



II. Horticultural performance of ‘Honeycrisp’ grown on a genetically diverse set of rootstocks under Western New York climatic conditions

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ABSTRACT

A field experiment with 31 rootstocks representing a genetically diverse group of rootstocks featuring ‘Honeycrisp’ as the scion was planted in 2010 at Geneva, NY USA. Rootstocks included three from the Malling series (UK), nine from the Budagovsky series (Russia), 16 from the Cornell Geneva series (USA) and three from the Pillnitz series (Germany). Over the first 8 years (2010–2017) we measured final tree size (trunk cross-sectional area: TCA) and cumulative yield. In the last 4 years we measured fruit soluble solids, bitter pit incidence, biennial bearing, and leaf zonal chlorosis. Tree size varied dramatically with the largest trees on B.70-20-20 and smallest trees on B.71-7-22. Setting the most vigorous rootstock at 100% we categorized rootstocks into 5 size categories: sub-dwarfing class (10–25%), dwarfing class (25–35%), semi-dwarfing class (35–50%), semi-vigorous category (50–70%) and vigorous class (70–100%). Cumulative yield varied 8 fold between the highest yielding rootstock (CG.3001) and the lowest yielding rootstock (B.71-7-22). We calculated theoretical yield per ha by multiplying cumulative yield per tree by a theoretical optimal tree density (trees/ha) based on tree size (TCA). The dwarfing rootstocks G.814, G.41TC, G.11 and B.10 had the highest yields per hectare while the most vigorous rootstocks B.70.20.20 and B.71-7-22 were the least productive. Theoretical cumulative yields varied from a high of 400 t/ha to a low of 50 t/ha, an 8-fold difference. Rootstock also influenced the incidence of bitter pit with the lowest levels of bitter pit with the rootstocks B.10, CG.2034, B.71-7-22, G.41N, CG.4003, G.202N, G.214, and Supporter 3. Considering bitter pit, yield, and optimum tree density, the theoretical yield of bitter pit free fruit varied from a high of 340 t/ha to a low of 35 t/ha, almost a 10-fold difference. The dwarfing rootstocks B.10, G.11, G.41TC, G.214 and G.814 had the highest yields per hectare of bitter pit free fruit. Rootstocks B.9 and M.26 had significantly lower cumulative bitter pit free yield/ha. These data indicate that rootstock not only has a large influence on mature tree cumulative yield but also bitter pit incidence which combine to create a large economic impact of rootstock choice on the long-term economic result of an orchard. This leads to the need for “designer rootstocks” which combine the rootstock characteristics needed to maximize the economic potential of each scion cultivar.

1. Introduction

The large majority of apple trees planted in modern orchards are composites of two or three genotypes (rootstock, interstem and scion) combined by grafting. Most commercial orchards make use of clonally propagated rootstocks and interstems to induce dwarf trees and to increase productivity per unit of land. The most widely used clonal rootstock in the world is ‘Malling 9’ (M.9) and its sport mutations, it is also the oldest dwarfing rootstock technology to be adopted by apple growers as some of the original clones may have been planted as early as the 1700’s under the name of ‘Paradis Jaune de Metz’ (Wertheim,

1998). Other apple rootstocks, derivatives of M.9, are also popular but suffer from some of the same drawbacks as M.9 clones such as susceptibility to the apple replant disease complex, fire blight caused by *Erwinia amylovora* Burill, and insect pests such as the woolly apple aphid (*Eriosoma lanigerum* Hausmann) (Fazio, 2014; Fazio et al., 2015). A set of more contemporary rootstocks emerging from the Budagovsky and Geneva® breeding programs are being evaluated in the NC-140 collaborative rootstock testing project in North America (Autio et al., 2013, 2017). One such trial that includes 31 apple rootstocks with ‘Honeycrisp’ as the grafted scion was planted in the year 2010 at 11 sites in the U.S. and Canada. ‘Honeycrisp’ apple has become an

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important new cultivar but it has a low vigor level in the scion which has caused problems filling allotted space in many growing areas of the world (Robinson et al., 2011; Rosenberger et al., 2001). The 2010 NC140 rootstock trial was designed to identify rootstocks that had sufficient vigor and productivity to maximize the performance of ‘Honeycrisp’. Results of the developmental years (1–5) of this study from all 11 sites were included in the report by Autio et al. (2017). In addition individual cooperators have used this trial to evaluate rootstock induced phytohormone concentration changes in the scion (Lordan et al., 2017), and to measure leaf and fruit nutrient concentration during the initial orchard growth and establishment (Neilsen and Hampson, 2014). Here we present results on the horticultural performance of the 31 rootstocks at the mature phase (years 5–8) from only one location, the Geneva trial. Bitter pit is a physiological disorder of some apple varieties including ‘Honeycrisp’ and ‘Fuji’ which manifests itself by small indentations (pits) that can be distributed uniformly on the surface of the apple (Prange et al., 2011; Raese and Drake, 1997). Sometimes the incidence of these pits is greater in areas more distant from the stem end (lower 1/3 of the apple or calyx end) (Jarolmasjed et al., 2016). The incidence and size of bitter pits may increase after apple are cold stored for weeks or months (Wargo and Watkins, 2004). Mineral nutrient concentrations in apple fruit have been associated with the formation of bitter pits, where lower levels of calcium, higher levels of potassium and nitrogen may increase the incidence (Baugher et al., 2017; Ford, 1979; Perring and Jackson, 1975). Larger fruit size which is positively correlated with low crop load is also associated with increase in bitter pit (Robinson and Lopez, 2012). Apple rootstocks, given their diverse effect on the nutrition of the canopy have been implicated in the physiology of bitter pit (Fazio et al., 2013, 2018).

Leaf vein chlorosis also referred to as zonal chlorosis is a physiological disorder of ‘Honeycrisp’ that appears as blotchy yellow colorations on leaves with no distinct border likely caused by overloading of sorbitol and starch products (Chen and Cheng, 2004). Low crop load and vegetative growth have been linked to the incidence of this leaf disorder (Fleck et al., 2011; Snyder-Leiby and Wang, 2008). Inheritance of this disorder in ‘Honeycrisp’ progenies was localized to linkage group 9 of the apple genome near the MdMYB1 locus that controls red fruit color (Howard et al., 2019).

Alternate bearing also referred to as biennial bearing is a phenomenon common to some apple cultivars like ‘Fuji’ and ‘Honeycrisp’ where high crop load one year affects negatively flower induction and fruit set of the next year which is then followed by another high crop load year (Wunsche and Ferguson, 2005) thus resulting in trees that bear fruit on alternate years giving good yields biennially instead of annually (Samuoliene et al., 2016). Phenotypic and genetic differences in the tendency of some scion varieties to fall into alternate bearing mode were described in progeny from ‘(Red) Delicious’ (biennial) and ‘Granny Smith’ (strongly annual) where quantitative trait loci (QTLs) were detected on linkage groups 4, 8 and 10 of the apple genome (Durand et al., 2017; Guitton et al., 2012). The exact physiological pathway that controls alternate bearing is not yet known and may involve timing of flower initiation, the availability of carbohydrate and nutrient resources and the hormonal status of the tree when meristems are ready to change from vegetative to reproductive modes. Rootstocks from a diverse genetic background have been recently implicated in the ability to influence alternate bearing of some cultivars perhaps through the induction of different hormone levels (Lordan et al., 2017) or by changes in crop load and carbohydrate storage (Reig et al., 2019).

Tree vigor in commercial apple orchards is largely controlled by the choice of rootstocks where some rootstocks can dwarf the tree all the way down to 10% of the growth of a normal tree on its own roots. The ability of rootstocks to dwarf apple trees has been leveraged to increase the productivity of orchards two to three-fold and reduce inputs (fertilizers, water, pesticides) and human accidents drastically. The dwarfing effect of apple rootstocks has been ascribed to 2–3 loci Dw1

and Dw2 and possibly a third locus (Fazio et al., 2014; Foster et al., 2015; Harrison et al., 2016). Dwarfing rootstocks have been shown to have a dramatic effect on the cumulative yield and yield efficiency (tree productivity/tree size) which determine the optimal spacing to capture light energy and convert it to fruit (Autio et al., 2013; Fallahi et al., 2018).

The objective of this study was to study the effect of a genetically diverse set of 31 rootstocks for their potential to maximize the performance of ‘Honeycrisp’ apple with emphasis on mature tree size, cumulative yield, cumulative yield efficiency, biennial bearing, leaf zonal chlorosis, fruit size and, bitter pit incidence.

2. Materials and methods

2.1. Trees and design

A rootstock field trial was planted in 2010 at the New York State Agricultural Experiment Station (Geneva, NY, USA), using ‘Honeycrisp’ as the scion cultivar (Autio et al., 2017). Trees were planted in a randomized complete block design, with 4 replications and with each block containing 2–3 trees of each rootstock. Blocking was done by initial tree diameter. Tree spacing was 1.2 m × 3.5 m. Rootstocks included three from the Malling series: M.26EMLA, M.9T337, and M.9Pajam2; nine from the Budagovsky series: B.10 (B.6 2-3 96), B.64-194, B.67-5-32, B.7-20-21, B.7-3-150, B.70-20-20, B.70-6-8, B.71-7-22, and B.9 (Kazlouskaya and Samus, 2011); six Cornell Geneva® released rootstocks: G.11, G.41N, G.41TC, G.935N, G.935TC, G.202N, G.202TC, G.214, G.222 and G.814 where the “N” and “TC” distinctions refer to normal propagation and tissue culture propagation respectively; six experimental Geneva rootstocks: CG.2034, CG.3001, CG.4003, CG.4004, CG.4013, CG.5087; and three rootstocks from the Pillnitz series: Piau51-11, Piau9-90, Supporter 3 (Supp. 3). Table 1 describes the origin, parentage and vigor class of each rootstock.

2.2. Tree performance measurements and fruit quality analysis

Tree trunk circumference (30 cm above the graft union), yield, and number of fruits were assessed every year. Trunk-cross-sectional area (TCA) and fruit size were then calculated. We calculated a theoretical yield/ha by multiplying cumulative yields per tree by a theoretical optimal tree density (trees/ha) coefficient based on tree size (TCA) (500 trees/ha for seedling size rootstocks to 5000 trees/ha for sub-dwarfing rootstocks). Tree height from the ground and tree spread (average of tree spread in the alley and in the row) were measured in the Fall of 2017. Biennial bearing was calculated as follow: (year 1 yield) – (year 2 yield)/(year 1 yield + year 2 yield), where 0 indicates no alternate bearing and 1 complete alternate bearing. Yield efficiency represents yield (kg) by TCA (cm²). Near harvest the severity of leaf zonal chlorosis was evaluated by visually assessing the percentage of leaves with chlorosis.

At harvest for the 1st and 2nd picks, a 30-fruit sample was collected for each rootstock replicate, from 2014–2017. Ten of the fruits in each sample were then used to assess soluble solids (Brix). The remaining 20 apples of each sample were preconditioned 1 week at 10 °C and then stored at 3 °C for six months. After storage, all of the apples contained in each sample were individually examined for any external signs of superficial bitter pit. The incidence of bitter pit of each sample was calculated as the percentage of fruit with bitter pit symptoms.

Climatic data were recorded for each year from the closest automatic weather station. Tree transpiration from May through October was calculated using a modified Penman-Monteith equation (NEWA.org) (Robinson et al., 2017). The trees were trickle irrigated as needed during the growing season using the Cornell apple irrigation model (NEWA.org).

Table 1

Apple rootstocks in the NC-140 Trial planted in 2010 with ‘Honeycrisp’ as the scion in Geneva, NY.

Rootstock	Type	Origin	Parentage	Tree size	References
B.62-396	Dwarf	Michurinsk College, Russia	B.13-14 x B.9	M.9-M-26	Kuldoshin and Sadowski, 1999
B.64-194	Semi-Dwarf	Michurinsk College, Russia	Unknown	M.7-MM.106	Kuldoshin and Sadowski, 1999
B.67-5-32	Semi-Dwarf	Michurinsk College, Russia	Unknown	M.7	Kuldoshin and Sadowski, 1999
B.7-20-21	Semi-Dwarf	Michurinsk College, Russia	Unknown	M.7	Kuldoshin and Sadowski, 1999
B.7-3-150	Semi-Dwarf	Michurinsk College, Russia	Unknown	M.7-MM.106	Kuldoshin and Sadowski, 1999
B.70-20-20	Vigorous	Michurinsk College, Russia	57-469 × 57-344	Seedling	Kuldoshin and Sadowski, 1999
B.70-6-8	Semi-Dwarf	Michurinsk College, Russia	Unknown	M.7-MM.106	Kuldoshin and Sadowski, 1999
B.71-7-22	Super Dwarf	Michurinsk College, Russia	Unknown	M.27	Kuldoshin and Sadowski, 1999
B.9	Dwarf	Michurinsk College, Russia	Unknown	B.9	Kazlouskaya and Samus, 2011
CG.2034	Dwarf	Geneva Res. Station, New York, USA	Dolgo crab × Mallings 27	M.27	Personal communication (Fazio G.)
CG.3001	Dwarf	Geneva Res. Station, New York, USA	P.2 × Robusta 5	M.9	Personal communication (Fazio G.)
CG.4003	Dwarf	Geneva Res. Station, New York, USA	(Antonovka Kamienaja × Ottawa 3) × Robusta 5	M.26	Norelli et al., 2003
CG.4004	Dwarf	Geneva Res. Station, New York, USA	722506-004 × OP	M.26	Personal communication (Fazio G.)
CG.4013	Dwarf	Geneva Res. Station, New York, USA	Ottawa 3 × Robusta 5	M.26	Norelli et al., 2003
CG.5087	Dwarf	Geneva Res. Station, New York, USA	Ottawa 3 × Robusta 5	M.26 to M.7	Norelli et al., 2003
G.11	Dwarf	Geneva Res. Station, New York, USA	M.26 × Robusta 5	M.9	Norelli et al., 2003
G.202N	Dwarf	Geneva Res. Station, New York, USA	M.27 × Robusta 5	M.26	Norelli et al., 2003
G.202TC	Dwarf	Geneva Res. Station, New York, USA	M.27 × Robusta 5	M.26	Norelli et al., 2003
G.214	Dwarf	Geneva Res. Station, New York, USA	Ottawa 3 × Robusta 5	M.26	Norelli et al., 2003
G.222	Semi-dwarf	Geneva Res. Station, New York, USA	M.27 × Robusta 5	M.26	Personal communication (Fazio G.)
G.41N	Dwarf	Geneva Res. Station, New York, USA	M.27 × Robusta 5	M.9	Personal communication (Fazio G.)
G.41TC	Dwarf	Geneva Res. Station, New York, USA	M.27 × Robusta 5	M.9	Personal communication (Fazio G.)
G.814	Dwarf	Geneva Res. Station, New York, USA	Ottawa 3 × Robusta 5	M.26	Norelli et al., 2003
G.935N	Dwarf	Geneva Res. Station, New York, USA	Ottawa 3 × Robusta 5	M.26	Norelli et al., 2003
G.935TC	Dwarf	Geneva Res. Station, New York, USA	Ottawa 3 × Robusta 5	M.26	Norelli et al., 2003
M.26	Dwarf	HRI-East Mallings, UK	M.16 × M.9	M.26	Preston, 1974; Proctor et al., 1974
M.9-Paj2	Dwarf	Reselected at CTIFL, FR	Unknown	M.9	Hatton, 1917; Webster and Hollands, 1999
M.9-T337	Dwarf	Reselected at HRI-East Mallings, UK	Unknown	M.9	Hatton, 1917; Webster and Hollands, 1999
PiAu.51-11	Semi-Dwarf	Pillnitz, Germany	M 4 open pollinated	M.7	Fischer and Sadowski, 1999
PiAu.9-90	Semi-dwarf	Pillnitz, Germany	Unknown	M.7	Fischer and Sadowski, 1999
Supp.3	Semi-dwarf	Pillnitz, Germany	Unknown	M.9	Fischer and Sadowski, 1999

2.3. Data analysis

Statistical analyses were performed using Mixed Models Procedure with rootstock genotype as a fixed effect and blocking and interaction as the random effects. Mean separation was determined using least significant difference test (LSD) with a *P* value of 0.05. Pearson correlation was carried out to study correlations among all the traits evaluated. Rootstock genotype means were used in multivariate analysis to generate two-way similarity cluster diagrams based on genotype similarity and variable similarity. The Ward's minimum variance criterion was used. Data were analyzed using the JMP statistical software package (Version 12; SAS Institute Inc., Cary, North Carolina) for the calculation of genotypic means, multivariate cluster analysis and correlation.

3. Results

3.1. Tree vigor

‘Honeycrisp’ tree size measured by the size of the trunk-cross-sectional area (TCA) in the fall of 2017 (end of 8th year) was strongly influenced by rootstock genotype (Fig. 1). Using the size of the largest trees (B.70-20-20 rootstock) as 100% we categorize rootstocks into 5 size categories. Rootstocks B.71-7-22, CG.2034 and B.9 were in the smallest group (sub-dwarfing class - 10–25% of B.70-20-20), while G.11, G.41, B.10, M.9-T337, Supp.3, G.935, M.9-EMLA, M.9-Pajam2, CG.4003 and G.214 were larger (25–35%) and fell into the dwarfing class. In the semi-dwarfing class (35–50%) were CG.5087, G.814, G.222, G.202 and CG.3001, while rootstocks Piau51-11, CG.4013, B.67-20-21, Piau-9-90, B.7-3-150, B.70-6-8 fell in the semi-vigorous category (50–70%). Rootstocks B.64-194 fell into the vigorous range (70–100% of B.70-20-20). Tree height and tree canopy spread measured in the fall of 2017 were 0.83 (*P* < 0.001) and 0.96 (*P* < 0.001) correlated respectively to the TCA (data not presented).

3.2. Cumulative yield and yield efficiency

Cumulative yield per tree over the first 8 years was greatest for CG.3001(120 kg/tree) followed by G.814 (110 kg/tree) (Fig. 2). Following the top 2 rootstocks was a large group of rootstocks that had a cumulative yield between 80 and 100 kg/tree (B.7-3-150, CG.4004, B.64-194, CG.5087, B.70-6-8, G.214, G.202N, B.70-20-20, G.41N, G.202TC, B.7-20-21, B.10, G.935N, PiAu51-11, G.41TC, G.222, G.11, M.9T337, Supp3, G.935TC). There was a smaller group of rootstocks that yielded 70–80 kg/tree (M.9Pajam2, PiAu9-90, CG.4013, B.67-5-32, CG.4003 and M.26EMLA), while the lowest yielding rootstocks were B.71-7-22, CG.20134 and B.9 with less than 55 kg/tree. Cumulative yield efficiency was highest with rootstocks G.11, B.9 and G.41TC, followed by B.10, G.41N, M.9T337, G.214 and G.814 (Fig. 3). The lowest yield efficiencies were measured on rootstocks B.70-20-20, Piau9-90, B.67-5-32, B.64-194, B.70-6-8, B.70-20-21, B.7-3-150, CG.4013 and Piau51-11. The intermediate yield efficiency group in this experiment featured well known rootstocks like M.9-Pajam2, and both G.935 and G.202 either N or TC, and experimental rootstocks such as CG.4004, CG.5087 and CG.4003.

The calculated theoretical yield per ha obtained by multiplying cumulative yields per tree by a theoretical optimal tree density (trees/ha) coefficient based on tree size (TCA) showed that the dwarfing rootstocks G.814, G.41TC, G.11 and B.10 had the highest yields per hectare while the most vigorous rootstocks B.70.20.20 and B.71-7-22 were the least productive (Fig. 4). Theoretical cumulative yields varied from a high of 400 t/ha to a low of 50 t/ha, an 8-fold difference.

3.3. Biennial bearing

Mean biennial bearing index (BBI) measured over six years was lowest (< 0.5) in G.41TC, CG.4003, G.814 and G.202N (Fig. 5). It was highest (> 0.7) in rootstocks B.67-5-32, Piau9-90, B.71-7-22 and CG.4013. The intermediate group (> 0.5 and < 0.7) featured the rest of

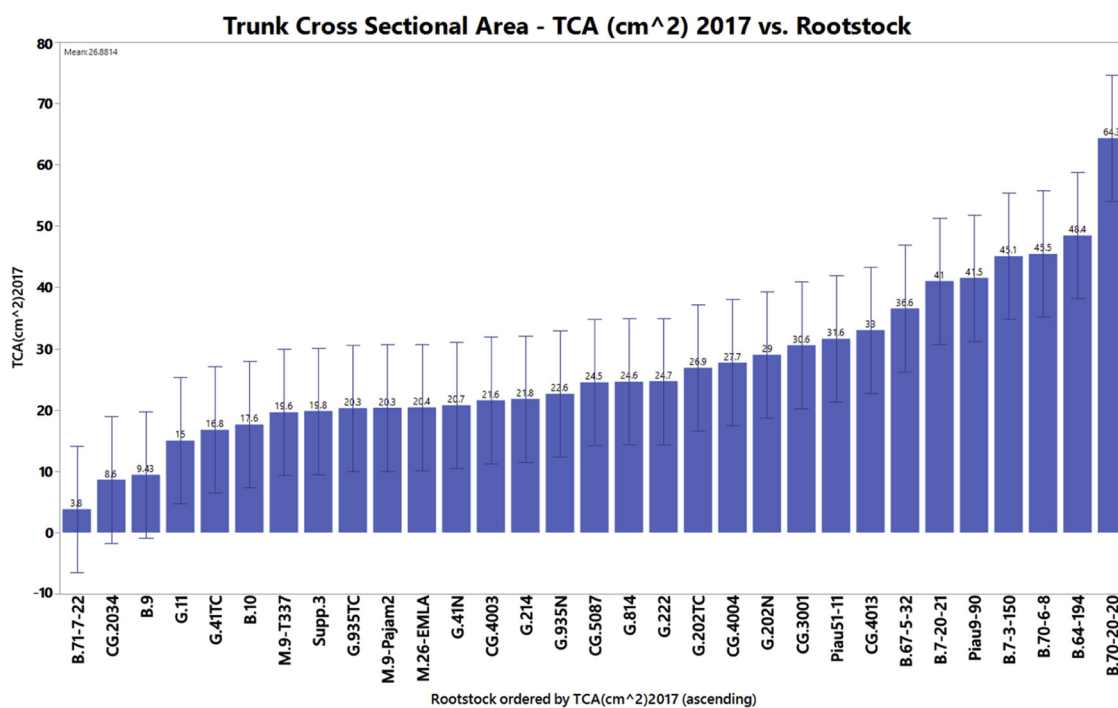


Fig. 1. Genotypic means for the trunk cross sectional area (TCA) (which correlate to the whole tree size) for 31 rootstocks after 8 years when grown at Geneva, NY. LSD for TCA = 10.3.

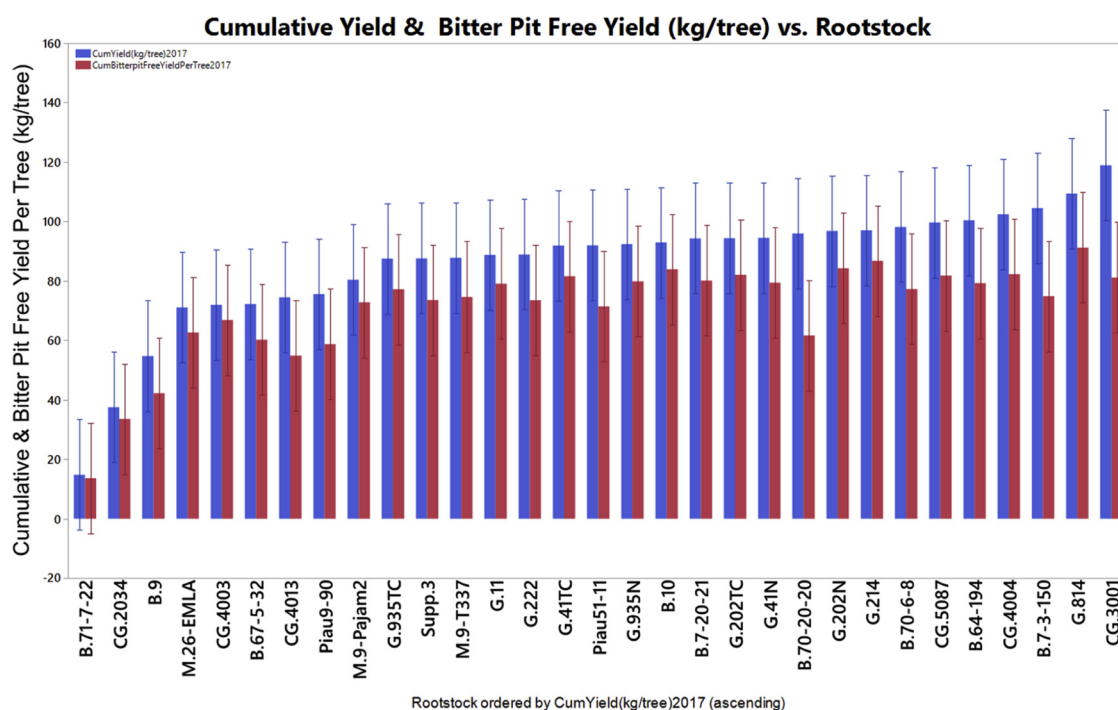


Fig. 2. Genotypic means for cumulative yield (blue) and bitter-pit free cumulative yield per tree (red) for 31 rootstocks after 8 years when grown at Geneva, NY. LSD for Yield/tree = 18.6. LSD for Bitter Pit free Yield/tree = 18.1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the rootstocks in this trial. Biennial bearing indices, where not very correlated with tree vigor as dwarfing rootstocks Supporter 3, M.9 Pajam2 and B.9 exhibited fairly high yield fluctuations.

3.4. Leaf zonal chlorosis

Leaf zonal chlorosis measured over three years (2014, 2015 & 2017)

was influenced by apple rootstocks (Fig. 6). While environmental conditions influenced the overall rating for this physiological disorder, there was strong correlation between years according to rootstocks (between 2014 and 2017 $r = 0.59$; $P < 0.001$). Higher values (red in Fig. 6) were observed in the lower cluster of rootstocks (G.814, CG.2034, PiAu9-90, and CG.5087), whereas lower values of zonal chlorosis (blue in Fig. 6) were observed by the rootstocks cluster of B.7-

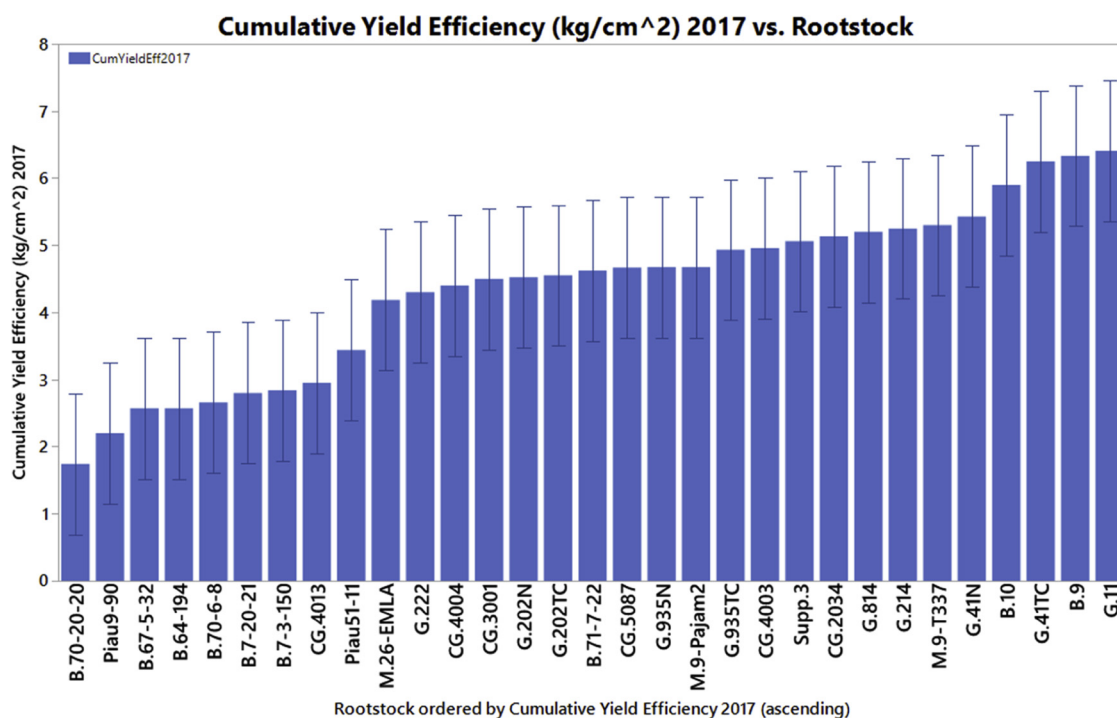


Fig. 3. Genotypic means for cumulative yield efficiency (kg of apples per cm² of the trunk cross sectional area) for 31 rootstocks after 8 years when grown at Geneva, NY. LSD for Yield Efficiency = 1.05.

20-21, B.70-6-8. While higher rootstock vigor seems to be slightly associated with the lack of zonal chlorosis, there are dwarfing rootstocks that also displayed low to average (gray in Fig. 6) levels of this disorder (G.222, M.9-T337, B.10 and CG.4003).

3.5. Fruit size, and soluble solids

Rootstock had a significant effect on fruit size (Fig. 7). Fruit size was small (blue in Fig. 7) for rootstocks B.71-7-22, B.9, CG.2034 and CG.4003, while CG.5087 and B64-194 had larger fruit size (red in Fig. 7). Years 2015 and 2017 were more similar than 2016 which was a very dry year, cumulated rainfall from May through October was

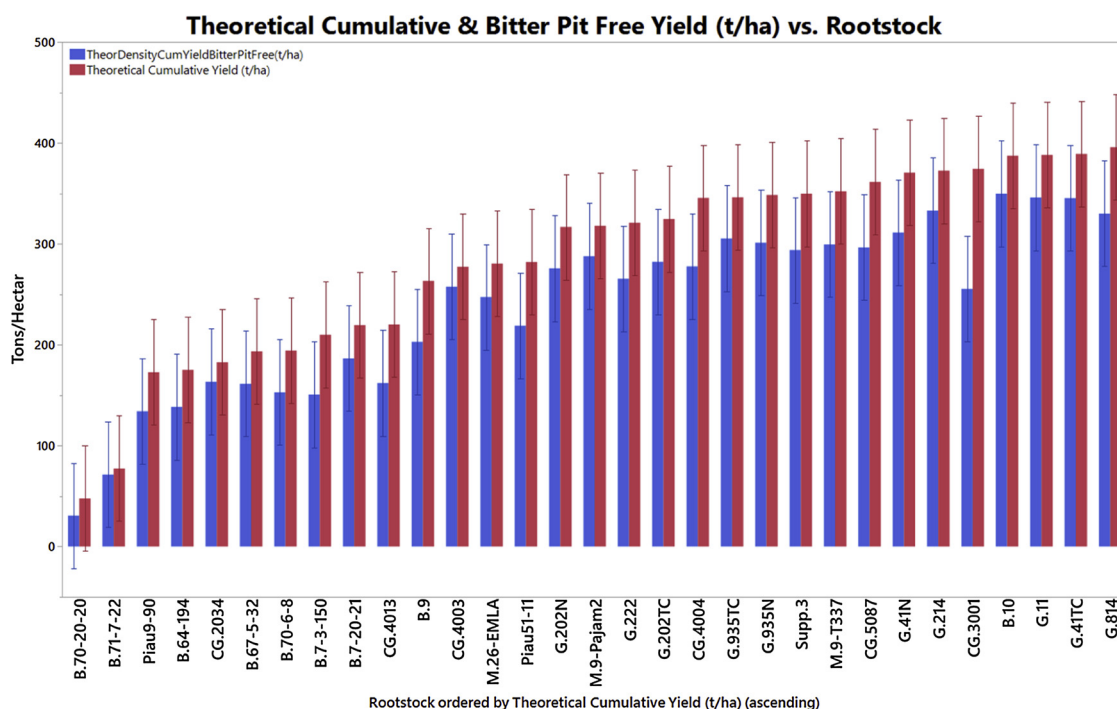


Fig. 4. Genotypic means for cumulative yield and bitter pit free yield (t/ha) (calculated by multiplying cumulative yields per tree by a theoretical optimal tree density (trees/ha) based on tree size potential (500 trees/ha for seedling size rootstocks to 5000 trees/ha for sub-dwarfing rootstocks) of 'Honeycrisp' apple grown on 31 rootstocks after 8 years at Geneva, NY. LSD for Theoretical cumulative yield/ha = 59.4 and LSD for Theoretical Bitter Pit free yield/ha = 52.3.

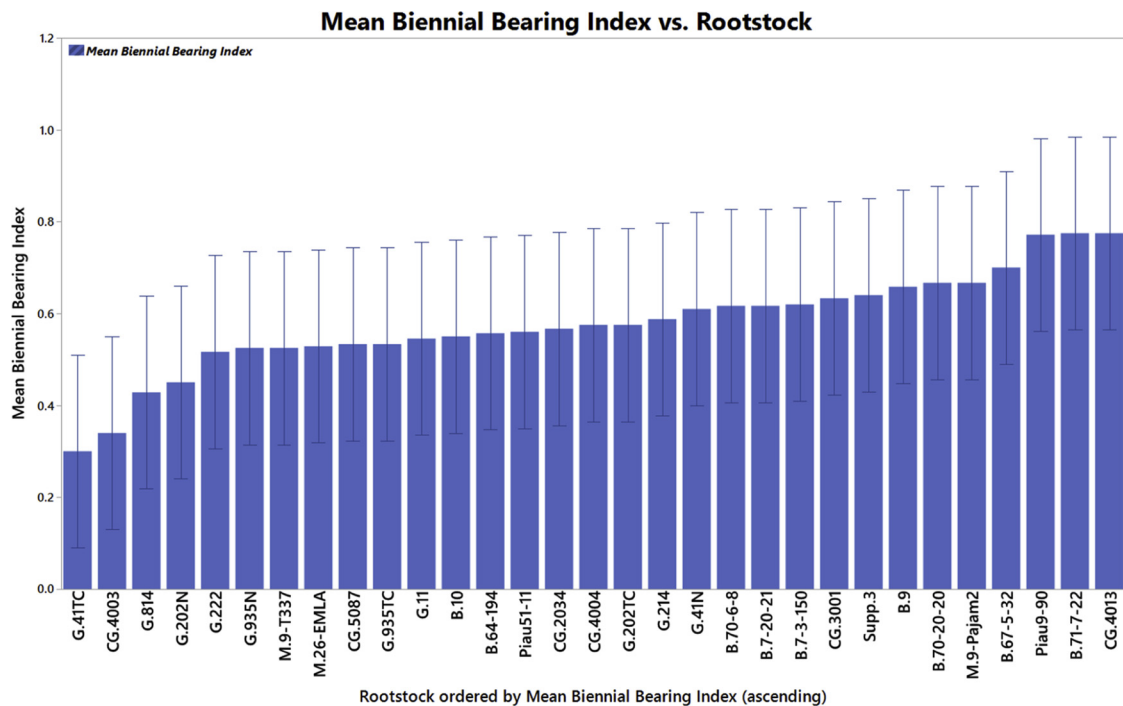


Fig. 5. Genotypic means for biennial bearing index (BBI) of ‘Honeycrisp’ apple grown on 31 rootstocks over 6 years (3rd–8th years) at Geneva, NY. LSD for Biennial Bearing Index = 0.21.

~4000 m³/ha vs 1400 m³/ha, 2015–2017 vs 2016 respectively (Fig. 8).

Rootstock influenced fruit soluble solids (brix) values (Fig. 9). Certain rootstocks (G.11 CG.2034, B.9, G.935TC, G.41N, G.202N CG.4004 and Supp. 3) seemed to induce consistently lower soluble solids (blue in Fig. 9) over 3 harvest years, whereas CG.4003 PiAu51-11, and PiAu9-90 had consistently high soluble solids (red in Fig. 9). There was generally good consistency between results in 2015 and 2016 but often opposite results with 2017. In the first 2 years, B.71-7-22, CG.3001, CG.5087, G.41N and G.935TC had low soluble solids but in 2015 and 2016 they all had high soluble solids in 2017.

3.6. Fruit bitter pit incidence

Rootstock influenced fruit bitter pit incidence (Fig. 10). One cluster with somewhat consistent low bitter-pit (blue in Fig. 10) featured rootstocks B.10, CG.2034, B.71-7-22, G.41N, CG.4003, G.202N, G.214, and Supp. 3. A second cluster of low to medium bitter-pit levels featured rootstocks M.9-T337, G.814, G.11 and G.935N. Consistently high bitter-pit levels (red in Fig. 10) were observed on rootstock B.70-20-20, B.7-3-150, CG.3001, CG.4013, and PiAu9-90. B.9 generally had low incidence of bitter pit but in the very dry year of 2016 it had high incidence of bitter pit.

Using the percent bitter pit incidence we calculated yield of bitter pit free fruits. Rootstock had a significant influence on yield of bitter pit free fruits (Fig. 2) Cumulative yield of bitter pit free fruit over the first 8 years was greatest for G.814, followed by G.214, G.202N, B.10, G.202TC, G.41TC, G.11 and CG.5087 (red bars in Fig. 2). Following the top rootstocks was a large group of rootstocks that had a cumulative yield of bitter pit free fruit between 60 and 80 kg/tree. The rootstocks with the lowest yields of bitter pit free fruit were B.71-7-22, CG.2034 and B.9 which were also the smallest trees.

Considering both tree size and bitter pit incidence we calculated the theoretical yield of bitter pit free fruit per ha (obtained by multiplying cumulative yields per tree by percentage of bitter pit free fruit and by the theoretical optimal tree density (trees/ha) coefficient based on tree size (TCA). Theoretical cumulative yields/ha of bitter pit free fruit varied from a high of 340 t/ha to a low of 35 t/ha, almost a 10-fold

difference (Fig. 4). The dwarfing rootstocks B.10, G.11, G.41TC, G.214 and G.814 had the highest yields per hectare of bitter pit free fruit (blue bars in Fig. 4). A second group included G.41N, G.935TC and N, M.9T337, CG.5087, Supp. 3, M.9Pajam2, G.202TC and N, CG.4004 and G.222. Rootstocks B.9 and M.26 had lower cumulative bitter pit free yield/ha along with several other un-released rootstock selections. The most vigorous rootstocks B.70.20.20 and B.71-7-22 had the lowest yield of bitter pit free fruit.

4. Discussion

4.1. Tree size and yield

Our results of mature tree size were similar to what Autio et al. (2017) reported at the end of year 5, where sub-dwarfing rootstock B.71-7-22 and vigorous (standard seedling size) B.70-20-20 represented the ends of the spectrum of rootstocks. The classes of dwarfing potential described in Autio et al. (2017) are congruent with the findings in this experiment. The highest cumulative yield per tree (2011–2017) was obtained on rootstock CG.3001, however the highest bitter pit free yield was produced by G.814 with G.214 and B.10 as second and third respectively. When the per tree yields were adjusted to how many trees could be planted per hectare of land based on the dwarfing capacity the theoretical cumulative yield per hectare for each rootstock, G.814, G.11, G.41TC, B.10, G.41N were the superior rootstocks where in the meta-analysis performed in Autio et al. (2017), G.814 was the most efficient also. The low theoretical cumulative yield with the most vigorous rootstocks B.70-20-20 and B.71-7-22 indicates that it is counterproductive to try to increase vigor of a weak scion cultivar (‘Honeycrisp’) with non-precocious, vigorous rootstocks. Our results also indicate that if the rootstock is too dwarfing for a weak growing scion like ‘Honeycrisp’ that even when planted very close theoretical yields are less than the best semi-dwarfing rootstocks. These results show that when evaluating rootstocks it is not enough to rank them by yield efficiency which is the common way to rank rootstocks. Although cumulative yield efficiency (kg of apples per cm² of the trunk cross sectional area) is a way to capture how well the rootstock is partitioning

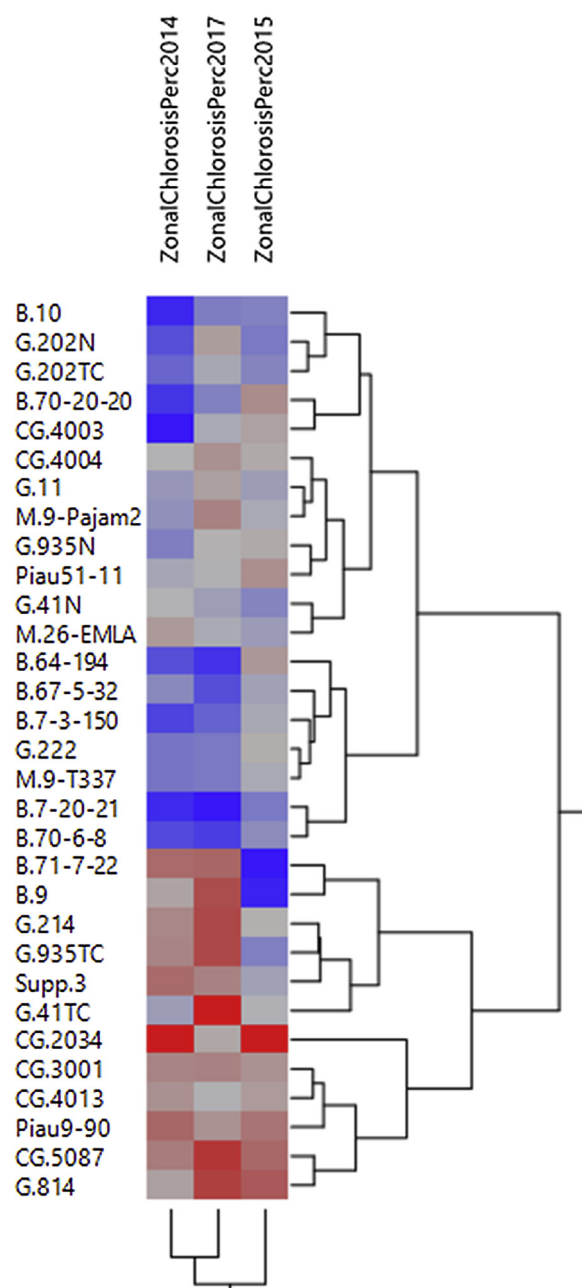


Fig. 6. Two-Way similarity cluster analysis of zonal chlorosis genotypic means over three growing seasons of ‘Honeycrisp’ apple grown on 31 rootstocks at Geneva, NY. Higher values are red whereas lower genotypic means are blue and average values are gray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

photosynthesis product toward producing fruit instead of vegetative growth (vigorous rootstocks that produce less apples per TCA are considered yield inefficient whereas dwarfing rootstocks that are able to produce more apples per TCA are yield efficient), it is also important to assess if the vigor of the rootstock is sufficient to fill the space and if the rootstock has high yield efficiency. A specific case was B.9 which was one of the most yield efficient rootstocks but because it was excessively dwarfing, its theoretical yield was less than half of the best rootstock’s theoretical yield (G.814). Further affecting the ranking of rootstocks for theoretical yield per ha was the incidence of bitter pit. Once that characteristic of ‘Honeycrisp’ was considered, the relative ranking of B.9 improved substantially, since it had low incidence of bitter pit, but it still had significantly less yield/ha of bitter pit free fruit

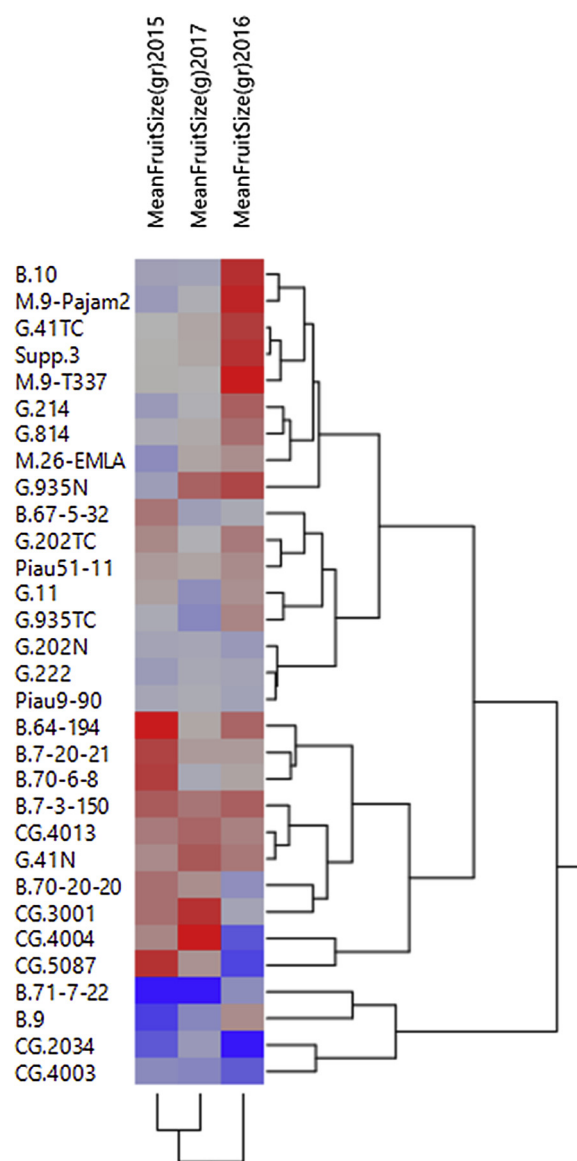


Fig. 7. Two-Way similarity cluster analysis of fruit size as affected by apple rootstocks of ‘Honeycrisp’ apple grown on 31 rootstocks at Geneva, NY. Higher values are red whereas lower genotypic means are blue and average values are gray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(205 t/ha) compared to the best rootstocks (~330 t/ha) which were B.10, G.11, G.41TC, G.214 and G.814. Considering the high farm gate fresh market price for ‘Honeycrisp’ apples (\$1.65/kg) (Lordan et al., 2018), the extra yield of the best rootstocks compared to B.9 would be worth ~\$222,000 per ha. This large economic impact illustrates the practical importance of rootstock evaluation to find the rootstocks which have the best combination of vigor, productivity and fruit quality to match specific scions to maximize yield of bitter pit free fruit. It is likely that in each geographic region different rootstocks may be the optimum for ‘Honeycrisp’. Our results unfortunately are limited to the climate in the Northeastern USA.

The tendency of some apple varieties to bear fruit heavily in one season and poorly the next season referred to as alternate or biennial bearing is dependent on the genetic components of each cultivar where ‘Honeycrisp’ and ‘Fuji’ are strongly biennial while ‘Gala’ is much less biennial (Guillon et al., 2012). Apple rootstocks can influence bienniality (Barritt et al., 1997) by means of influencing crop load, vigor, hormone concentration and gene expression of the scion (Jensen et al., 2012;

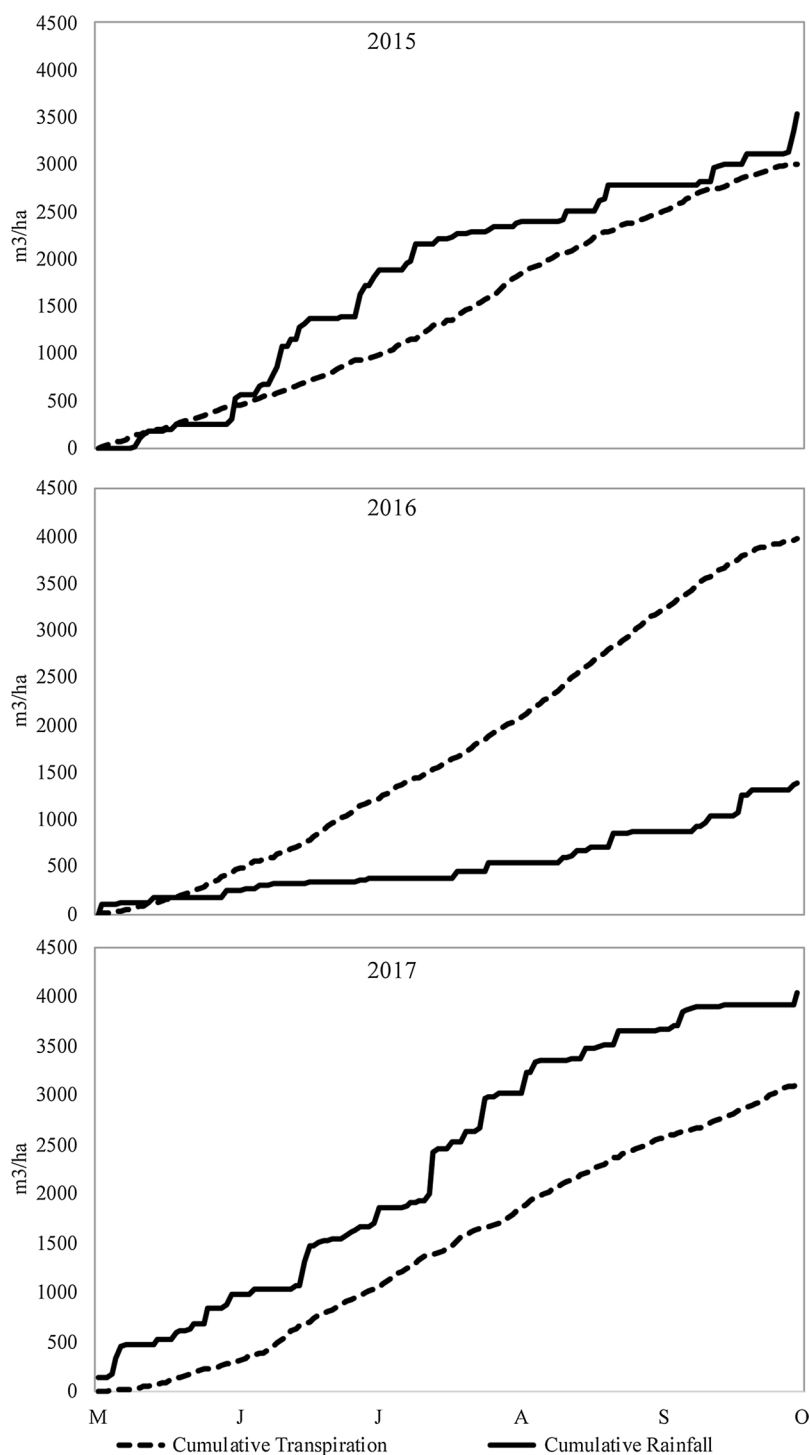


Fig. 8. Cumulative rainfall and tree transpiration (m^3/ha) from May through October at Geneva Ny. Tree transpiration was calculated using a modified Penman-Monteith equation (NEWA.org) (Robinson et al., 2017).

Lordan et al., 2017; Tworowski and Fazio, 2016). In this trial, G.41TC, CG.4003 and G.814 displayed the lowest levels of alternate bearing, and CG.4013 (semi-dwarf) and B.71-7-22 (sub-dwarf) displayed the highest levels of alternate bearing, indicating as in Barritt et al. (1997), that vigor control is not always related to the suppression of alternate bearing. More research is needed to fully understand all the variables that influence this trait that causes large losses in production in apple orchards worldwide.

4.2. Fruit quality

Rootstock did influence fruit soluble solids (brix) but the results varied between years. Fruit in the 2015 season were harvested in two picks according to color maturity, suggesting that the trends observed in rootstocks were not due to differences in maturity, rather more correlated with crop load (Robinson and Lopez, 2012) and may be one of the reasons why apples may taste different when grown on different rootstocks.

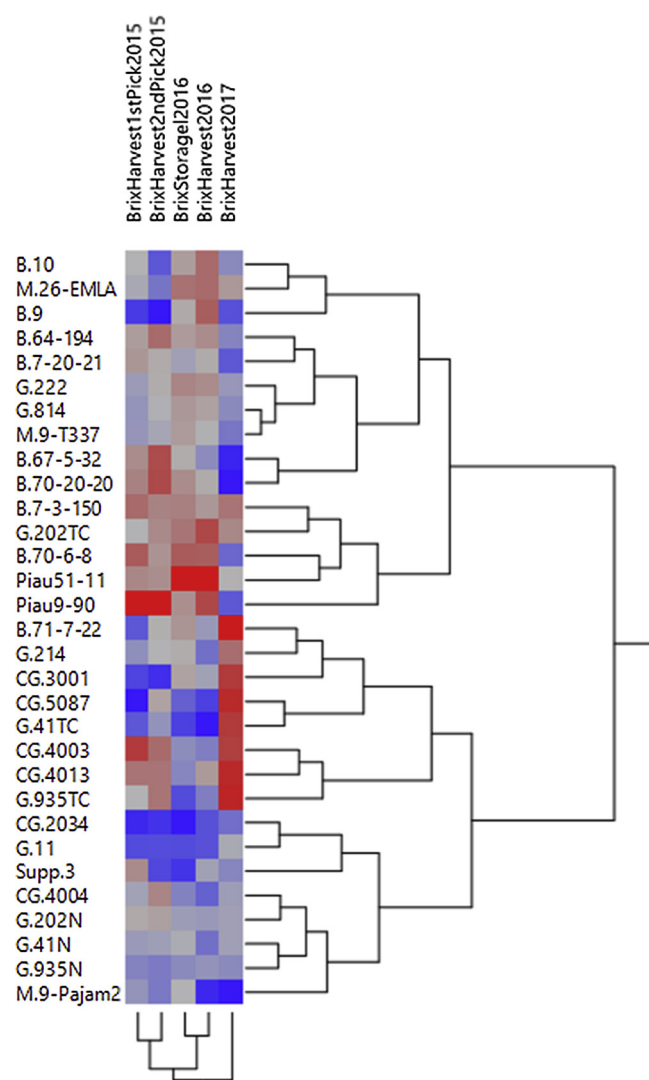


Fig. 9. Two-Way similarity cluster analysis of genotypic means for fruit brix or soluble solid content of different harvest years and storage conditions of ‘Honeycrisp’ apple grown on 31 rootstocks at Geneva, NY. Higher values are red whereas lower genotypic means are blue and average values are gray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. Zonal leaf chlorosis

‘Honeycrisp’ trees are sensitive to a leaf physiological disorder caused by over-loading of carbohydrates in leaves that causes damage to the photosynthesis systems (Chen et al., 2010; Fleck 2011; Snyder-Leiby and Wang, 2008) and often referred to as leaf zonal chlorosis. Rootstocks have also been shown to have an influence on this physiological disorder, with the degree of influence affected by season and perhaps management practices (Autio et al., 2017). In our study zonal chlorosis is less prevalent with the more vigorous rootstocks. This indicates that in conditions where vegetative growth is more active these vegetative sinks can utilize carbohydrates produced in the leaves thus limiting the buildup of starch granules which cause cell rupture and the zonal chlorosis (Cheng and Robinson, 2006). However, some semi-dwarfing rootstocks (G.222, M.9-T337, B.10 and CG.4003) also had low values for zonal chlorosis indicating an unknown rootstock mediated mechanism to prevent the buildup of starch granules in the leaf.

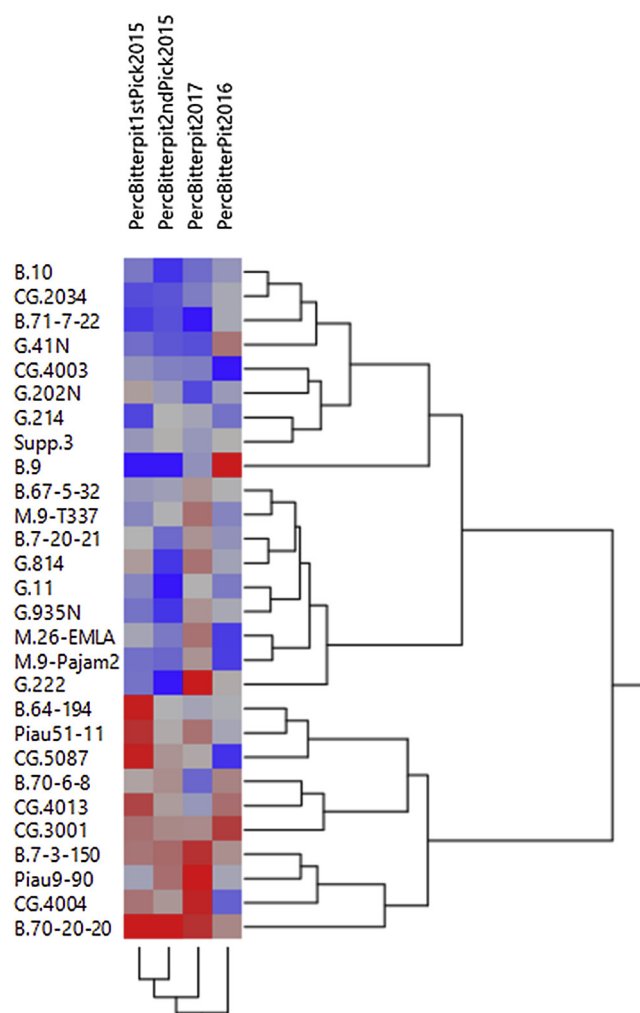


Fig. 10. Two-Way similarity cluster analysis of rootstock induced mean percent bitter-pit incidence for years 2015–2017 of ‘Honeycrisp’ apple grown on 31 rootstocks at Geneva, NY. Higher values are red whereas lower genotypic means are blue and average values are gray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusion

This experiment using a genetically diverse set of rootstocks showed dramatic differences in tree size, yield, yield efficiency, biennial bearing and bitter pit incidence on the fruit which were induced by the rootstock. However, in ranking rootstocks for a particular climate and a particular scion variety, it is important to not only consider yield efficiency but also the vigor of the rootstock which must be sufficient to fill the space rapidly and combined with high yield efficiency. Our data also indicate that rootstock not only has a large influence on mature tree cumulative yield but also bitter pit incidence which combine to create a large economic impact of rootstock choice on its long-term economic result of an orchard. The best rootstocks had theoretical yields of bitter pit free fruit of 10 times the poorest performing rootstocks. A final important factor is that when scion cultivar vigor is low as with ‘Honeycrisp’ the best rootstock may not be the same as for a more moderate vigor scion cultivar or even a vigorous scion cultivar which need more dwarfing power from the rootstock compared to weak scion cultivars (Reig et al., 2018). This leads to the need for “designer rootstocks” which combine the rootstock characteristics needed to maximize the potential of each scion cultivar in a particular climate.

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