Apple Dwarfing Rootstock Cold Hardiness: Comparing Performance of The Geneva® Series Rootstocks in Cold and Mild Winter Conditions

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Apples typically have sufficient cold hardiness to survive most winters in New York. However, as climate changes and winters become milder, trees may not receive the right temperature cues for maximum protection and develop insufficient cold hardiness. We found that, all Geneva®-series rootstocks outperformed M.9 in cold hardiness but certain Geneva®-series rootstocks may exhibit reduced reliability as the climate warms, while others show potential as climate-resilient germplasm.

The evolution of dormancy in fruit and other deciduous trees serves as a proactive physiological response to safeguard against the unfavorable growing conditions that occur during winter (Campoy *et al.*, 2011). Exposure to freezing temperatures and low light levels during the dormant season requires a set of defense mechanisms to maintain the viability of plant tissues until favorable growing conditions resume in the spring. As a result, temperate deciduous tree species have developed a complex system for accruing, maintaining, and losing cold hardiness that relies not only external factors (e.g., day length and temperature) but also genetic factors that balances the amount of time the plant spends relying on carbohydrate reserves with an ability to survive unpredictable winter weather (Maurya and Bhalerao, 2017; Vitasse *et al.*, 2014). As a result of the long history of apple breeding, combining different genetic backgrounds to produce superior fruit, or in the case of rootstocks, superior rooting and dwarfing, apple scions and rootstocks may also have large differences in the rate that cold hardiness is developed in early winter (acclimation), differences in the tolerance to the coldest temperatures of midwinter, different responses to warm spells and "false spring" events during dormancy, and differences in how fast cold hardiness is lost as spring approaches (deacclimation). Even though cold hardiness is commonly referred to as a binary and qualitative trait (e.g., "hardy" vs "non-hardy"), the reality is that cold hardiness is a dynamic phenotype that shifts during winter. As a result, describing and categorizing the hardiness of apple scions and rootstocks is complicated and needs to be examined in the context of the phase of winter (early, mid, late) and the intensity of winter (annual variation).

Historically, winter damage in commercial apple systems is infrequent in most areas of apple production given that orchard systems are expected to be productive for 20 years or more (Lordan *et al.*, 2019). Winters that do result in extensive damage are often referred to as "test winters". Before high-quality methods for testing cold hardiness became available, these extreme winters were important data points for researchers (Quamme *et al.*, 2004). Regions such as the Hood River Valley in Oregon historically experienced one test winter every nine years while much harsher regions at the edge of viable apple production such as New Brunswick experienced test winters as often as every five years (Brown *et al.*, 1964; Coleman, 1991). When these extreme events occur, they often result in severe economic consequences. For example, in the winter of 1983-1984, approximately 1/7th of all apple trees in Ontario were killed due to low temperatures in late winter (Rochette *et al.*, 2004).

Phenotyping the changing dynamics of cold hardiness throughout winter in tree species is a challenging endeavor. Controlled experiments in the field (*in situ*) are impractical given the size of the apple tree (even on a dwarfing rootstock) and the difficulty of applying a controlled freeze treatment outside of the laboratory. Opportunistic observations of tree damage following extreme weather events have long been relied upon for gleaning broad trends in hardiness between cultivars (Maney, 1942) but serve as a general observation at a single timepoint. In contrast to observing damage in the field, progress has been made in the establishment of lab-based assessments of cold hardiness and freeze damage. One of the first methods used for quantitatively and reproducibly estimating the cold hardiness of plants is the measurement of electrical conductivity that results when tissue samples are exposed to freezing temperatures (Dexter *et al.*, 1932). This method uses an estimation of freeze damage to plant tissues resulting from the catastrophic perforation of the cell membrane from ice nucleation. When plant tissues freeze, cells can lyse and release cellular ions and other metabolites. By measuring the electrical conductivity of a tissue sample in distilled water before, and after freezing, we can estimate the amount of cellular damage that occurs from the freeze treatment. Comparing levels of damage that occur at many different freezing temperatures can then be used as a point of comparison to rank the cold hardiness of different plant samples. This method is now a standard practice for evaluating how cold hardiness changes across winter in woody plant tissues (Kovaleski and Grossman, 2021) and is the method we used in this study.

Replication of cold hardiness experiments between years can show strikingly different outcomes given the wide differences in temperature that can be observed between a mild and severe winter- highlighting the importance of multi-year experiments and that interpretations of data must be done in the context of the environment in which they were taken (Coleman, 1985; Ozherelieva and Sedov, 2017). In addition, while an improvement over field observation, phenotyping cold hardiness with electrolyte leakage is laborious as multiple tissue samples collected at many different winter timepoints are needed to generate a reliable estimate of season-wide cold hardiness and tissue damage.

These constraints make it difficult to design an experiment that examines a large cohort of cultivars and also properly samples throughout the dormant season. Many experiments compromise on at least one of these criteria, for example: Cline *et al.* (2012) and Cline *et al.* (2021) looked at only two timepoints during the winter, at the beginning of December and February, while Quamme and Hampson (2004) collected data during November and February. In each case, researchers focused on determining cold hardiness in early winter, before trees had fully acclimated in eastern Canada, and again in February when trees would have achieved their maximal cold hardiness for the year. Conversely, Coleman (1985) focused solely on the hardiness of apples as they began deacclimating in spring. While each paper contributed to our understanding of apple cold hardiness, each is constrained by the difficulties facing researchers attempting to generate high-resolution datasets on winter hardiness. The study presented here aims to satisfy both challenges, by evaluating a large number of apple rootstocks and scions monthly throughout winter and repeated over four winter seasons.

Given the critical role of the scion cultivar in apple production, much of the research into winter hardiness of apples has focused on phenotyping scions. However, apples are mechanically grafted, combining the high fruit yield and quality traits of the scion with growth control, nutrition, and water uptake traits of the rootstock. In most high-density apple production, apple rootstocks are grafted so that 6-10 inches of trunk (referred to as the rootstock shank) remains above the soil surface. Thus, a whole-tree assessment of cold hardiness should include the relative status of both the rootstock *and* scion phenotypes. Previous studies examining rootstock hardiness measuring injury by exposing young trees to controlled freezes, but often at a limited range of temperatures (Moran *et al.*, 2011; Moran *et al.*, 2018). Given that the rootstock shank and graft union is believed to be the last tissue to enter dormancy in fall (Stokstad, 2019), it is also important to evaluate this tissue as a potential ‘weak link’ in the whole tree’s cold hardiness status. Additionally, the rapid change in apple production from large widely spaced apple trees to that of high-density plantings on dwarfing rootstocks has led to the widespread planting of cultivars such as ‘M.9’ that are prone to injury (Marini and Fazio, 2018). The objective of this study was to comprehensively examine the cold hardiness ability of apple dwarfing rootstocks across multiple winter seasons with a focus on the modern rootstock releases comprising the Geneva® series (Marini and Fazio, 2018).

Material and methods

The experiment was conducted over four winter seasons starting in the fall of 2021 and concluding in the spring of 2025. Results from within each season will be referred to as 2021-2022, 2022-2023, 2023-2024, and 2024-2025. The results of the first year of this study have been previously reported (Londo *et al.*, 2023). During 2021-2022, 22 cultivars were tested from November to March, split between 5 fresh-market scion cultivars and 17 rootstock cultivars. In 2022-2023, the experiment began in November and concluded in April. In each of the seasons 2023-2024 and 2024-2025, sampling began in September and concluded in April.

Long-term weather data for Geneva, NY was sourced from the National Centers for Environmental Information (NCEI). The daily high and low temperature, starting from January 1st, 1969, and running to the termination of the experiment was used to assess the weather conditions of the experiment winters compared to long-term averages. The 56 available years of weather data were ranked by the severity of the winter using the mean daily temperature from November 1st to March 30th for each winter, averaged for each year. Temperature patterns within each winter were visualized to compare across seasons by calculating a two-week rolling average of the mean daily temperature.

The rootstock and dessert scion cultivars used in this study were located at Cornell’s AgriTech experiment station located in Geneva, NY. Scion genotypes were all grafted on ‘M.9’ rootstocks as part of a long-term scion comparison study. The rootstock genotypes used in the study were sampled from adjacent own-rooted stoolbed plantings. Dormant one-year old stem sections approximately 7-10 mm in diameter were sampled to assess cold hardiness using electrolyte leakage assays (Kovaleski and Grossman, 2021). Samples 2.5 cm in length were cut from stem internode sections to avoid inclusion of vegetative buds. Three replicate stem tissue samples were prepared for each apple genotype for each experimental freezing treatment for each sampling timepoint during winter. Each tissue sample was placed in a 50 mL centrifuge tube with 30 mL of distilled water and exposed to one of 10 temperature treatments. Freeze treatments consisted of 9 temperatures below freezing (from -10 °C to -50 °C in 5 degrees intervals, which translates to 14 °F to -58 °F in 9-degree intervals) and one unfrozen control (4 °C, or 39 °F). Samples were placed inside a large programmable freezer (Tenney TC30RC2; New Columbia, PA) and a ramping freezing protocol was used. The ramp consisted of a 4°C hold for 1 hour, decreasing to -5°C at 1°C/minute. The freezer then held at -5°C for 2 hours to assure all samples had frozen, then began a decreasing temperature ramp of -5°C/hour with 1 hour holds at each freezing set point. Sample tubes were manually removed from the freezer at the conclusion of each freezing set point hold.

Following freezing exposure, sample tubes were moved to the laboratory and left at room temperature to thaw while shaking on a large flatbed shaker for 24 hours to ensure thorough mixing of the sample and leakage of any cellular solutions. An initial electrical conductivity (EC, measured in mS) of each sample- denoted as Ri- was taken using a Mantech Automax 402 autotitrator equipped with a Mantech 4510 conductivity meter. Samples were then placed in a -80 °C (-112 °F) freezer overnight to fully kill the tissue, maximizing membrane perforation and the electrolyte leakage for each given sample to allow for damage standardization during data analysis. Samples were thawed and shaken a second time, followed by a second conductivity reading- denoted as Rf. The index of injury (IoI) for each sample was calculated following a modified version of the methods found in Lim *et al.* (1998), where the conductivity readings of the three unfrozen controls (4 °C; 39 °F) for each genotype-timepoint combination were averaged and used as the minimum leakage expected for any piece of tissue of that genotype-timepoint combination (denoted as Ro). The IoI calculation normalizes the Ri and Rf of each reading by its corresponding Ro and uses the corresponding ratio as an expression for the proportion of damage to that tissue sample. Across the experiment a total of 16,800 sample EC measurements were collected. After eliminating outlier values 16,168 sample points remained. A log-logistic curve was then fit to the EC data using the ‘drc’ library in R (Ritz *et al.*, 2015) and from the regression curve, the temperatures which resulted in 25% of maximum tissue leakage was determined. This value, referred to as the Lethal Temperature for 25% of Tissue, or LT25, has been shown to correlate with the temperature that results in tissue damage and browning of the cambium tissue in apples (Jason Londo, unpublished data).

Ranking Rootstock Hardiness: At each timepoint throughout the experiment, LT25 values for each rootstock genotype were compared to the average LT25 of the other sampled rootstocks, producing a relative comparison of how much more or less cold hardy that cultivar was for that particular month and winter. These individual values calculated on a per-month basis were then combined to create an average deviation from the monthly normalized values for every cultivar across the entire experiment, expressed in both Fahrenheit and Centigrade. Each rootstock was then compared to 'M.9' using an ANOVA to determine whether it was significantly more cold hardy. The 'fdr' method from the 'stats package in R (R Core Team, 2024) was used to control for the family-wise error rate with an alpha of 0.05.

Consistency Analysis: The first winter of this study, 2021-2022, was the most similar to historical patterns of temperature change during New York winters, a canonical "cold" winter. To understand how the rootstock genotypes respond to mild winter conditions, we examined the difference in maximum cold hardiness the genotypes attained in the three mild winters (2022-2023, 2023-2024, and 2024-2025) compared with the response in 2021-2022. The midwinter cold hardiness values in January and February for each rootstock from 2021-2022 were used as the baseline for a cultivar's maximum achievable cold hardiness during a cold winter. The reported magnitude of difference from cold to mild winters was calculated by subtracting the midwinter hardiness values for the two months of each of the mild winters from the midwinter hardiness values of 2021-2022. To compare the consistency of cultivars statistically, the proportion of cold hardiness achieved in each mild winter compared to the cold winter baseline was calculated (i.e., the LT25 from a mild year was divided by the LT25 from a cold year) and these percentages were compared to 'M.9' using ANOVA. The 'fdr' method from the 'stats' package (R Core Team, 2024) in R was used to control for the family-wise error rate with a significance level of 0.1.

Deacclimation Rates: Deacclimation is the loss of cold hardiness that occurs when temperatures rise during winter or as the season approaches budbreak in spring. Field deacclimation rates were estimated by taking the change in cold hardiness between two monthly timepoints in late winter, representing the loss of cold hardiness that occurred under field conditions. These rates were calculated for the rootstocks and scions by comparing the cold hardiness values observed in April relative to values observed in March in 2023-2024 and 2024-2025. ANOVA was used to test significant differences between the rootstock and scion deacclimation rates using the 'stats' in R (R Core Team, 2024).

Results

Examining the trends in winter temperature data revealed that the average temperature during winter from October 1st to April 30th for two of the study years (2022-2023 & 2023-2024) were among the warmest years in the previous 56 years- ranking as the 5th and 4th warmest, respectively, while 2024-2025 was the 20th warmest winter. The winter of 2021-2022 was comparatively much colder, ranking as the 31st coldest in the dataset.

Each winter had unique temperature features that likely affected the cold hardiness levels we measured for apple stem tissue (Figure 1). As noted above, winter temperatures during 2021-2022 were colder than the other three examined winter seasons with the coldest minimum temperature reaching -11°F (-23.9 °C), and temperature decreases from the start of winter to the end of winter followed a standard U-shaped pattern (consistent decreasing temperatures to midwinter, then warming toward spring). The early winter temperatures of 2022-2023 were quite similar to 2021-2022, with a notable steep drop in temperature in late December (December 24-25, culminating in a low of 4°F (-15.6 °C). Immediately following this acute low temperature event, temperatures rose and were unseasonably warm through January before a second acute cold event occurred on February 4th and 5th with lows of -7 °F (-21.7 °C) and -1 °F (-18.3 °C), respectively. The early seasonal cold, warm snap in January, and return to cold temperatures in February are an excellent example of a "false spring" temperature event. Winter conditions in 2023-2024 again were similar to the early seasons of 2021-2022 and 2022-2023. However, midwinter temperatures were considerably more mild in 2023-2024 with the minimum temperature only reaching 5 °F (-15 °C). Conditions during 2024-2025 were again similar to the previous winters during the early wintertime period and with midwinter low temperatures remaining mild, with minimum temperatures reaching -3 °F (-19.4 °C) on January 22nd, 2025. However, 2024-2025 contrasted with the two previous mild

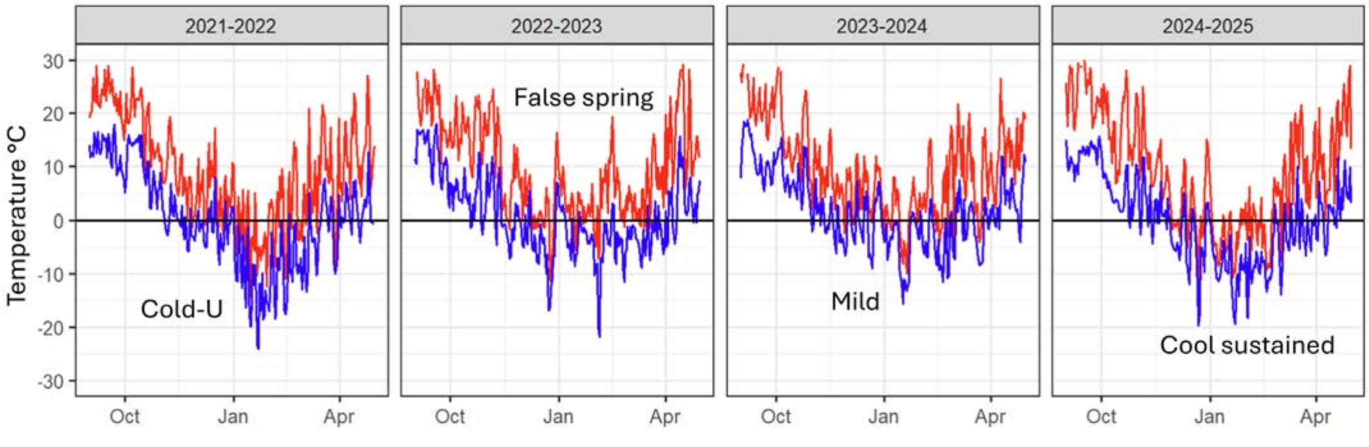

Figure 1. Comparison of temperature patterns between the four seasons in this study. Red line denotes daily maximum temperatures, and blue line denotes daily minimum temperatures in °C. 2021-2022 had a typical U-shaped pattern with midwinter cold. 2022-2023 had a false-spring event in midwinter. 2023-2024 was U-shaped, but very mild. 2024-2025 was also U-shaped but had sustained midwinter cold temperatures.

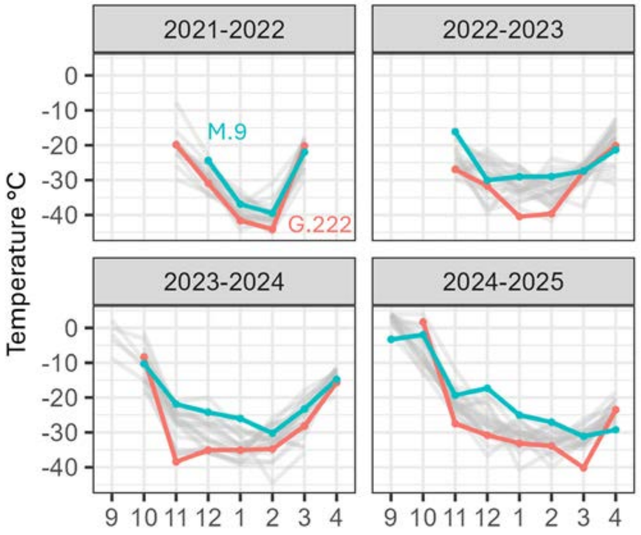

Figure 2. LT25 values for rootstock cold hardiness across the four years of the study, contrasting cold sensitive ('M.9', blue line) and cold hardy ('G.222', red line) rootstocks. X-axis denotes month of the year. Gray lines indicate cold hardiness of the other genotypes in the study to demonstrate the range in variation.

winters in that midwinter daily high temperatures remained cool. The result of this temperature pattern was an overall mild winter but with a period during January and February where both highs and lows were cold, resulting in a more sustained "cool-cold" winter. Thus, when examining patterns of cold hardiness change across winter, we consider 2021-2022 a cold winter, 2022-2023 a mild-false spring winter, 2023-2024 a mild winter, and 2024-2025 a cool-cold winter.

Rootstock Performance During Mild Winters: Midwinter cold hardiness estimates measured during the cold conditions of 2021-2022 were significantly lower than those of the following three mild winters and ranged from 10-15°F hardier on average. As previously reported (Londo *et al.* 2023), all rootstocks evaluated in 2021-2022 had U-shaped responses, achieving deep midwinter cold hardiness (Figure 2). When examining mild winters, initial early winter acclimation patterns were highly consistent among rootstocks, all rootstocks appear to utilize early winter temperature patterns and gain comparable cold hardiness. However, by mid-winter, large differences in cold hardiness response were noted and variation between rootstocks became apparent. This difference was most easily seen when contrasting cold hardiness at the January and February timepoints of 2021-2022 with the cold hardiness achieved in the mild winters of 2022-2023, 2023-2024, and 2024-2025 (Figure 2).

To better convey the pattern of shifting cold hardiness we differentiate between rootstocks that slowed or stopped acclimation in midwinter and instead maintained relatively low levels of cold hardiness, with those who continue to gain cold hardiness.

Rootstocks that stop developing additional cold hardiness in mild winters are less resilient as they are at higher risk of freeze damage if an acute cold event were to occur in mid to late winter. In our study, 'M.9' was the least consistent of the rootstocks tested when comparing cold and mild winter responses (i.e., it acclimated the least during mild winters). Of the 17 rootstocks tested in this experiment, 'M.9' averaged nearly 19 °F (10.6 °C) less hardy in January/February of 2022-2023, 2023-2024, and 2024-2025 than in 2021-2022. In contrast, 'G.484' and 'G.890' were highly consistent in the level of cold hardiness achieved in mild winters and was nearly the same as in 2021-2022, averaging 3.5 °F (2 °C) and 6.7 °F (3.7 °C) less hardy in mild midwinters.

Cold hardiness levels change during winter when comparing the early, mid, and late portions of the season. We used 'M.9' as our standard for a cold sensitive rootstock as point of comparison and when examining all rootstocks, we noted that nearly all Geneva® series rootstocks are more cold hardy across all four years of the study during the early (Nov-Dec) and mid (Jan-Feb) points of winter (Figure 3). In contrast, most Geneva® series rootstocks were *less* cold hardy than M.9 during late winter. When examining the whole winter pattern of cold hardiness, five rootstocks, 'B.9', 'G.11', 'G.202', 'G.484', and 'G.969' were not significantly different from 'M.9' while the remaining 11 rootstocks were significantly more cold hardy. Comparatively, 'G.11' performed the poorest of the Geneva® series rootstocks with cold hardiness only 0.6 °F (0.3 °C) more hardy than 'M.9'. In contrast, 'G.222' and 'G.257' were the hardiest rootstocks observed in the experiment, each just over 11 °F (6.1 °C) more hardy than 'M.9' on average. In total, 10 of the 14 Geneva® series rootstocks were significantly more cold hardy than 'M.9.' Additionally, most of the Geneva® series rootstocks performed as well or better than the cold-hardy rootstock 'Ottawa 3', one of the parent genotypes used in the breeding and selection of the Geneva® series rootstocks (Table 1).

Rootstock and Scion Deacclimation Deacclimation: is the loss of cold hardiness that occurs when temperatures begin rising in late winter and early spring as the tree prepares for the new growing season. Comparatively large differences in the deacclimation rate response were observed when comparing between the rootstock and scion genotypes (Figure 4). During this period, scions deacclimated an average of 5.3 °F (3.0 °C) while rootstocks deacclimated 17.8 °F (10.0 °C) on average. The fastest-deacclimating rootstocks ('G.210', 'G.222', 'G.257', and 'G.935') all had nearly identical rates of deacclimation- averaging between 21.5 (12.0 °C) and 22.0 °F (12 .2 °C). For the slowest-deacclimating rootstocks, 'M.9' and 'G.935' similarly had nearly identical deacclimation rates of 9.9 °F. By contrast, the fastest deacclimation rate of the scion group ('Evercrisp', 9.1 °F, 5.1 °C) was slower than the slowest of the rootstocks. Over the two years of data collec-

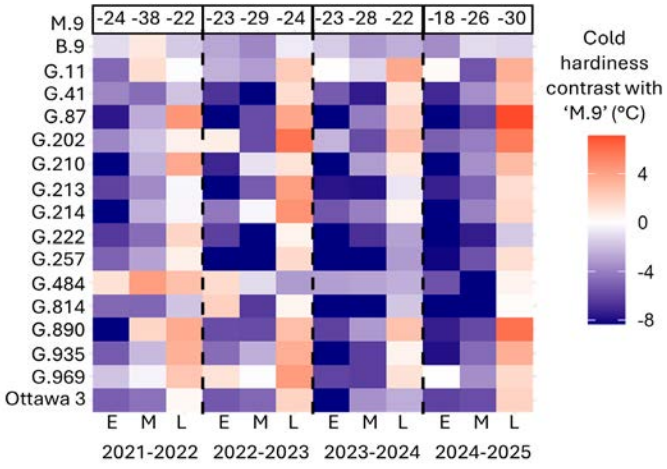

Figure 3. Heatmap comparison of cold hardiness across the four winters of this study. Data for each phase of winter represents average cold hardiness for early (Nov-Dec) mid (Jan-Feb) and late (Mar-Apr) portions of the winter. Cold hardiness level for M.9 used as reference. Heat map indicates if the rootstock was less cold hardy (red) or more cold hardy (blue) relative to M.9. Cold hardiness levels denoted in °C.

tion, 'Snapdragon' deacclimated only 2.0 °F (1.1 °C) on average.

Discussion

The results from the first year of this study were published in the spring 2023 issue of NYFQ (Londo et al 2023), and while slight variation in cold hardiness was noted among rootstocks, all rootstocks performed well during 2021-2022. After examining temperature patterns across the four winters of data discussed here, the conditions during the 2021-2022 season were substantially colder than in the following three winters. Historical trends of midwinter temperatures have been trending upward in New York State, increasing by up to 1.4 °F per decade since 1965 (Burakowski *et al.*, 2008). The effects of midwinter warming may already be manifesting through disorders such as rapid apple decline- where lethal rootstock damage is observed following mild winters and primarily on 'M.9' rootstocks (Stokstad, 2019). Considering the widespread use of 'M.9' as a dwarfing rootstock in high-density apple orchards, we used 'M.9' as our contrast point for evaluating the performance of the more modern Geneva®-series rootstocks developed by the Cornell-USDA rootstock breeding program. While there are many anecdotal observations that 'M.9' is relatively weak in cold climates, its performance has not yet been examined with monthly resolution throughout the winter season and in comparison, with the Geneva®-series. As a result of the difference in winter conditions captured across this study, the context of this discussion focuses on comparisons between the three most recent winter seasons with 2021-2022. It was our goal to use this difference to try and preview how warming winter conditions may impact the long-term winter resilience and suitability of dwarfing rootstocks.

Our results demonstrate that all the Geneva®-series rootstocks currently commercially available outperform 'M.9' during the dormant season. However, the improved performance of the Geneva®-series rootstocks is not as simple as more cold hardy at all points in winter and most of the enhanced hardiness was apparent during early and mid-winter sampling. Of all the rootstocks, 'G.11' was the second-weakest rootstock in the study and while it was numerically 0.6 °F (0.3 °C) more cold hardy than 'M.9'- it was not statistically significant. As 'G.11' is a progeny selection of a cross between 'M.9' and the cold-hardy 'Robusta 5'(Robinson *et al.*, 2006), it may be that 'G.11' inherited the alleles associated with poorer winter hardiness from 'M.9'. Interestingly, 'G.41' is a full sibling of 'G.11' but was observed to be significantly more cold hardy than 'M.9', averaging 7.4 °F (4.1 °C) more cold hardy during the dormant season. These paired but contrasting results set up the intriguing possibility of including cold hardiness as a selection target in future rootstock breeding efforts for mild-winter resilient dwarfing rootstocks.

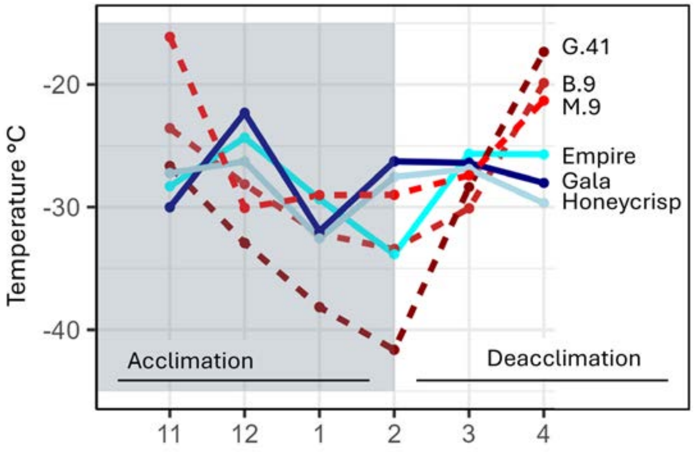

Figure 4. Cold hardiness curves for the winter of 2022-2023. Lines indicate the LT25 values in °C throughout winter. X-axis denotes month of the year. Acclimation portion of the winter shaded in gray with deacclimation portion unshaded. Response shows rapid deacclimation response observed in all dwarfing rootstocks relative to scion cultivars.

Table 1. Comparison of rootstock cultivar hardiness relative to the winter hardiness of 'M.9'. Difference in average hardiness denoted as °F or °C. *NS signifies 'non-significant.' Controlling for Type I error was performed using the false discovery rate (FDR) method at an alpha of 0.05.

Rootstock	°F Hardier	°C Hardier	Significance
B.9	3.8	2.11	NS
G.11	0.64	0.36	NS
G.41	7.39	4.11	< 0.01
G.87	6.18	3.43	< 0.05
G.202	2.05	1.14	NS
G.210	7.01	3.9	< 0.01
G.213	7.43	4.13	< 0.001
G.214	5.03	2.79	< 0.05
G.222	11.34	6.3	< 0.0001
G.257	11.28	6.27	< 0.001
G.484	2.36	1.31	NS
G.814	9.5	5.28	< 0.001
G.890	4.74	2.63	< 0.05
G.935	5.27	2.93	< 0.05
G.969	1.7	0.94	NS
Ottawa 3	7.38	4.1	< 0.01

Another surprising finding in the study was the relatively similar performance of 'B.9' compared to 'M.9'. While 3.8 °F (2.1 °C) more cold hardy on average, 'B.9' was not significantly different from 'M.9'. Previous research has demonstrated that 'B.9' can be quite cold hardy, depending on the set of cultivars being contrasted, and has been shown to be more cold hardy than 'M.9' in some experiments (Liu et al, 2021; Quamme and Brownlee, 1996). One possible explanation for the relatively poor performance of 'B.9' in this study is previous cold hardiness comparisons have all been conducted in winters conditions more similar to historically "cold" winters. Here we see that in mild winters, 'B.9' may not be stimulated sufficiently to achieve deep cold hardiness levels. Relatedly, this observation does concur with reports of winterkilled trees on 'B.9' and 'M.9' in the Champlain valley in 2004 due to a midwinter deep freeze, while hardier Geneva®-series rootstocks were more likely to survive (Robinson *et al.* 2006). In this experiment, 'B.9' performed the strongest in late winter and early spring, when it averaged 5.5 °F (3.1 °C) more cold hardy than the other rootstocks in the study- compared to being 4.6 °F (2.6 °C) less hardy on average in the midwinter months of January and February (Figure 3).

In contrast, 'G.222' and 'G.257' were two of the hardiest rootstocks in the experiment, more than 10°F (5.6 °C) more hardy on average than 'M.9' (Figure 2, Figure 3). This difference resulted from a much faster gain in cold hardiness during the early winter acclimation phase of the cold hardiness response, and maintenance of deep hardiness during midwinter. Even in the mild winter conditions of 2023-2024, both 'G.222' and 'G.257' had calculated winterkill temperatures below -30 °F (-34.4 °C) by mid-December. Both rootstocks maintain their high levels of cold hardiness through midwinter into early spring and appear to represent examples of rootstocks which perceive and respond to mild winter conditions as if they are cold. The season-to-season repeatability of this resilience to warm temperatures will be monitored for several more years to increase confidence in the observation.

This study did not focus on the cold hardiness dynamics that occur in scion cultivars, yet we included a brief comparison of five dessert apples in order to contextualize differences between rootstocks and scions during winter. While research into winter damage to apples in early spring is generally focused on damage to floral buds (Pfleiderer *et al.*, 2019), the susceptibility of rootstocks to warming temperatures during spring compared to scions is additional evidence towards the important role that rootstocks play in winter survival of orchards. Scion genotypes in this study were in general, less cold hardy than rootstock genotypes in midwinter. However, when examining the process of field deacclimation, the loss of cold hardiness as temperatures warm in mid-late winter, we observed large and significant differences in the deacclimation sensitivity of scions and rootstock genotypes. Specifically, all scion cultivars deacclimated at a much slower rate than do the rootstock genotypes (Figure 4). Functionally, these results suggest that the different portions of grafted apple trees (rootstock shank vs. scion) may simultaneously have different levels of cold hardiness and respond independently to warm temperatures during winter. As a result, acute cold events during winter may impact the different portions of the grafted apple, resulting in scion damage in some cases (e.g., midwinter acute cold) and rootstock shank in others (e.g., acute cold after false springs). Anecdotally, midwinter warm spells are a key factor in causing winter damage or winterkill in New York State (McNicholas and Forshey, 1982, Robinson *et al.*, 2006) and are frequently brought up as a cause of rapid apple decline (Singh *et al.*, 2019; Stokstad 2019). These results show that, given that rootstocks are quicker to deacclimate in mid-late winter than scions, rootstock selection and scion selection are both key to avoiding tree damage during winter, particularly as climate change results in more mild and chaotic winters in the Northeastern U.S.

Conclusions

As upstate New York winters become more erratic and warm spells in January and February set the stage for cold damage from extreme temperature swings, new orchard plantings should account for the increased risk of cold damage by selecting rootstocks that have improved upon 'M.9' in cold hardiness and winter resiliency. The overall strong cold hardiness of the Geneva®-series rootstocks throughout the winter demonstrates the improvements that decades of rootstock breeding efforts have realized. Every Geneva® rootstock tested in this experiment was more resilient and achieved stronger cold hardiness than 'M.9' in mild winters, though 'B.9', 'G.11', 'G.202', 'G.484', and 'G.969' were not significantly different. Given the poor relative performance of these rootstocks in mild winters, it is our opinion that these rootstocks represent riskier choices in the future as New York winters continue to warm yet remain chaotic. The most cold hardy rootstocks of the study were 'G.41', 'G.222', and 'G.257' and these genotypes outperformed 'M.9' in whole-winter cold hardiness and also retained deeper levels of cold hardiness under mild conditions. As shown in this study, cold hardiness in apple rootstocks is a dynamic process and we will continue monitoring performance of Geneva®-series rootstocks in the years to come.

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