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Advances in the development and utilization of fruit tree rootstocks: a case study for apple

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1 What are rootstocks?

All commercial temperate zone fruit trees are composed of an aerial 'scion' cultivar grafted or budded on another cultivar which serves as the support root system referred to as the 'rootstock.' The practice of budding or grafting desirable scion cultivars on rootstocks has been practiced for centuries due to the highly heterozygous nature of tree fruits (Tukey, 1978), most of which do not reproduce 'true to type' by seed. Thus, in general, the seed from a desirable fruit variety will not result in a tree which produces the same fruit characteristics as the parent. To overcome this problem, fruit growers learned many centuries ago that a desirable genotype could be propagated asexually by budding (a single bud) or grafting (a small section of shoot with several buds) onto other plants with roots (usually the same or a closely related species) and then allowing only the bud of the desirable cultivar to grow and develop into each tree's canopy, thus creating multiple trees of the desirable cultivar (Cummins, 1973; Larsen, 1976). For example, all of the 'Red Delicious' apple (*Malus domestica*) trees in the world originated from a single tree discovered

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in Peru, Iowa, in the 1800s. Thereafter, buds from the original tree were budded onto other apple seedlings, and later interspecific hybrid clones, that serve as rootstocks to produce the millions of 'Delicious' trees that have been grown around the world from until the present day. Similarly, 'Montmorency' sour cherry (*Prunus cerasus*) is a 400+ year-old cultivar that originated in France, but comprises the majority of sour cherry production in the United States, where it is grown primarily on *Prunus mahaleb* seedling rootstocks. The general history of all major fruit cultivars, including subtropicals such as *Citrus* as well as temperate zone fruit and nut trees, is similarly based on the propagation of superior fruiting genotypes on different rootstock genotypes. Not only does this provide a way to reliably reproduce the superior traits of the scion, but also a way to adapt its production to different localized soils, climates, and production systems.

Historically, seedlings were used as rootstocks for deciduous fruit tree species such as apple, pear (*Pyrus communis*), peach (*Prunus persica*), tart and sweet (*Prunus avium*) cherry, apricot (*Prunus armeniaca*), and plum (*Prunus domestica* and *Prunus salicina*) (Sax, 1949). The classic way to produce a rootstock is to plant seeds and when the young seedling is 30–50 cm tall, bud or graft onto that seedling the desirable scion cultivar. However, with the exception of some peach and almond rootstocks, since each seedling rootstock is a unique genotype, there can be considerable variability in its own growth characteristics as well as the characteristics it may impart to the scion due to the heterozygosity of each fruit species, resulting in variability in tree performance in the orchard. Potential variations in seedling rootstocks include vegetative vigor, tree shape, and size, yield, precocity of fruit bearing, fruit size, and susceptibility to root diseases and abiotic stresses. Nevertheless, almost all commercial orchards used seedling rootstocks until the twentieth century. While this chapter focuses mostly on apple, it exemplifies the various inherent rootstock properties and rootstock-induced qualities on grafted scions that can be found in other temperate fruit rootstocks.

2 History and modern use of clonal rootstocks in apple

Several millennia ago (possibly by the fourth century AD), rootstocks that had unique desirable characteristics began to be selected and propagated asexually by rooted cuttings or via stoolbed or layerbed techniques (Tukey, 1964). One such apple rootstock named 'Paradise' was dwarfing. It was propagated vegetatively in Europe and used in home gardens for several centuries before the modern era of rootstock improvement (Lindley, 1828; Loudon, 1822). A number of other dwarfing apple rootstocks were in use and propagated clonally by the late nineteenth century, but duplication of names and confusion of rootstock identity hindered adaptation for commercial production. To solve

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this problem, Hatton at East Malling Research Station (EMRS) in the United Kingdom (UK) began collecting and categorizing apple rootstocks from all over Europe. These were named using the letters EM (East Malling) and roman numerals I-IX (Hatton, 1917, 1919). Later, the EM designation was changed to simply M and the numbers from Roman to Arabic numbers. The series was expanded to 16 genotypes in 1914, and later additional rootstocks 17–24 were listed in 1924.

The most dwarfing rootstocks of the Malling series (M.8 and M.9) initially were considered too dwarfing for commercial orchards and more suitable for home gardens. However, from the semi-dwarfing Malling rootstock series (M.2, M.4, M.7, M.13 etc.), several were adopted by commercial apple growers in England and other European countries (Hatton, 1920). By the late 1950s, clonal rootstocks began to replace seedling rootstocks in most of Europe, North America, Australia, and New Zealand. This facilitated the development of planting systems at double or triple the planting density of trees on seedling rootstocks, which typically were planted at 150 trees/ha. At roughly the same time in the 1960s, Don Heinicke in the United States and Don McKenzie in New Zealand independently developed the central leader tree training system for use with semi-dwarfing clonal rootstocks (Heinicke, 1975; McKenzie, 1964, 1985). This planting system revolutionized apple growing and was adopted worldwide. Its primary advantage was earlier production because of greater precocity of the semi-dwarfing Malling rootstocks and greater cumulative production due to the higher planting density (Palmer et al., 1989; Sansavini et al., 1981; Sansavini and Musacchi, 2000).

The more dwarfing rootstocks of the Malling series, particularly M.9, began to be used in some German and Dutch orchards in the 1960s, leading to the development of the slender spindle tree form by Bob Wertheim in the late 1960s (Wertheim, 1978). These dwarf slender spindle trees were planted at 1500–2000 trees/ha. Initially, this concept was only accepted in Northern Europe where land for orchards was limited (Wertheim, 1981; Wertheim and Callesen, 2000). In areas of the world where land was more plentiful, most growers preferred to plant semi-dwarfing rootstocks on large land areas.

In France, a different tree form that could be used with semi-dwarfing or dwarfing clonal rootstocks, named the Vertical Axis, was developed by Jean Marie Lespinasse in the mid-1970s. Trees were planted at a density of 1000–1500 trees/ha. Although in France this tree form was developed mostly with M.9, growers in many other parts of the world mostly used semi-dwarfing clonal Malling rootstocks in the 1980s and 1990s (Barden, 1995; Crassweller and Smith, 2001).

In the late 1980s, many research and extension personnel around the world began to evaluate and promote higher tree densities on M.9 rootstock trained to various versions of the slender spindle tree form. However, growers in most regions were hesitant to adopt M.9 rootstock. A notable exception was Northern Italy where Herman Oberhofer, an extension specialist, began to take groups of growers to Holland to observe high-density orchards on dwarfing rootstocks, and within 10 years the vast majority of Northern Italy apple farms had converted to slender spindle on M.9 rootstocks (Comai and Widmann, 1972).

Through the 1990s and 2000s, most other apple-growing areas of the world switched from clonal semi-dwarfing rootstocks to clonal dwarfing rootstocks (Hampson et al., 2002; Robinson et al., 1991a). This happened more rapidly in some countries than others. In some countries, an intermediate step was taken by using a semi-dwarfing rootstock with the scion grafted on M.9 as an interstock. These interstem trees were more dwarfing than those on semi-dwarfing rootstocks, but not as dwarfing as those directly on M.9 rootstock (Domoto, 1982; Ferree et al., 1982; Koike and Tsukahara, 1988; Lord, 1983). In almost all regions of the world that used interstem trees, these have now been replaced by fully dwarfing rootstocks. Currently, most areas of Europe, North and South America, and Australia, New Zealand, and South Korea, use dwarfing stocks and planting densities greater than 2000 trees/ha and some as high as 6000 trees/ha. However, in some areas of the world, particularly China, Japan, and India, adoption of dwarfing clonal rootstocks has been slow and growers continue to use seedling, or semi-dwarfing, rootstocks with limited use of interstem trees (Ma et al., 2013; Tamai et al., 2002, 2003).

3 Rootstock improvement efforts

After the initial effort to name and categorize European rootstocks in the early 1900s, Preston at EMRS conducted controlled crosses of rootstocks which resulted in the release of M.26 in 1959 and later M.27 in 1975 (Preston, 1967; Preston and Belcher, 1982). M.26 was a cross of M.16 and M.9 and found widespread acceptance around the world since it was slightly more vigorous than M.9, but less vigorous than M.7. M.27 has found only limited use because it is even more dwarfing than M.9 and often with reduced fruit size (Wertheim and Scholtens, 1994).

The introduction of Malling rootstocks to Australia and South Africa revealed an important weakness, their susceptibility to woolly apple aphid (*Eriosoma lanigerum*) (Dozier et al., 1974). These aphids colonize the tops of trees, but in areas with cold winters, they are killed and then re-colonize slowly the next year. However, in areas with mild or warm winters, they colonize the root system and then re-infest the aerial parts of the tree rapidly the next year. The need for woolly apple aphid–resistant rootstocks led to a joint breeding program between EMRS and the Merton Research Station in the UK. Crosses of Malling rootstocks with Northern Spy resulted in a new series of rootstocks, the

Malling-Merton (MM) series numbered from 101 to 114. All are semi-dwarfing. Of these, the most important were MM.104, MM.106 and MM.111 (Preston, 1966). They were adopted by growers in many apple regions in the world and were utilized in the Central Leader system at densities from 500 to 800 trees/ha. MM.106 is highly productive, but also highly susceptible to *Phytophthora* root rot, which limited its use in wet soils (Browne and Mircetich, 1993). MM.111 is less productive and slightly more vigorous than MM.106, but is very durable and tolerant to drought stress (Atkinson et al., 1997; Tworkoski et al., 2016).

The need for better rootstocks has prompted many institutions around the world to make crosses for breeding objectives that have varied by institution, and have been as simple as improved rooting in the propagation bed or as complex such as multiple resistances to rootstock biotic and abiotic stresses. Rootstock breeding programs have been conducted in Sweden (Alnarp 2), Poland (P series) (Czynczyk and Omiecinska, 1989), Germany (Supporter® and Pillnitz series) (Fisher, 1994), Czech Republic (JTE series) (Dvorak, 1983; Webster and Tobutt, 1994), Romania (Voinesti series) (Mazilu et al., 1999), Russia (Budagovsky series) (Kuldoshin and Sadowski, 1999; Webster and Tobutt, 1994), China (SM series) (Gao et al., 2011; Rong et al., 2011; Wan et al., 2011), Japan (Morioka series) (Bessho and Soejima, 1992; Tsuchiya, 1988), Canada (Ottawa, KSC, SJM and Vineland series) (Elfving et al., 1993; Embree, 1985; Khanizadeh et al., 2005; Spangelo et al., 1974), New Zealand (IFO series) (Bus et al., 2008), Michigan, USA (MAC series) (Carlson and Perry, 1986), and Geneva, New York, USA (Geneva® series) (Cummins and Aldwinckle, 1974; Fazio et al., 2015b). There are now more than 100 named rootstocks in the world (Table 1).

One of the more impactful breeding programs started in 1937 at the Michurinsk Research Station in Russia. The primary objective of this program was increased winter hardiness. They used Russian red leaf rootstock as their source of cold hardiness and M.8 as their source of dwarfing. They released Budagovsky 9 (B.9) in 1975 as an M.9-sized stock with greater cold hardiness than M.9 (Czynczyk, 1979). It has had a worldwide impact and has been planted widely in the United States and Northern Europe. Researchers in the United States (LoGiudice et al., 2006; Russo et al., 2008b) showed B.9 is also resistant to fire blight (caused by *Erwinia amylovora*). The nature of the resistance is unusual since the young plant is sensitive to fire blight, but with age the grafted tree shows field-level resistance. Other rootstocks which have had limited acceptance are B.491 and B.118. A fourth and more recent rootstock, B.10 (B.62-396) is rapidly gaining acceptance in the United States (Autio et al., 2017a,b). It is slightly more vigorous than M.9, but is highly productive like M.9 and shows fire blight tolerance similar to B.9. Several other selections from the Budagovsky breeding program have been evaluated in North America, but none has shown high productivity and dwarfing (Autio et al., 2017a,b).

Table 1 A partial listing of apple rootstocks worldwide, with origin, characteristic vigor, parentage, and tree size relative to industry standards

Roostock	Type	Origin	Parentage	Tree size	References
B.54-118	Semi-dwarf	Michurinsk College, Russia	Unknown	–	Hulko et al. (1999), Kuldoshin (1999)
B.9	Dwarf	Michurinsk College, Russia	Unknown	M.9	Hulko et al. (1999), Kuldoshin (1999)
B.10	Dwarf	Michurinsk College, Russia	Unknown	M.9	Hulko et al. (1999), Kuldoshin (1999)
B.118	Semi-Dwarf	Michurinsk College, Russia	Unknown	M.9	Hulko et al. (1999), Kuldoshin (1999)
B.490	Dwarf	Michurinsk College, Russia	Unknown	M.9	Hulko et al. (1999), Kuldoshin (1999)
B.491	Dwarf	Michurinsk College, Russia	Unknown	M.9	Hulko et al. (1999), Kuldoshin (1999)
CG.2022	Dwarf	Geneva, USA	Malling 9 × Ottawa 11	M.27	Russo et al. (2007)
CG.2034	Dwarf	Geneva, USA	Dolgo crab × Malling 27	M.27	G. Fazio, pers. comm.
CG.4003	Dwarf	Geneva, USA	(Antonovka Kamienaja × Ottawa 3) × Robusta 5	M.26	Norelli et al. (2003)
CG.4004	Dwarf	Geneva, USA	722506-004 × OP	M.26	G. Fazio, pers. comm.
CG.5257	Dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.26	G. Fazio, pers. comm.
CG.6006	Semi-dwarf	Geneva, USA	PK-14 × Robusta 5	M.26 to M.7	G. Fazio, pers. comm.
CG.8189	Semi-dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.7-MM.106	G. Fazio, pers. comm.
G.202	Dwarf	Geneva, USA	M.27 × Robusta 5	M.26	Norelli et al. (2003)
G.210	Semi-dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.7	Norelli et al. (2003)
G.214	Dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.26	Norelli et al. (2003)
G.222	Dwarf	Geneva, USA	M.27 × Robusta 5	M.26	G. Fazio, pers. comm.
G.814	Dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.7	Norelli et al. (2003)
G.890	Semi-Dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.26 to M.7	Norelli et al. (2003)
G.935	Dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.26 to M.7	Norelli et al. (2003)
G.969	Semi-dwarf	Geneva, USA	Ottawa 3 × Robusta 5	M.7	Norelli et al. (2003)
JM.1	Dwarf	Morioka, Japan	Unknown	M.9	G. Fazio, pers. comm.

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JM.2	Dwarf	Morioka, Japan	Unknown	M.7	Norelli et al. (2003)
JM.4	Dwarf	Morioka, Japan	*M. prunifolia* Seishi × M.9	M.26	Norelli et al. (2003)
JM.10	Dwarf	Morioka, Japan	*M. prunifolia* Seishi × M.9	M.9	Norelli et al. (2003)
JTE-B	Dwarf	Czech Republic	Unknown	M.7	Norelli et al. (2003)
JTE-C	Dwarf	Czech Republic	Unknown	M.7	Norelli et al. (2003)
Mark	Dwarf	Michigan, USA	M.9 open pollinated	M.9	Carlson and Perry (1986)
M.26	Dwarf	HRI-East Malling, UK	M.16 × M.9	M.26	Preston (1974), Rogers and Beakbane (1957), Proctor et al. (1974)
M.27	Dwarf	HRI-East Malling, UK	M.13 × M.9	M.27	Preston (1974), Barritt et al. (1995)
M.7	Semi-dwarf	East Malling, UK	Unknown	M.7	Hatton (1917), Preston (1967)
M.9	Dwarf	Reselected at HRI-East Malling, UK	Unknown	M.9	Hatton (1917), Van Oosten (1977), Van Oosten and Groene (1984), Webster and Hollands (1999)
MM.106	Semi-dwarf	East Malling, Uk	Northern Spy × M.1	MM.106	Preston (1955, 1966)
P.1	Semi-dwarf	Skierniewice, Poland	M.4 × Antonovka	M.7	Czynczyk and Omiecinska (1989)
P.2	Dwarf	Skierniewice, Poland	M.9 × Antonovka	M.9	Czynczyk and Omiecinska (1989)
P.16	Dwarf	Skierniewice, Poland	Longfield × M.11	M.9	Czynczyk and Omiecinska (1989)
P.22	Dwarf	Skierniewice, Poland	M.9 × Antonovka	M.27	Czynczyk and Omiecinska (1989)
PiAu.51-11	Dwarf	Pillnitz, Germany	M 4 open pollinated	M.26	Norelli et al. (2003)
PiAu.51-4	Semi-dwarf	Pillnitz, Germany	M 4 open pollinated	M.26	Norelli et al. (2003)
PiAu.56-83	Semi-dwarf	Pillnitz, Germany	M 11 open pollinated	M.9	Norelli et al. (2003)
V.1	Dwarf	Vineland, Ontario, Canada	"Kerr" open pollinated	M.9-M.26	Elfving et al. (1993), Hampson et al. (2012)
V.2	Semi-dwarf	Vineland, Ontario, Canada	"Kerr" open pollinated	M.7	Elfving et al. (1993), Hampson et al. (2012)
V.3	Dwarf	Vineland, Ontario, Canada	"Kerr" open pollinated	M.27-M.9	Elfving et al. (1993), Hampson et al. (2012)
V.4	Semi-dwarf	Vineland, Ontario, Canada	"Kerr" open pollinated	M.7-MM.106	Elfving et al. (1993), Hampson et al. (2012)
V.7	Semi-dwarf	Vineland, Ontario, Canada	"Kerr" open pollinated	M.7	Elfving et al. (1993), Hampson et al. (2012)

Another breeding program that has had significant impact has been the German program at Pillnitz. Fisher has released four rootstocks, the Supporter® series 1-4. Supporter® 4 is similar to M.26, being highly productive, and has been planted to some extent in several European countries (Fischer et al., 1997). It has had little importance outside of Europe because it is susceptible to fire blight and replant disease (Autio et al., 2013; Auvil et al., 2011).

The breeding program in Poland has released a number of cold-hardy rootstocks which have been used in Poland and to a limited extent in other European countries. The most important have been P.22 (very dwarfing, similar to M.27) and P.16 (similar to M.9, but more winter hardy). While these have been tested worldwide, their implementation has been somewhat slow because they did not offer significant improvements over the current standard rootstocks (Marini et al., 2006).

Mark rootstock, bred by Robert Carlson and released by Michigan State University in the early 1980s, had its most significant impact in the United States from 1985 to 1995. Mark is slightly more vigorous than M.9 and is winter hardy and very productive. However, as the trees aged, a proliferation of non-organized tissue developed just below the soil line, leading to weak tree growth and small fruit size (Travis and Rytter, 1995; Travis et al., 1999; Warmund et al., 1993).

Of the four Canadian breeding programs, Ottawa 3 has had the most impact. It is very winter hardy and very productive, with vigor similar to M.9. It was planted to a limited extent in the late 1980s and early 1990s, but problems with transplant losses, virus sensitivity, and difficulty in propagation limited its use (Ferree, 1992; Rioux et al., 1984; Spangelo et al., 1974). Currently, five rootstocks from Vineland, Ontario, are under development and may have importance in the future (Hampson, 2012; Hampson et al., 2012). The KSC and SJM rootstocks have not had commercial importance.

Another impactful rootstock breeding program has been at the Geneva campus of Cornell University. The program was started by James Cummins in 1969 and was joined by Herb Aldwinckle in 1971 to develop a series of rootstocks that not only conferred high productivity and dwarfing, but also resistances to the most important rootstock diseases and biotic stresses (Aldwinckle et al., 1972; Cummins and Aldwinckle, 1974). They extensively used 'Robusta 5' rootstock as a parent since it is resistant to fire blight and other diseases (Gardner et al., 1980). Other parents were either M.9, M.26, M.27, or Ottawa 3. They screened all progeny for resistance to fire blight and tolerance/resistance to crown and root rot caused by *Phytophthora cactorum*. They also screened for woolly apple aphid resistance and selected for low number of root suckers or burr-knots (Cummins et al., 1983). These were then selected for high productivity, dwarfing, and cold hardiness. Interestingly, some of the Geneva® rootstocks also have shown tolerance/resistance to apple replant disease (ARD), although that was not a breeding objective. The program was converted to a joint breeding venture between Cornell University (Geneva) and the USDA-ARS in 1998, and it continues to make crosses and release new rootstocks under the leadership of Gennaro Fazio. The breeding objectives have evolved through time. While these include previous objectives of fire blight resistance, crown rot resistance, cold hardiness, low root suckers, and low burr-knots, newer objectives include replant disease tolerance, specific nutrient uptake (especially Ca), low chill induction requirement, drought tolerance, water-use efficiency (WUE), tolerance to sodic soils, tolerance to particular soil pH levels (high and low), and graft union strength (Fazio et al., 2015b). As of 2019, 14 rootstocks have been released by the Geneva® program and several have achieved importance in the United States and some other parts of the world. Those that are being produced in large volumes (>500,000 plants per year) include, in order of importance, G.41, followed by G.11, G.935, G.969, G.890, and G.213. The total worldwide sales of these rootstocks was 8.8 million in 2017.

Currently in the world, there are only five to seven rootstock breeding programs. In addition to the Geneva® program, there are three programs in China, one in New Zealand, and one in Russia. A unique objective of one of the Chinese programs is apomixis in rootstocks, which would allow propagation of rootstocks by seed. This would drastically change the propagation industry in the world. Primary objectives of these programs include cold hardiness (Russia, China), fire blight resistance (New Zealand), and drought tolerance (China) (Gao et al., 2011; Ma et al., 2012; Sha et al., 2011; Wan et al., 2011; Zhang et al., 2011).

4 Rootstock propagation

Apple rootstocks are propagated either by seed, cuttings, layering, stooling, or by tissue culture. When propagated by seed, the grafted trees are usually vigorous, but also variable in tree size and productivity due to the variability inherent in seeds (Visser and Schaap, 1967). Thus, almost all apple rootstocks in the world are propagated asexually by cuttings, layerbed, or stoolbed. Only since about 2008 have apple rootstocks been propagated commercially by tissue culture (Castillo et al., 2015).

Propagation in all areas of the world, except some Asian countries including China, is mostly done by layerbed or stoolbed. However, in China most rootstocks are propagated by rooting of hardwood cuttings (Kwon et al., 1999; Yoshida and Muramatsu, 1998). This is due to the difficulty of propagating Malling stocks (which are used in the west) by cuttings (Sun and Bassuk, 1991), while rootstocks used in China have the genetic makeup to root well from cuttings.

Typically, propagation by stoolbed (plants planted vertically) or by layerbed (plants planted on an incline and then laid flat at the end of the first season) is done by planting rootstock plants in a row in a shallow trench (Hartmann et al., 1997). After the first year's growth, the plants are cut back to three buds on each shoot for a stoolbed or the shoots are laid horizontal along the ground in the bottom of the trench for a layerbed. Later in the spring of the second year, when shoots from the 'mother' plants reach about 30 cm tall, sawdust, peat, or soil is mounded up to cover the lower parts of the new shoot. The sawdust is kept moist by irrigation and additional layers of sawdust or soil are mounded up through the season to a height of 30 cm. In the late summer and fall and during the winter in climates with mild winters, the shoots develop roots from one to five nodes along the lower stem of the 1-year-old shoot. These shoots are harvested from the mother plants in late fall, winter, or early spring by cutting the stem below the new roots, but leaving intact the mother plant. The process is repeated each year by sweeping away the sawdust or soil from the mother plants in the spring, exposing the horizontal shoots in the layerbed or the upright plant in the stoolbed, and then adding more sawdust or soil again as new shoots reach 30 cm in height.

The ability to produce roots in a stoolbed or as a rooted cutting differs among rootstocks (Villeneuve, 1986). A related rootstock trait is the tendency to produce burr-knots which are aboveground masses of root initials. Burr-knots are considered a defect and create a risk of rootstock infection by the bacteria that causes fire blight (Marini et al., 2003). Good rooting in a stoolbed generally is associated with a tendency to produce burr-knots. Many of the Malling stocks produce burr-knots, but also can be propagated easily in a stoolbed, while many of the Geneva® rootstocks root poorly in a stoolbed and do not produce burr-knots.

The stoolbed/layerbed method has been used for several centuries to propagate apple rootstocks, with only small improvements in technique. This method is an extension of what happens naturally with some apple trees where root-derived suckers come up from the ground season after season (Costante et al., 1983). Rootstock clones that root well with this system have been successful commercially, while those that root poorly in this system usually have been discarded (Robinson et al., 1997). However, the 2005 introduction of G.41 (which does not root well in a layerbed) stimulated the development of improved new techniques. Adams (2010) found that applications of the gibberellin biosynthesis inhibitor, prohexadione-calcium, to the shoots of rootstock layerbeds when the shoots were 90–100 cm tall, resulted in a reduction in shoot growth, but better rooting at the base of the shoot. Fazio (unpublished data) also observed in commercial nursery settings that planting G.41 in a vertical position in a stoolbed at double or triple the normal density resulted in better rooting of each shoot. This was due to the more limited number of shoots produced by each stooling mother plant (3–5 on a high-density stool plant vs. 10–15 from a layerbed plant) and the competition for resources between shoots. Lastly, Adams (2010) showed that if the stoolbed was established using tissue culture mother plants, rooting was improved significantly, and the increased rooting lasted for several years. These three improvements in stool/layerbed technology have allowed the successful stoolbed propagation of difficult-to-root rootstocks such as G.41.

A second important method of apple rootstock propagation has been the use of hardwood cuttings. This is the main method of propagation of rootstocks in China, but it is uncommon in other parts of the world. The most common rootstock in China is *Malus prunifolia*, which roots readily from cuttings (Yao et al., 2001). Typically, dormant (hardwood cuttings) are dipped in a synthetic auxin (indolebutyric acid, IBA) and then planted in a rooting bed of sand/soil in a plastic-covered high tunnel greenhouse and kept in high humidity until cuttings have rooted. They are then transplanted to a nursery where they are budded with a scion variety (Rong et al., 2011; Wen et al., 2018). This is seldom successful with Malling or Budagovsky rootstocks due to their low rooting percentage (Bassuk and Howard, 1980). Recently in the United States, several of the new Geneva® rootstocks have been propagated by softwood cuttings. Typically, green cuttings consisting of the tops of tissue-cultured plants are removed and dipped in rooting hormone (IBA), planted in a rooting bed of artificial media (vermiculite and peat moss), and kept under a plastic tunnel with misting until rooted. When the source of the green wood is micro-propagated material, these cuttings are more successful (Quamme and Hogue, 1994). These rooted plants are transplanted to a nursery and then budded in the late summer with a scion variety (Fleming, pers. comm.).

The newest large-scale commercial method of propagation is via tissue (tip) culture. Tissue culture consists of harvesting a shoot apex (an explant) and growing it on an artificial medium with a complete set of nutrients (Castillo et al., 2015; Geng et al., 2015). The plant hormones (or synthetic versions of plant hormones) are placed in the medium and their relative concentration is modified to obtain specific growth characteristics. By varying the balance of auxins and cytokinins, the explant is induced first to multiply by producing callus and shoots. These plants are divided and subdivided multiple times in an iterative process that produces thousands of new explants from an original plant. Later, the hormone balance is modified by increasing auxins to induce rooting. These small, sterile, rooted plantlets are then transplanted into a soil-less medium and grown in a mist tunnel for several weeks for the first phase of acclimation ('hardening off'). Then they are moved to larger pots in a regular greenhouse to acclimate to higher light levels, and finally are moved to the open air. These rooted plants can then be planted in a nursery and budded with a scion variety. This method was tried in the 1980s for propagating M.9

and Mark, but problems arose when the plants developed differently in the field, with many more burr-knots and vigorous growth (James and Thurbon, 1979; Webster and Jones, 1989). This may have been due to epigenetic effects of the hormones used in the tissue culture process, or it may have been simply a mix up of plant material and the propagation of a seedling instead of M.9 or Mark. This occurred before the era of DNA fingerprinting, thus the problem was never resolved. Nevertheless, because of those bad experiences in Europe, the use of tissue culture to propagate apple rootstocks was banned and fell into disfavor. In the mid-2000s, Gennaro Fazio began working with various tissue culture labs in the United States in an effort to propagate G.41 via tissue culture since it is difficult to propagate by stoolbed or cuttings. Field trials of trees from these tissue-cultured rootstocks performed similarly to stoolbed propagated rootstocks (Autio et al., 2005, b); by 2010, commercial quantities of G.41 and other Geneva® rootstocks were being propagated by tissue culture. This success stimulated others in the world to accept tissue-cultured Geneva® rootstocks. By 2017, there were more than three million Geneva® rootstocks being propagated by tissue culture each year.

Important advances in both the techniques of apple rootstock tissue culture and the improvements in tree performance from tissue-cultured plants have been achieved. Each tissue culture company has developed proprietary methods to achieve commercial success. These individual trade secrets are not widely shared. However, the results in the nursery and in the orchard have been published. Adams (2010) showed that liners from tissue-cultured plants have more roots and a more fibrous root system than stoolbed plants. The improvement in rooting carried over to the stoolbed where liners from a stoolbed that had tissue-cultured mother plants had more roots than liners from a stoolbed started with conventional plants. Because of the more fibrous root system, tissue culture plants establish better in the orchard. In addition to propagation benefits, micro-propagated plants feature a more vigorous root system with many more primary roots than conventional liners. Some nurseries are offering these well-developed root systems in a potted tree nursery production system that can be transplanted with few losses even during mid-summer.

Currently, the price of a stoolbed-produced rooted rootstock liner or a rooted cutting is less than a tissue-cultured, rooted rootstock liner. Nevertheless, all three methods are used commercially to propagate apple rootstocks worldwide. However, the stoolbed/layerbed method predominates.

5 Rootstock evaluation

Systematic rootstock evaluation began with the work of Hatton at EMRS in the early 1900s (Hatton, 1917). Their published work was a guide for growers and

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researchers alike. Individual researchers in Europe and North America continued individual comparative trials of rootstocks through the 1960s (Carlson, 1974; Nelson and Tukey, 1955). Later researchers in other countries also began comparative rootstock trials, including New Zealand, Australia, South Africa, Japan, and more recently China (Bergh, 1992; George and Nissen, 1986; Racsko et al., 2011; Tustin and Cashmore, 1994; Tustin et al., 1993). However, the trial results in one climate and soil type often differed from results of other trials in other climates. This led to substantial confusion and differing opinions among researchers and growers. In 1976, a group of researchers in eastern North America launched a coordinated rootstock testing program named the NC-140 project (Ferree, 1991, 1992; Ferree and Perry, 1989). This group began conducting uniform multilocation orchard comparisons of rootstocks and met annually to compare results. The project was later expanded across the United States and now includes participants from Canada and Mexico as well. The group also conducts comparative research trials with peach, cherry and pear rootstocks (Cowgill et al., 2017). Over the 45-year existence of this project, it has conducted 18 trials of apple rootstocks (approximately one every 3 years). With each new trial, the latest rootstocks from around the world have been included. The primary rootstock characteristics evaluated in the coordinated NC-140 trials include tree survival in various climates, level of dwarfing, precocity, yield, yield efficiency, fruit size, number of root suckers, and burr-knots. A similar group of researchers from Europe was organized in 2003 and is conducting coordinated uniform multilocation rootstock trials in several European countries (Kviklys, 2011). Another group led by Leo Rufato began multilocation coordinated trials in Brazil in 2014.

In addition to coordinated trials, individual researchers have focused on evaluations of cold hardiness, graft union strength, virus susceptibility, tolerance to replant disease, nematode tolerance or resistance, and mineral nutrient profiles.

6 Rootstock effects on scion traits and mechanisms

Rootstock genotype has numerous effects on the scion, including vigor, precocity, yield efficiency, partitioning of carbon, mineral nutrient profile, branch angle, and graft union strength (Fig. 1). In addition, rootstock tolerance or susceptibility to soil characteristics, climate stress, and biotic stresses determine if the tree survives, is stunted, or grows well.

6.1 Dwarfing

The most desirable rootstock characteristic is dwarfing. In most cases, seedling rootstocks confer the most vigor. The current list of clonal rootstocks range in

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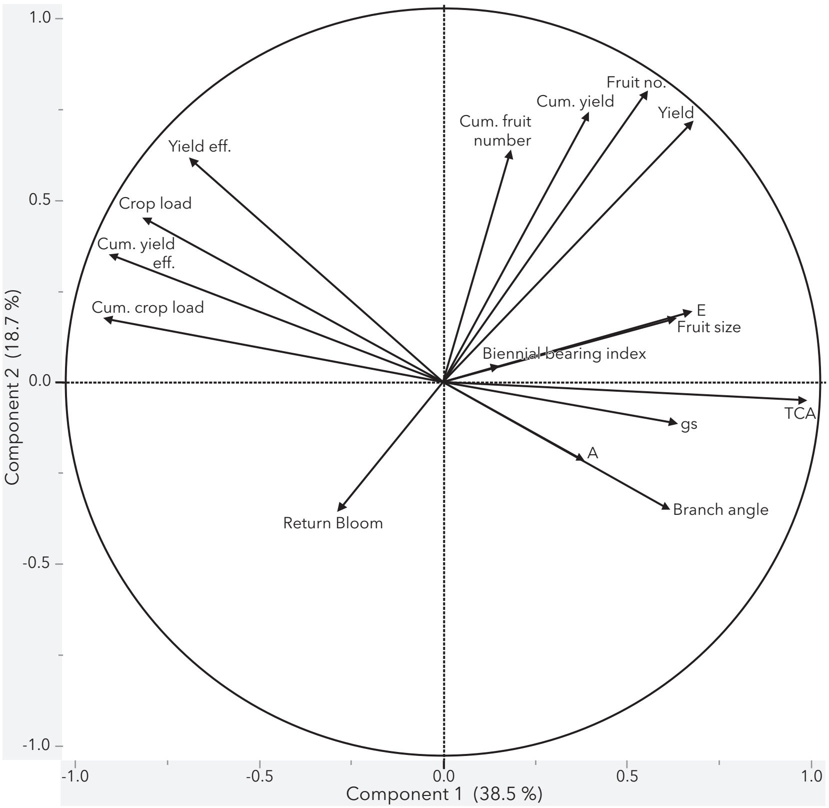

Figure 1 Principal components (PCA analysis) of variables affected by rootstocks: cumulative fruit number, cumulative yield, fruit number, yield, mean biennial bearing index, fruit size, transpiration (E), trunk cross-sectional area (TCA), stomatal conductance (*gs*), carbon assimilation (A), branch angle, return bloom, cumulative crop load, cumulative yield efficiency, crop load, and yield efficiency. The arrows indicate the effects that are positively correlated (in the same quadrant) and those that are negatively correlated (opposite quadrants).

vigor from 100% to only 10% of seedling (Table 1). This vast range of dwarfing has allowed a 10- to 20-fold increase in planting density in modern orchards. Although the mechanism of dwarfing has been studied intensively for more than 50 years, the complete explanation of apple dwarfing is still not clear. In the last 10 years, the genetic basis of dwarfing has been linked to several genes, *Dw1* and *Dw2*, and possibly a third (Fazio et al., 2014; Foster et al., 2015; Harrison et al., 2016). The physiological expression of these genes is less clear as they have not been characterized yet at the molecular level. Physiologists have measured effects of dwarfing rootstocks on root-supplied hormones and distinct carbon partitioning, with dwarfing rootstocks inducing a much greater use of carbon for fruit production compared to root system development. This is probably why trees on dwarfing rootstocks have much smaller root systems. It has been shown that dwarfing in apple is not caused by restricted water supply to the scion (Olien and Lakso, 1986). While the rootstock may cause some changes in vessel size, xylem element and vascular resistance to water is similar in vigorous and dwarfing rootstocks (Tworkoski and Fazio, 2011). In contrast, dwarfing in peach has been linked to water stress induced by dwarfing rootstocks (Johnson et al., 2011). Currently, the physiological basis for dwarfing appears to be a combination of root-supplied signals (maybe hormones) to the scion, inducing increased flowering, and reduced partitioning of carbon to the root system and early termination of vegetative growth (Foster et al., 2017; Van Hooijdonk et al., 2010).

6.2 Precocity

Precocity or induction of early bearing is defined as the earliness of an apple tree to flower and begin fruiting (Fazio et al., 2014). The physiological trait of juvenility describes young trees that are grown from seeds which do not produce any flowers or fruits for several (5–8) years, a phenomenon that seems to be linked to changes in methylation of the apple genome (Hafiz et al., 2008). As the trees age, they transition from juvenility to a reproductive stage of flowering and fruiting. The basis of juvenility may be linked to a plethora of root signals, including hormones. Gene-altering approaches that modulate genes involved in flower induction have been shown to reduce this juvenile phase for breeding purposes (Kotoda et al., 2006; Schlatholter et al., 2018; Schouten et al., 2009); however, thus far they have not proven successful in graft transmissible alteration of the juvenile period. When a mature (non-juvenile) apple scion is grafted on a seedling rootstock (which is juvenile), the scion may revert to a juvenile-like phase and flowering may be delayed for 5–8 years after grafting. However, when grafted onto a precocious clonal rootstock, there is no reversion to a juvenile-like phase, with the potential for flowering to occur in the first or second year in the orchard (Schmidt, 1986). Rootstocks differ in their effect on scion precocity (Fallahi and Mohan, 2000). Most of the semi-dwarfing rootstocks from the Malling series, and the Budagovsky series, are more precocious than seedling rootstocks, but flowering is still delayed 3–5 years after grafting. However, the dwarfing Malling, Budagovsky, and Geneva® rootstocks are much more precocious, with flowering in the first year in the orchard or even in the nursery. G.11 rootstock is highly precocious and can have flowers itself in the nursery. Interestingly, many of the semi-dwarf Geneva® rootstocks are also highly precocious such as the more dwarfing rootstocks. Precocity was a selection factor for semi-dwarf Geneva® rootstocks, since the lack of precocity is a serious flaw in Malling and Budgovsky semi-dwarfing rootstocks. Precocity induced by the rootstock has a large effect on orchard economics, since early production in years 1–5 is important for repaying the capital investment in a new orchard. The increase in precocity of dwarfing rootstocks has allowed the planting of much higher tree densities, with associated higher orchard establishment costs, since the investment can be paid off rapidly (Lordan et al., 2018a; Reig et al., 2019).

6.3 Yield efficiency and harvest index

A primary criterion to compare rootstocks has been the calculation of yield efficiency, which is defined as the weight of fruit produced (kg) per unit of trunk cross-sectional area (TCA in cm^2) measured at a set distance above the graft union (Robinson et al., 1991b). This is a rootstock-scion performance efficiency measurement since it relates the tree's fruit output relative to the size of tree as measured by TCA, which tends to be proportional to canopy size up to a point. This facilitates the comparison of trees on rootstocks of vastly different vigor and tree size on an orchard-area basis. However, this measure was developed for comparing trees on rootstocks of varying vigor that were minimally constrained by allotted orchard space in evaluation trials for which the filling of orchard space and canopy maturation typically took 6–10 years. It has recently been recognized that, as long as the primary determinant of canopy size is rootstock vigor, yield efficiency allows comparative evaluation of differences in rootstock-induced productivity relative to vegetative growth. However, as orchards have become more dense, with a primary training/production system focus on filling allotted orchard space and reaching full production rapidly, the point at which the canopy completes the filling of its allotted space occurs much earlier, and therefore pruning intervention to maintain the canopy in that space becomes a confounding factor to yield efficiency calculations, since the canopy's productive area is no longer expanding but the TCA continues to increase for the life of the tree. Therefore, yield efficiency comparisons are primarily of value only until the allotted orchard space is filled. Furthermore, as modern orchards are trained and pruned to more two-dimensional 'fruiting wall' canopy architectures, the inherent rootstock effect on yield efficiency is further confounded due to non-rootstock–based horticultural interventions.

When fruit production over several years (traditionally 10 in rootstock comparison trials, perhaps less for higher density training systems) is summed and the cumulative production is divided by the tree TCA (at the point at which allotted orchard space is filled), an estimate of harvest index is obtained (Palmer, 2011; Strong and Azarenko, 2000). Harvest index is the measure of fruit production compared to vegetative production (branches, leaves, trunk, and roots) of the tree. However, harvest index is difficult and expensive to measure, thus the measure of cumulative yield efficiency is used since final TCA is an estimate of the cumulative vegetative growth of the tree. In the few cases where harvest index has been measured directly, dwarfing rootstocks (M.9) were found to partition 70–80% of annual carbon into fruit and only 20–30% to vegetative growth, while vigorous rootstocks induce much more partitioning of carbon into vegetative growth (>50%) (Strong and Miller Azarenko, 1991).

An annual estimate of partitioning of carbon into fruit vs. vegetative growth can be obtained from the ratio of fruit production (kg) to the incremental increase in TCA (cm^2 increase); however, this estimate of annual harvest index is less commonly used by rootstock researchers. If this annual estimate was used more, it could show how the partitioning of carbon between fruit production and vegetative production changes over time, and would allow the identification of rootstocks that will be problematic over time as the orchard matures since they continue to have a high fraction of carbon partitioned into vegetative growth even when the tree is mature.

Rootstock vigor is linked loosely to yield efficiency, with most vigorous, semi-vigorous rootstocks, and semi-dwarfing having lower yield efficiency than dwarfing stocks. Interestingly, many of the semi-dwarfing Geneva® rootstocks have yield efficiencies that are similar to dwarfing rootstocks (Reig et al., 2018; Russo et al., 2007). This is because high yield efficiency was a selection criterion for semi-dwarfing Geneva® stocks. The increase in yield efficiency has resulted in much higher yields per ha for dwarf trees if the dwarf trees are planted at their optimum tree density, as predicted from their inherent tree size (Lordan et al., 2018b). The indiscriminate use of high yield efficiency values to plan orchard designs has resulted in serious errors for the apple industry when scion vigor is low, and growers choose the most dwarfing rootstocks available because of their high yield efficiency. This has resulted in many orchards where the trees do not fill the space allocated to each tree, resulting in moderate yields per ha even though the yield efficiency of the rootstocks is high. Nevertheless, if rootstock vigor is sufficient to fill the space quickly, then the high yield efficiency of a dwarfing rootstock will result in higher yields than a less-efficient rootstock. This improved mature production is an important factor for sustainable long-term profitability of high-density orchards on dwarfing rootstocks, compared to medium and low-density orchards on semi-dwarfing or vigorous rootstocks (Lordan et al., 2018a).

It seems clear that the impact of rootstocks on carbon partitioning and flowering is intertwined with the dwarfing effect of the rootstock on the scion. Since a dwarfing rootstock induces the partitioning of 70–80% of annual fixed carbon into the fruit, the amount of carbon left for vegetative growth is a small fraction of that available in a tree on a vigorous rootstock. The mechanism of increased yield efficiency of dwarfing rootstocks is not completely clear. Evidence to date indicates that increased root-supplied hormones differ among rootstocks (Adams et al., 2018; Lordan et al., 2017) and may cause increased flower initiation and fruit set, which leads to early production in the first or second years accompanied by higher partitioning of carbon to fruits. However, that explanation does not fully explain the dwarfing effect of rootstocks, since shoots of the scion on a dwarfing rootstock also stop growth earlier in the season that those on a vigorous rootstock. Nor does it explain why interstems of varying length decrease vigor and increase early bearing in apple trees (Carlson and Oh, 1975).

6.4 Influence on leaf and fruit nutrient concentrations

Recently, there has been great interest in rootstock effects on fruit mineral nutrient profiles. This has been driven by the widespread planting of the variety 'Honeycrisp,' which suffers from several fruit disorders including the calcium-related disorder bitter pit (Baugher et al., 2017; Biggs and Peck, 2015; Rosenberger et al., 2004). While the modulation of nutrients in the scion by rootstocks had been described in the past (Lockard, 1976; Rom and Rom, 1991; Tukey et al., 1962), the types of rootstocks used in such research were genetically very similar (Duan et al., 2017; Gharghani et al., 2010; Jin et al., 2012). Wide crosses performed in the Geneva® breeding program have revealed significantly different nutrient profiles induced by rootstocks (Fazio et al., 2012, 2013). Some rootstocks cause greater levels of K in the leaves or in the fruit, while others induce higher levels of Ca in the fruit or the leaves. Such rootstock-induced differences have been shown for several other nutrients, including N, P, S, Mg, and B (Reig et al., 2018). Changes in soil pH, for example, caused differences in the expected absorption curves for metal ions such as manganese and iron, indicating that some rootstocks perform better at certain pH values than others (Fazio et al., 2012). Soil pH is one of the most important predictors of soil fertility, and developing a set of rootstocks well adapted to specific pH profiles may improve orchard performance and open marginal land to apple cultivation. The genetic inheritance of nutrient absorption and translocation to different parts of the scion is quite complex, as there are many mechanisms that contribute to a rootstock's differential efficiency for a particular nutrient (differential evapotranspiration, crop load, root morphology, water availability and use efficiency, interaction with soil biota, active and passive transport, vessel composition, and size etc.) and the genetic landscape described by Fazio et al. (2013) shows a very dynamic multi-locus model intertwined with between-nutrient to nutrient positive and negative correlations. It is possible to identify rootstocks with high calcium effects on the scion; however, given the complex genetic nature of each nutrient profile, the combinatorial probability of developing a rootstock that features multiple desirable nutrient profiles decreases with the addition of more nutrient requirements (Fazio et al., 2015a; Reig et al., 2018). Therefore, nutrient-based selection of new apple rootstocks may have to be limited to a few nutrients at a time.

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6.5 Branch angle and hormones

Within rootstock breeding populations, breeders have noticed the induction of differences in scion branch angle as well as level of sylleptic branching. Fazio and Robinson (2008a,b) reported certain Geneva® rootstocks induced flatter scion branch angles than other Malling stocks. G.935 is particularly adept at this in a nursery environment; it consistently promotes more feathers (sylleptic branches) than other traditional rootstocks. More recently, Lordan et al. (2017) showed that certain Geneva® rootstocks (e.g. G.11 and G.41) had higher levels of root-supplied cytokinins and abscisic acid than other Malling stocks (Lordan et al., 2017). This hormone profile was somewhat associated with flatter branch angles. Flatter branch angle also is associated with the potential for more flowers (Lauri and Lespinasse, 2001). This trait is potentially quite valuable in high-density orchard production systems, since trees with flat branch angles require less branch manipulation to control tree vigor.

7 Rootstock tolerance to abiotic and biotic stresses

7.1 Cold hardiness and lack of winter chilling

In northern climates, fall, mid-winter, and early spring cold temperatures are a serious risk and limitation to apple tree survival (Moran et al., 2018). In warmer climates, the lack of winter cold (sufficient to complete the endodormancy to ecodormancy transition) is also a limitation to uniform bud burst in the spring. Rootstocks can affect both cold hardiness and the chilling requirement for bud burst in the spring.

When fully cold-acclimated, apple flower buds can withstand temperatures of −30°C; however, roots can only withstand temperatures of −10°C. Soil buffering capacity for cold winter temperatures and snow cover usually protect roots from the temperatures below −10°C. However, if there is little snow cover and there are prolonged air temperatures below −30°C, then damaging soil temperatures below −10°C can occur in the root zone. A second type of rootstock damage during winter can affect the rootstock shank (the trunk-like portion of the root system below the graft union). If cold winter temperatures occur with no snow cover, the part of the rootstock that is exposed above ground and the part just below the soil surface can be damaged. If the entire cambium is killed in this zone just above and below the soil line, the tree will die in the spring about blossom time or during mid-summer when temperatures get hot (Embree and McRae, 1991; Prive et al., 2001).

The hardiness of the rootstock shank varies considerably among rootstocks. Differential tolerance to cold temperatures has been studied and certain Malling stocks such as M.7 are quite sensitive to winter damage at moderately cold temperatures of −20°C. In 1990, Quamme classified the rootstocks available at the time for winter hardiness. He classified M.7 as very tender, M.2, M.4, M.9, MM.106, and P.16 as tender, M.26, MM.111, MM.104, P.1, and J.9 as moderately hardy and Antonovka seedling, A.2, Beautiful Arcade, O.3, O.8, B.9, P.2, P.22, and P.18 as hardy (Quamme, 1990; Quamme et al., 1997). Under severe climatic conditions in Poland, tree mortality was greater on M.9 than on M.26 or B.9 (Czynczyk and Zagaja, 1984). Following the mid-winter cold event of 2004, Robinson et al. (2006) found tree survival with 'Honeycrisp' and 'McIntosh' as the scions was greatest (~90%) for O.3, V.1, V.3, G.16, G.30, and Mark. B.118, M.9T337, B.9, M.9 Nic 29, Supporter 4, M.26, and MM.111 had only 50% survival, while M.7 and MM.106 had very poor survival. Moran et al. (2011a) froze non-grafted rootstocks and found that G.41, G.11, G.30, B.9, P.2, and M.26 had similar hardiness, whereas G.935 had greater root hardiness than M.26 (Moran et al., 2011a,b). More recently, Moran et al. (2018) found that the Geneva® and Vineland series rootstocks exhibited a high degree of winter hardiness in January, but that some were more tender in the fall (October) or in the spring (April). G.30 was not hardy below −15°C in October or in April, while CG.4013 was not hardy below −15°C in the fall and CG.5257 was not hardy below −15°C in April. However, in November or in March, they had hardiness similar to mid-winter levels.

On the other extreme of low winter temperatures is the situation in some apple-growing regions of the world of too little winter cold to satisfy the endodormancy chilling requirement. Without adequate chilling, bud burst of the scion in the spring is delayed and variable, with a high percentage of buds failing to grow and subsequently dying (Midgley and Lotze, 2011; Rufato et al., 2010). Rootstocks can affect the percentage of buds on the scion that grow in spring following insufficient chilling. Recently, researchers in Brazil found that G.213 rootstock had a greater percentage of buds that grew in the spring after mild winters compared to M.9 or Marubakaido rootstocks. The same research revealed that other Geneva® rootstocks, such as G.210 or G.814, also may have a positive effect of bud development in climates with too little winter chilling (Macedo et al., 2018). Preliminary studies indicate that these rootstocks have higher levels of root-supplied cytokinins which may stimulate bud growth of the scion. Experiments conducted in Geneva, New York, that subjected 'Gala' budded on similar rootstocks found that budbreak occurred after accumulation of 550 chilling hours, about 150 less than the standard requirement for 'Gala.'

7.2 Drought tolerance and WUE

Apple tree WUE is a complex trait defined by the amount of photosynthesized carbon per unit of water transpired, and is commonly measured seasonally (units of seasonal dry-matter growth/units of water) or by measuring CO_2, O_2, and H_2O flux of tree canopies during short periods (Glenn, 2014). WUE in combination with phytohormones and root morphology are thought to be associated with drought tolerance in apples (Tworkoski et al., 2016; Zhang et al., 2014). Phenotypic diversity for WUE physiological and morphological components were found in domesticated apple and related wild species (Bassett et al., 2011), and several genes responding to water deficit have been described in apple roots (Bassett et al., 2014). While WUE may be related to tolerance to drought stress, the effective measure of tolerance to drought stress should be the maintenance of productivity and marketable fruit quality after the occurrence of stress (Atkinson et al., 1997). This is a difficult parameter to measure, because beyond the effect of apple rootstocks, soil conditions, scion variety, crop load, and other physiological variables all contribute to that parameter (Atkinson et al., 2000; Ebel et al., 2001; Lo Bianco et al., 2012).

7.3 Fire blight

One of the most serious risks to orchards on susceptible rootstocks is the bacterial disease fire blight. Although fire blight infects blossoms through the nectary in open flowers, it can travel in the plant through the xylem and then infect the cambium of the rootstock. If the rootstock is sensitive to fire blight, the cambium connecting the top of the tree and the root system is killed and the tree collapses a few months later or the next year (Norelli et al., 2001). Some of the Malling semi-dwarfing rootstocks, such as M.7 and MM.111, are partially resistant and thus there was little tree death in the era when they were the predominant rootstocks. However, M.9 and M.26 are extremely susceptible, and with the increased use of M.9 since the late 1990s, there have been numerous fire blight epidemics that have killed millions of trees and have cost apple growers millions of dollars in losses (Aldwinckle et al., 2004; Russo et al., 2007). A recent (2018) epidemic in Washington (USA) caused the death of an estimated 10% of the trees. Because of this risk, the primary objective of the Geneva rootstock breeding program was to develop fire blight–resistant rootstocks. If the rootstock is resistant, some flowers and then branches in the scion may become infected, but they can be removed by pruning and the tree will survive. The Geneva rootstock program has now released 14 fire blight–resistant rootstocks. The new rootstocks from New Zealand (IFO series) also are reported to be resistant.

The basis of the fire blight resistance used in the Geneva breeding program was the rootstock 'Robusta 5,' which is a descendant of an Asiatic crab apple species *Malus X robusta*. The Geneva progeny of 'Robusta 5' have broad resistance to fire blight strains, but there exists some variability in resistance to all known strains (Fazio et al., 2008). G.41 has some of the strongest resistance, while G.935 has shown some susceptibility to one strain. Nevertheless, they all have provided growers with a level of protection to the risk of tree death due to fire blight. Genetic inheritance of the 'Robusta 5'-type of resistance has been described as having a strain-specific component on chromosome 3 identified as a gene belonging to the NBS-LRR class of resistance genes (Broggini et al., 2014a,b; Fahrentrapp et al., 2013; Kost et al., 2015). Other minor QTLs on linkage groups 5, 7, 11, and 14, which do not seem to be strain-specific, were detected in a non-rootstock population ('Idared' × 'Robusta 5') (Wohner et al., 2014). Another non-strain–specific locus was discovered on linkage group 7 in a rootstock population derived from a cross between 'Ottawa 3' and 'Robusta 5' (Gardiner et al., 2012). Cis-genic approaches with the *LG03* gene proved only partially successful, suggesting a more complex pathway of resistance than just one gene recognition of the pathogen (Kost et al., 2015). There is some evidence of graft transmissible benefits conferred to the grafted scion from fire blight–resistant rootstocks (Jensen et al., 2003, 2011, 2012), including reports by large-scale apple growers that they see less mortality and incidence of strikes when a resistant rootstock is used.

A unique situation was discovered with B.9 rootstocks. It was shown to be susceptible when inoculated with the bacteria, but when used as a rootstock and the scion was inoculated, it exhibited good field-level resistance (LoGiudice et al., 2006; Russo et al., 2008a,b).

7.4 Apple replant disease (ARD)

When apple trees are replanted in the same orchard in which apples and pears were planted previously, the new trees often are stunted and do not grow well. This problem has been named apple replant disease (ARD) and is caused by a complex of several microorganisms which thrive on the roots of the previous apple trees in the soil where the trees grew. Mazzola (1998) has reported that the most important pathogens associated with the disease include *Phythium, Phytophthora* spp., *Rhizoctonia solani,* and *Cylindrocarpon* spp., as well as the root lesion nematode (*Pratylenchus penetrans*) and bacteria (Mazzola, 1998). Research trials and grower observation indicate that M.26 is very sensitive to ARD (Robinson, 2011). In virgin soils, M.26 produces a larger tree than M.9, but in replant soils it often is similar in size or smaller than M.9. All rootstocks exhibit less vigorous growth on replant soils than virgin soils. This has resulted in the use of soil fumigation to kill pathogenic microorganisms prior to planting (Peryea and Covey, 1989; Yao et al., 2006), which sometimes (depending on soil type) is not effective.

Beginning in 2000, Merwin and students evaluated Geneva® rootstocks for replant disease tolerance and found that G.65, CG.6210, and G.30 show greater tolerance to the disease than Malling stocks (Isutsa and Merwin, 2000). Rumberger et al. (2004) found that trees on M.7, M.26, and G.16 remained smaller when growing in the previous tree rows compared with previous grass lanes, whereas the growth of trees on G.210 and G.30 planted in the two locations was similar. Leinfelder and Merwin (2006) suggested that using G.30 and G.210 rootstocks and planting in the previous grass lanes instead of the old rows may be an effective strategy against ARD. Based on field trials, Robinson et al. (2006) found that G.935 and G.202 had good tolerance to ARD. In a replant study in Washington, Mazzola et al. (2009b) found that G.11 and G.30 were more tolerant to lesion nematode than M.7, M.9, M.26, MM.106, and MM.111 (Mazzola et al., 2009a,b). Trees on M.26, MM.106, and MM.111 were more susceptible to *Pythium* spp. than trees on B.9 and rootstocks in the Geneva® series. Auvil et al. (2011) also reported that trees on several Geneva® rootstocks in several Washington locations outperformed the industry standards (B.9, M.9, and M.26) on replant sites (Auvil et al., 2011). In replant trials in North Carolina (USA), trees on G.30 and G.210 performed better in replant soils than trees on M.26 and M.7 (Parker et al., 2014).

The mechanism of ARD tolerance of Geneva® rootstocks is not clear. It is possible that the early screening for resistance to *Phytophthora* root rot fungi also co-screened for tolerance to other soil microorganisms. It is also possible that the root systems of the tolerant Geneva® rootstocks simply have a faster turnover rate and can essentially outgrow the pathogens (Atucha et al., 2013). What is remarkable is that the microbial community in the rhizosphere of these new rootstocks is drastically changed compared to the Malling stocks (Rumberger et al., 2007), possibly by deposition of specific exudates (Leisso et al., 2017, 2018). Regardless of the mechanism, this tolerance to ARD for replanting apple orchards on previous orchard land is becoming more important as soil fumigation options become more limited. In some parts of the United States and the world, soil fumigation is no longer an available option.

7.5 Viruses

Some plant viruses are lethal to many apple varieties, but other viruses are not lethal to most apple varieties and rootstocks. Viruses that can exist in the plant and cause few symptoms are termed latent viruses, which can be spread to new trees by grafting infected wood on clean rootstocks or by grafting clean wood on infected rootstocks. There are five main latent viruses: apple stem pitting virus (ASPV), apple stem grooving virus (ASGV), chlorotic leaf spot virus (ACLSV), apple mosaic virus (ApMV) and tomato ringspot virus (ToRSV) (Fuchs et al., 2018). Over time, all common commercial rootstocks from the Malling series became infected with one or more latent viruses. During the 1950s and 1960s, the Malling stocks were heat-treated to eliminate known viruses, and were given the designation East Malling-Long Ashton (EMLA). The clean versions of the Malling stocks were slightly more vigorous than the infected versions. In addition to the effort at the East Malling and Long Ashton research stations, the Dutch organization NAKB and the French organization CTIFL produced their own versions of clean M.9. The Dutch clean M.9 is referred as M.9T337 and the French version is referred as M.9Pajam1 and Pajam2.

A specific case of lethality was with MM.106 rootstock. When 'Delicious' scions were grafted on MM.106 and the trees were later infected with ToRSV through nematode vectors, the trees developed a brown (dead) line of cells at the graft union and the trees died (Tuttle and Gotlieb, 1985). More recently, several of the Geneva® rootstocks have shown susceptibility to one or more of the latent viruses. G.16 was very sensitive to the three most common latent viruses and required the use of virus-free budwood; otherwise, the trees die in the nursery or in the first year in the orchard. G.814 and G.935 have shown lesser susceptibility to latent viruses. The case of G.935 is still unclear, since it seems tolerant of individual viruses, but possibly combinations of viruses result in poor growth although the trees do not die. Nevertheless, the solution to these sensitivities is the use of virus-free bud wood since the common latent viruses are only transmitted by grafting.

Some apple-growing regions, such as the European Union, have very good virus elimination programs and require both rootstocks and scion wood to be virus-free. However, other areas, such as the United States, have allowed virus elimination programs to lapse due to limited government funding, and currently there are widespread latent virus infections in New York orchards (Fuchs et al., 2018). It is imperative that apple regions worldwide strengthen their virus elimination programs.

7.6 Tree anchorage and graft union strength

In the era when trees were expected to be freestanding (i.e., before trees were supported by posts or trellises), the anchorage of a rootstock was an important characteristic. Most of the semi-dwarfing rootstocks from around the world are freestanding, but some semi-dwarfing and the dwarfing rootstocks are not. M.7 is a semi-dwarfing rootstock that is freestanding in most cases, but with heavy rains and winds it can lean. In many orchards with M.7, about 30% of the trees exhibit significant leaning. In the previous era of semi-dwarfing rootstocks, many orchards with M.7 required tree support. However, with the adoption of the dwarfing rootstocks M.9 and M.26, tree support is required because the rootstock does not provide sufficient anchorage to support the tree with a heavy crop load. Support is also required because dwarfing rootstocks are much more precocious, resulting in a heavy crop on a young tree with small diameter limbs and trunk which can break down the canopy without support. Thus, in the dwarf tree era and high planting densities, rootstock anchorage has become an unimportant rootstock characteristic.

Another tree structural issue is rootstock-scion graft union strength, which has become more important with the adoption of dwarfing rootstocks. Both M.9 and M.26 have weak graft unions with some scion cultivars (e.g. 'Gala'), which requires good trellis support. Geneva® 30 also has exhibited poor graft union strength with 'Gala,' as high winds from a 1990 hurricane caused the breakage of mature trees at the graft union. Recent nursery and field observations indicate that unions of some newer cultivars, such as 'Cripps Pink' and 'Scilate' on G.41, are also brittle and trees break in wind storms, as well as when digging trees in the nursery or planting trees in the orchard. Since tree breakage can have significant economic consequences for nurserymen and orchardists, researchers have evaluated methods for determining union strength and flexibility (Adams et al., 2017). The amount of force required to break graft unions currently is used in the Geneva breeding program to classify graft union strength of rootstocks. Rehkugler et al. (1979) found that 18-year-old 'Golden Delicious' on M.9 could withstand only one-third of the force required to cause breakage on vigorous rootstocks (Rehkugler et al., 1979). Robinson et al. (2003) found the graft union of 'Gala'/G.30 was more brittle than 'Gala'/M.26, but the strength of the 'Gala'/G.30 graft union increased with tree age (Robinson et al., 2003). Adams et al. (2017) found that 'Scilate'/G.41 graft unions were weaker than 'Scilate'/M.9 graft unions, and that grafting method did not improve the graft union strength. Application of plant growth regulators to graft unions in the nursery did improve graft union strength: foliar applications of prohexadione-calcium and benzyladenine applied to the union in latex paint increased the flexural strength per scion cross-sectional area and the flexibility of the union. To avoid tree breakage problems, support should be provided in the nursery, as well as in the orchard so branches can be tied to multiple wires to prevent the twisting of trees in the wind.

8 Trends in apple (and other tree fruit) rootstock use

Over the last 100 years, total worldwide apple rootstock production has increased many fold. This is due to increased acreage worldwide, but also due to the tenfold increase in planting density as the world's apple growers moved from low-density orchards to high-density orchards. Our estimate of worldwide production of apple rootstocks is two million plants in 1950, but in 2019 we estimate there are more than 120 million rootstocks produced worldwide.

The apple-producing world before 1950 primarily used seedling rootstocks. Excluding China, starting in the mid-twentieth century a slow transition from seedling rootstocks to semi-dwarfing Malling rootstocks (MM.106, MM.111, and M.7) began and accelerated in the 1960s and 1970s so that by 1980, semi-dwarfing rootstocks accounted for an estimated 80% of all apple rootstocks in the world. However, starting in the 1970s, the use of M.9 increased from less than 10% of all rootstocks to almost 70% of all rootstocks by 2000, while the use of semi-dwarfing rootstocks declined rapidly during the 1990s. As M.9 gained in popularity, M.26 also grew to account for about 20% of rootstocks produced by the year 2000. Since 2000, M.9 has dominated the worldwide production of rootstocks, but in some countries, B.9 has increased rapidly and accounts for 20% of all rootstocks produced today. Since 2006, the production of the Geneva® rootstock series has increased rapidly in the United States and, in 2019, accounts for about 40% of all rootstocks produced. On a worldwide scale, the Geneva® rootstocks account for about 8% of all rootstocks. It is expected that their production will rise to account for 50% of worldwide apple rootstock production (excluding China) in the next 10 years.

Apple rootstock usage in China has followed a different path. Apple production in China before 1980 was small; however, due to government promotion of growing apples, production exploded in the late 1980s and 1990s. This resulted in China becoming the largest apple-producing country in the world by 2000, with currently five times the production of the second largest producer, the United States. Almost all Chinese apple production is based on vigorous and semi-vigorous rootstocks of *Malus prunifolia*, *M. baccata*, *M. hupehensis*, *M. micromalus,* and *M. seversei*. Although China has a vast orchard area, the planting densities are moderate, thus resulting in an estimated annual rootstock production of 30 million plants, which is similar to the European apple rootstock production.

This historical evolution of apple production tied to rootstock innovations presents a template for the likely evolution of other temperate zone tree fruit production systems as well. Clearly, sweet cherry production has undergone a similar, even more rapid evolution and expansion since the first development of vigor-limiting, precocious rootstocks (primarily the Gisela® series) in the 1980s and 1990s. Significant advances in genetic development and selection of vigor-limiting peach and pear rootstocks also have been made since the turn of the century, with the subsequent research into their utilization for production system innovations now in their early stages.

9 Future trends in apple rootstocks

In the previous century, the primary criteria in choice of apple rootstock has been "will it survive in my climate, is it the right vigor and is it available?" Cold damage and fire blight have been the two primary and economically important causes of tree death in North America. In addition, *Phytophthora* root rots and waterlogging have also caused tree death. Thus, the rootstock decision in the past was usually quite simple, with only one or two choices available to growers. However, with the proliferation of improved apple rootstocks available around the world, there is now a dizzying array of choices for apple growers. The Geneva breeding program alone has released 14 apple rootstocks and is poised to release four more in the next few years. Even so, availability of new rootstocks is still a problem for some growing regions.

Researchers are attempting to evaluate new rootstocks in different locations and provide advice to apple growers regarding which rootstocks will perform best in each region. With so many rootstock choices, Fazio has suggested the term 'designer rootstocks' to indicate the possibility of choosing a rootstock suited for the specific climate, soil, cultivar, and planting system a grower chooses. Robinson further defined the four variables that need to be determined specifically for each orchard before choosing a rootstock: (1) vigor of the variety, (2) vigor imparted by the climate, (3) vigor imparted by the soil, and (4) the space allocated to each tree. Each of these should be considered as pieces of a puzzle specific to each orchard or areas in an orchard for selecting the rootstock. Robinson has further suggested that a rootstock in a modern orchard should be able to grow well enough to fill the space allocated to the tree in 2 years and begin production in either the first or second year, depending on the quality of available nursery trees. If rootstock vigor combined with scion, climate, and soil vigor do not result in sufficient growth to fill the space in 2 years, then substantial economic penalties in lost yield accrue to the grower. When rootstock choices were relatively limited, growers often planted an available rootstock that was not well matched with all of the vigor factors (including tree spacing), resulting in trees that took 5–8 years to fill their allotted space or that grew too vigorously for the allotted space and then were difficult to manage in later years. Robinson has estimated that with high-priced varieties, the lost yield when trees fail to fill their space by the end of the second or third year can cost up to $250 000/ha in lost yield over the first 8 years of orchard life. This economic reality often is not appreciated by growers who never see the un-realized income from lower-than-potential yields due to the wrong rootstock choice.

The introduction of the 'Honeycrisp' apple in the United States in the mid-1990s brought new challenges to growers for rootstock selection. It is a weak-growing cultivar that often fails to fill the orchard space allocated to the tree in 2 years when grafted to dwarfing rootstocks. However, due to its high market price, 'Honeycrisp' has been very profitable for growers even though it often fails to achieve this goal. In addition, its susceptibility to the Ca-related disorder, bitter pit, has resulted in the quest for rootstocks that not only have the appropriate vigor level but also have a genetically programmed specific mineral nutrient profile for higher Ca uptake and a better translocated K/Ca ratio in the fruit to reduce bitter pit. A national project involving a group of US researchers from the NC140 rootstock evaluation group has begun a

5-year project to speed the discovery of such rootstocks that are more ideally matched to specific varieties in locations where apples are produced. Similarly, this effort is also examining potential rootstocks for new areas of production that historically have been limited by high soil pH and/or high salt tolerance and drought tolerance. The project intends to develop an online decision aid tool to help growers choose the right rootstock for their specific soil, climate, variety, and spacing.

The future of rootstock improvement will assuredly lead to greater combinations of resistance/tolerance to biotic and abiotic stresses and positive horticultural traits. In the short term, efforts to characterize existing rootstocks or existing breeding populations for all of the desirable rootstock traits can be done relatively rapidly (10 years). However, to breed new 'designer' rootstocks for specific combinations of important traits is a much longer process (30 years). To speed up progress, marker-assisted breeding will improve the efficiency of selecting rootstocks with desirable traits at an early stage, potentially reducing the time to develop a new rootstock to only 13 years (2–3 years to select for one or more desirable traits and 10 years for propagation and field evaluation). Another possible way to accelerate rootstock development is to use genetic engineering through cis-gene transfer of specific apple genes through CRISPR-Cas9 technology. By this method, a specific gene could be inserted to an elite rootstock that already has many positive attributes. This may reduce the time to develop a new rootstock to only 11 years (1 year for gene transfer and 10 years for propagation and field testing).

Limitations to rapidly introducing a new rootstock worldwide include virus-certification, bulk propagation, and the need by growers and researchers in each production region worldwide to establish objective rootstock trials to confirm the performance of a rootstock in a given climate with the target varieties. Most growers are hesitant to plant a new rootstock that has not been proven in their area. For growers, a new orchard is at least a 20-year investment and if the choice of rootstock (or variety) does not result in a productive orchard of marketable fruit for 20 years, there can be large economic penalties.

There are few tree fruit rootstock breeding programs in the world. Some focus on only a few horticultural traits, such as improved rooting or cold hardiness. However, the world apple community needs rootstock breeding programs to focus on multiple resistances to biotic and abiotic stresses, in addition to superior horticultural characteristics including high yield of premium-quality fruit. Such broad breeding objectives require a large team and many cooperators who will evaluate the rootstocks in different climates and soils. We predict that rootstock breeding programs with the vision of developing rootstocks with multiple resistances and superior horticultural performance will produce an increasing array of new valuable rootstocks over the next 30 years.

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