding, other traits were developed to withstand diseases or abiotic stresses like severe cold events (Khanizadeh et al., 2000). The process of localization (customization) refers to the adaptation of a product to serve the needs of a particular type of environment, climate, cultural practices, or other unique features. Breeding and selection of superior hybrids and other types of genetic manipulation followed by systematic field evaluation is the medium by which localization occurs for rootstocks. When such process is successful, the implementation of its products results in substantial gains in productivity. So, is high density production all that rootstock technologies can do?

We have learned that rootstocks technologies can go far beyond dwarfing and early bearing. A first of its kind research showed that gene expression of grafted scions could be dramatically altered by rootstock genotype (Jensen et al., 2010; Jensen et al., 2003). In addition, rootstock genotype was shown to alter the hormonal flux of mature grafted scions (van Hooijdonk et al., 2011; Tworkoski et al., 2016; Lordan et al., 2017; Adams et al., 2018). Rootstocks also alter the architecture of grafted scions by branch angle modification and production of sylleptic branching (Fazio and Robinson, 2008). Recent releases from the Geneva breeding program are known to have a significant effect on chilling hour requirement of grafted scions in mature trees, thereby increasing bud break and flower density of trees in low chill environments (Macedo et al., 2018). Apple rootstocks have demonstrated the ability to modulate the content of mineral nutrients (and nitrogen) in leaves and fruit of grafted scions (Fallahi, 2012; Neilsen et al., 2014; Fazio et al., 2020).

The cumulative yield of marketable fruit (total yield minus culls) is perhaps one of the most economically impactful parameters that can be influenced by choice of rootstocks (Lordan et al., 2019; Fazio et al., 2020; Reig et al., 2020). Numerous comparative studies have shown that apple rootstocks can modify several yield components like flowering, fruit number, fruit size, canopy formation, and bud renewal, which when combined, affect cumulative yield. In addition, several studies have shown that rootstocks can also affect the percentage of marketable fruit according to quality parameters (color, size, maturity, soluble solids, storage disorders associated with mineral nutrient content), resulting in the alteration of profitability of an orchard (Fallahi et al., 2002; Fallahi, 2012; Reig et al., 2019a; Reig et al., 2019b).

Significant progress has been made with regard to resistance to biotic stresses like fire blight (Russo et al., 2007; Fazio et al., 2008; Gardiner et al., 2012;), replant disease complex and its components (Mazzola, 1998; Rumberger et al., 2004; Leinfelder et al., 2006; Yao et al., 2006; Laurent et al., 2008; Shin et al., 2016; Zhu et al., 2017; Reim et al., 2020; Yim et al., 2020; Zhu and Salzgiver, 2020; Rufato et al., 2021), where apple root genotypes seem to play a very significant role on changing the composition of the soil microbiota by way of rhizo-deposits (Leisso et al., 2017). While trying to understand the role of root phenotypes, our lab in Geneva, NY, has leveraged custom made aeroponic systems to study root architecture, gene expression, and metabolomics, resulting in the identification of diverse architectural phenotypes (Figure 1), diverse metabolic profiles (Figure 2) and root-specific differentially expressed genes. These systems, in combination with specially built rhizhotron systems (Figure 3), have also been used to increase our understanding of the root x pH interaction (Al Farqani, 2019).

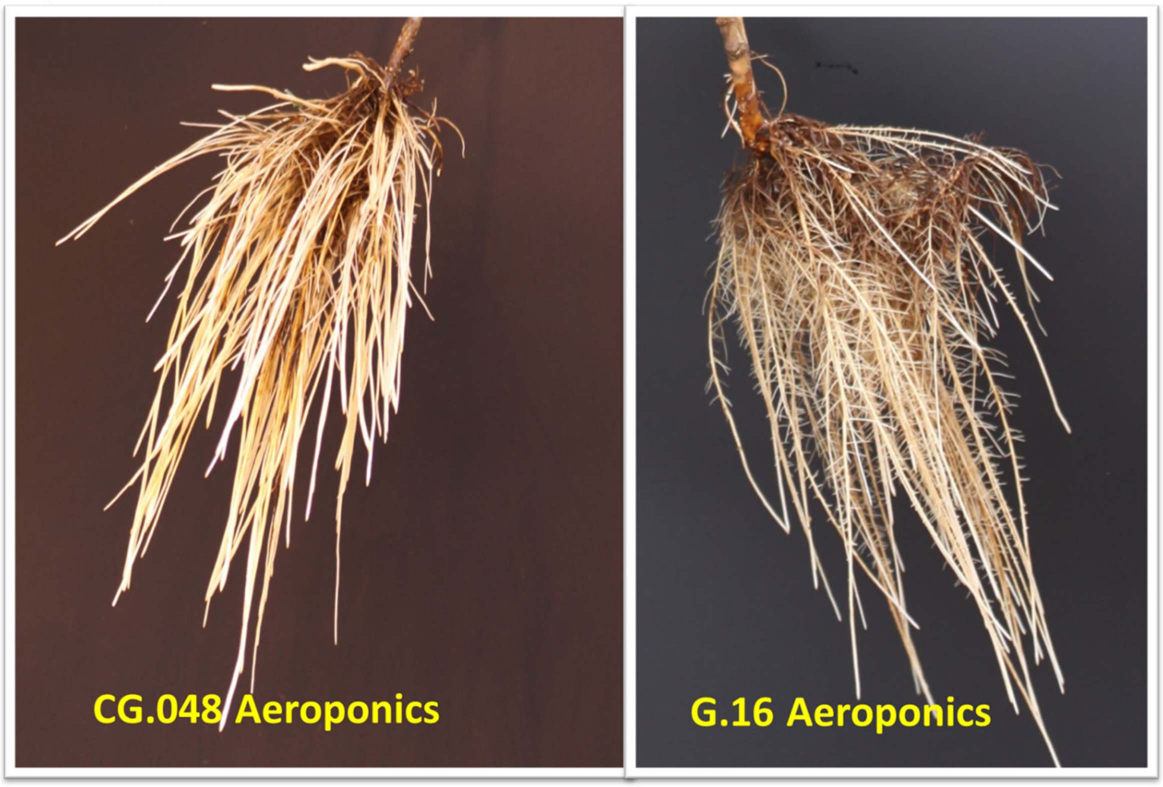

Figure 1. Root architectural differences among apple rootstocks raised in aeroponic systems. Aeroponic systems allow direct access to root tissue unencumbered by soil and other particles, thus providing cleaner options for transcriptomic studies and other observations. While the soil-less environment does not represent the myriads of interactions that roots have with soil particles and biota, it does reduce the variables acting upon roots when studying interactions with nutrients, pH, temperature etc.

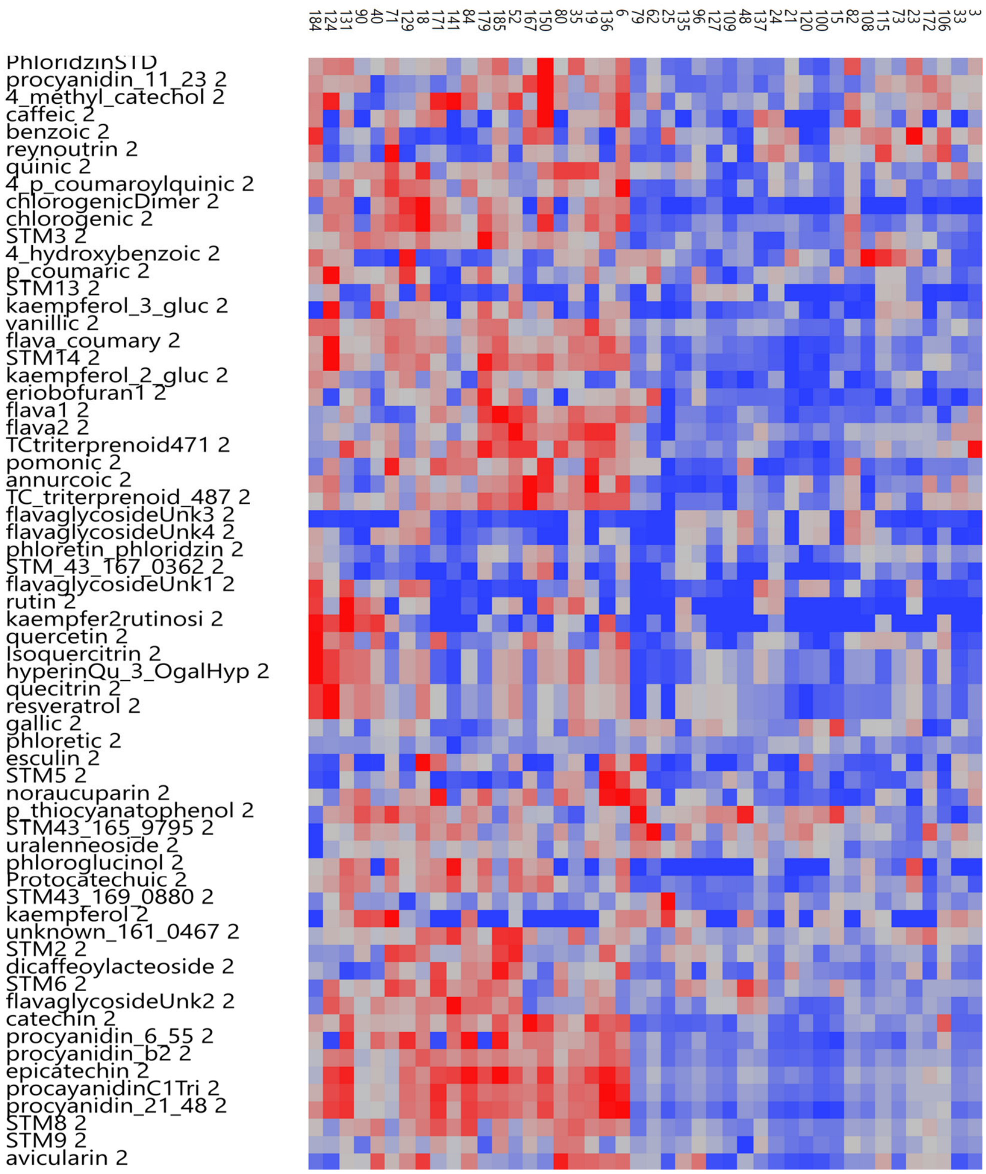

Figure 2. Phenotypic diversity of metabolic compound content (red=high, gray=medium, blue=low) in aeroponically grown roots harvested from 45 different rootstocks.

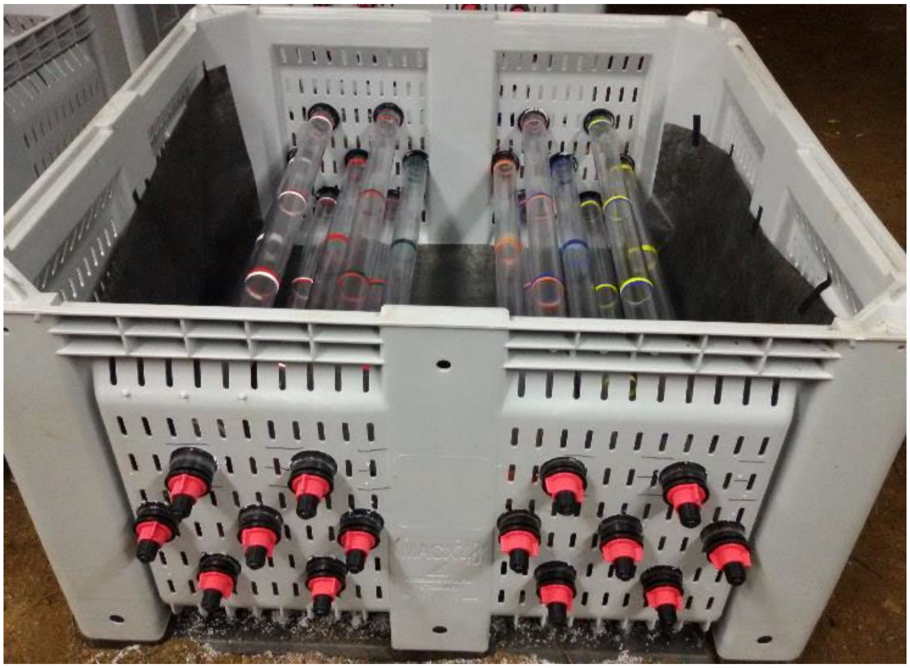

Figure 3. Tube rhizotron systems to study rootstock interactions with soil pH.

CONCLUSIONS

While our understanding of how rootstocks work and how they fit into the whole orchard system has increased significantly, there is still much to do with regards to questions associated with water availability, climate change, integration with robotics, remote sensing, integration with improved training systems, and the unraveling of interactions between apple rootstocks and apple viruses. We can imagine that in the next decade, we will be able to develop rootstock technologies that will address some of these problems. Unfortunately, working with tree fruit rootstocks means that the testing period of some of these solutions will need to be tested for multiple years, perhaps decades. In the meantime, the development of specific knowledge about pairing rootstocks to scions, soils, and training systems will go a long way to making tree fruit growers more successful and profitable.

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