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Research Paper

Effects of apple (*Malus* × *domestica*) rootstocks on scion performance and hormone concentration

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ABSTRACT

New apple rootstocks that are fire blight resistant are rapidly becoming available in recent years. Rootstock effect on vigor, yield, return bloom, branch angle, bud break, and hormone profile was assessed using 'Honeycrisp' as the scion cultivar. Three Budagovsky (B.9, B.10 and B.7-20-20), five Geneva (G.814, G.214, G.935, G.41 and G.11) and two Malling (M.9T337 and M.26) rootstocks were used for this trial. G.814 and G.214 were high productive rootstocks, more vigorous than M.9T337 that could be interesting for weak growing cultivars such as 'Honeycrisp'. B.9. B.10, G.41 and G.214 performed pretty similar to M.9T337, but they had slightly higher cumulative yields. High return bloom values were observed on G.935, M.9T337, and G.814, whereas B.72020 was the rootstock with the lowest values. In addition, B.72020 was the stock with more upright branches, while B.10 and G.11 had the flattest. On average, a few rootstocks had a low biennial bearing index, which included B.10 and G.814. Indole-3-acetic acid was the most abundant auxin in the xylem, being B.72020 and B.9 the stocks with higher content, while G.935 had the least. Regarding cytokinins (CK), the highest content was observed on G.11, and the lowest on G.814 and G.214. The highest ABA/CK ratio was observed on B.9, whereas B.72020 had the lowest value. On the other hand, B.72020 had the highest AUX/CK ratio value; and G.11 and G.935 the lowest. Fruit size was associated with high ABA/CK values. Trunk cross sectional area, branch angle, gas exchange variables, and biennial bearing were correlated with auxins and AUX/CK concentrations in xylem. Yield efficiency, crop load, leaf temperature, return bloom and bud break were correlated with ABA, CK, and ABA/CK in xylem. Since G.814, G.935 and G.11 had a very uniform bud break, these rootstocks could be suitable to test in areas where irregular bud break might be a problem. The high levels of endogenous ABA observed in Honeycrisp grafted on B.9 and G.11 suggests the possibility of these rootstocks tolerating drought stress by slowing evapotranspiration of the scion.

1. Introduction

Planting a new apple (*Malus* × *domestica* Borkh.) orchard nowadays encompasses a 15–25 year commitment. Cultivar and rootstock selection, and choice of training system are a few among other important key decisions that will affect an orchard's economic and environmental viability. Increasing light interception and improving its distribution through the canopy, planting with narrower spacing, increasing within row density, can boost quality and produce higher orchard yields (Lakso and Robinson, 2014; Palmer, 2011; Robinson, 2010; Tustin and van Hooijdonk, 2014). However, it has been shown that as planting density is increased there is a point where additional economic and productivity benefits decrease with each additional tree (Robinson, 2008; Robinson et al., 2007). The concept of high density orchards relies on high early yields are needed to pay back the initial intensive investment in trees and high density support infrastructure (posts, wire, irrigation, etc.). Tree vigor and its size and shape affect not only yield and precocity, but management costs (Giovannini and Liverani, 2005; Wertheim et al., 2001). Dwarfing apple rootstocks have made possible the transition of entire industries to higher tree density and training systems over the last 50 years. Although the transition has been mostly beneficial, there is a serious threat to high-density apple orchards, since many of them are planted on dwarfing rootstocks as M.9 and M.26 that are highly susceptible to the bacterial disease fire blight (*Erwinia amylovora* Burill), thus, limiting the establishment of new plantings in fire blight prone areas (Norelli et al., 2003; Russo et al., 2007). Climate change exemplified by the increase in average winter temperatures during the last decades, and insufficient chilling units accumulated in warm climates like Brazil, might hinder appropriate bud break on apple trees, compromising their productivity (Flaishman et al., 2010; Oukabli et al., 2003; Petri et al., 2012).

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Changing climate and increased disease pressure underscore an urgent need for new, highly productive apple rootstocks that are resistant biotic and abiotic stresses to fire blight and are adapted to the climatic stresses common in apple production areas of the world. A number of new apple rootstocks that are resistant to fire blight and other biotic stresses are rapidly becoming available. The Cornell University − USDA-ARS apple rootstock breeding program has developed rootstock genotypes which are resistant to fire blight and crown rot (*Phytophthora* spp.) (Cummins and Aldwinckle, 1983; Fazio et al., 2015). Moreover, the dwarfing rootstock B.9, from the Budagovsky breeding program, has recently been reported to have high degree of field resistance to fire blight (Russo et al., 2008a; Russo et al., 2008b). Dwarfing and semi-dwarfing fire blight resistant rootstocks from various breeding programs have been widely tested with 'Gala', 'Fuji', 'Golden Delicious' and 'McIntosh' cultivars through the NC-140 coordinated rootstock testing system (Autio et al., 2013; Autio et al., 2011; Marini et al., 2006a; Marini et al., 2014) resulting in the identification of several rootstocks amenable to widespread cultivation of those varieties. Still, the popularity of several weak-growing cultivars such as 'Honeycrisp' requires a re-evaluation of promising rootstocks when the scion cultivar is not vigorous (Robinson et al., 2011b).

Tree vigor and yield are the main variables assessed when testing rootstocks. However, other variables like branch angle, biennial bearing, and hormone profile may also play a role with the performance of these rootstocks (Fazio and Robinson, 2008; Hollender and Dardick, 2015; Lauri and Lespinasse, 2001; Tworkoski and Miller, 2007; Van Hooijdonk et al., 2011).

Plant hormones are organic substances that have the ability to affect physiological processes at concentrations far below those where either nutrients or vitamins would affect these processes (Davies, 2004). The role of hormones in regulating physiological processes and influence on biennial bearing has been widely described (Davies, 2004; Jackson, 2003; McLaughlin and Greene, 1991b; Ramírez et al., 2004). Bud break and dormancy release has been reported to be regulated by cytokinins (Saure, 1985; Young, 1989), and gibberellins (Lavender et al., 1973). Other hormones like auxins have been associated in controlling the vigor of the trees (Sorce et al., 2007; Sorce et al., 2006). Cytokinins are produced in the root meristems, where they travel all the way up the stem through the xylem (Davies, 2004). Auxins are primarily synthetized in leaf primordia (Davies, 2004), but Ljung et al. (2005) reported roots to contain multiple auxins sources as well. Phenotypic diversity for endogenous hormone production has been demonstrated (Tworkoski and Fazio, 2016; Tworkoski et al., 2016) hence, we may consider that different rootstocks will induce different hormone profiles to the scion, affecting its overall performance.

The collection and analysis of xylem exudates (Bangerth, 2008), has enabled the observation of hormone fluxes (Kamboj and Quinlan, 1997) and profiles on young apple trees grafted on Malling rootstocks (Tworkoski and Fazio, 2016; Tworkoski and Miller, 2007), suggesting that some physiological processes leading to dwarfing and productivity are slow and may require time for clear manifestation.

The aim of this study was to assess the performance of different rootstocks at a mature orchard production stage. Interaction among tree growth variables and how rootstocks may modify the vigor, yield, return bloom, branch angle, bud break, and hormone profile of the weak biennial bearing scion cultivar 'Honeycrisp' was examined.

2. Materials and methods

2.1. Trees and design

A rootstock trial was planted in 2010 at the New York State Agricultural Experiment Station (Geneva, NY, USA), using 'Honeycrisp' as the scion cultivar. 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 2 Malling: M.26 EMLA and M.9T337; 3 Budagovsky: B.7-20-20, B.10 and B.9; and 5 Cornell Geneva: G.11, G.41, G.935, G.214, and G.814.

2.2. Growth, yield and performance measurements

Tree survival, trunk circumference (30 cm above the graft union), number of suckers, yield and number of fruits were assessed every year. Trunk-cross-sectional area (TCA) and fruit size were then calculated. In 2016, crotch angle from the trunk (0° = flat, 90° = upright) was measured on 15 branches per tree and two trees per rep. Return bloom was measured in the spring of 2016 by dividing the number of flowering spurs per total number of spurs on 4 branches per tree and two trees per rep. 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. Percentage of bud-break on terminal buds was recorded every two days, with any bud showing 3 mm green tip considered broken (Belding and Young, 1989).

2.3. Physiological measurements

In 2016, carbon assimilation (A, μmol $CO2\ m^{-2}$ leaf area s^{-1}), transpiration (E, mmol H2O m^{-2}leaf area s^{-1}), and stomatal conductance (gs, mmol $m^{-2}\ s^{-1}$) were measured on two leaves on two trees per rep (16 leaves per treatment) on alternated days during two weeks (CIRAS-1 PP Systems, Haverhill, MA) (Tworkoski and Fazio, 2011). Average gas exchange values were calculated.

2.4. Hormone analysis

In 2016, xylem exudates were extracted at bloom, coinciding with the highest cytokinin concentration in xylem (Belding and Young, 1989), from two one-year-old branches from two trees per rep, using a similar methodology described by Sorce et al. (2007) and a pressure chamber (600 EXP Super Chamber, PMS Instrument Company, Albany, Oregon, USA). Samples from each replicate were pooled to produce an experimental unit and were stored at −80 °C until analyzed. The identification and quantification of the hormones were done by UPLC ESI–MS/MS (Lulsdorf et al., 2013; Zaharia et al., 2005) at the National Research Council Plant Biotechnology Institute (110 Gymnasium Place, Saskatoon, Saskatchewan, S7N0W9, Canada).

2.5. Data analysis

Response variables were modeled using linear mixed effect models. Mixed models including rootstock as fixed factor and block as a random factor were built to separate treatment effects for the TCA, fruit size, yield, yield efficiency, crop load, return bloom, branch angle, biennial bearing index, and hormone content. Yield was included as covariate to adjust fruit size. A mixed model including rootstock, day, and rootstock x day as fixed factors and tree nested to block and block as random factors was built to separate the treatment effects for bud break. For all the models, when the main effect (rootstock) was significant, pairwise comparisons between the rootstocks were made by LS means Student *t*-test. *P* values were corrected using the false discovery rate (FDR) to control for multiple comparisons (Benjamini and Hochberg, 1995). Adjusted *P* values ≤ 0.05 were considered significant. Residual analysis was performed to insure that model assumptions were met.

Multivariate projection methods (Principal Component Analysis, PCA) were applied to simultaneously analyze performance and physiological variables. For this purpose, we used the following variables: Cumulative TCA, yield (2015), fruit number (2015), cumulative yield and fruit number, fruit size (2015), average branch angle and biennial bearing index, return bloom (2016), yield efficiency (2015), crop load (2015), cumulative yield efficiency and crop load, carbon assimilation, transpiration and stomatal conductance. All the variables were analyzed in the same matrix.