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Return bloom on 'Golden Delicious' apple trees as affected by previous season's crop density on three rootstocks at 11 locations

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Abstract

'Golden Delicious' apple trees [*Malus* x *domestica* (Borkh.) Mansf] on three dwarfing rootstocks (M.9 NAKBT337, G.16 and M.26 EMLA) were grown at 11 locations and crop densities were adjusted to various crop densities, ranging from 3.0 to 14.0 fruit/cm^2 of trunk cross-section area, to determine if rootstock influenced the relationship between crop density and return bloom. Depending on the location, data were available for one to six years. In total there were 36 location-year combinations. Analysis of covariance was used to evaluate the separate and the interactive effects of previous season's crop density and rootstock on flower density expressed as flowers/cm^2 branch cross-sectional area. Flower density was negatively related to the previous season's crop density in a linear manner 43% of the time and rootstock significantly affected flower density 32% of the time. Since there was never an interaction between rootstock and previous season's crop density, the two factors affected flower density independently. Rootstock sometimes influenced flower density in seasons following both low and high crop densities, but the level of flower density was not consistently associated with any rootstock.

Biennial bearing is defined as an alternating cropping pattern, where a heavy crop one year inhibits blossom initiation and results in few blossoms the following year. Biennial bearing in apple has been extensively studied, but it is still not fully understood and remains a problem in commercial orchards (Monselise and Goldschmidt, 1982). Biennial bearing can be influenced by cultural practices, environmental conditions and genetics (Dennis, 2003). Rootstocks can alter gene expression patterns in apple scions (Jensen et al., 2003), so it is possible that rootstock may influence biennial bearing. Rootstock influenced biennial bearing in some citrus experiments (El-Zeftawi and Throton, 1975; Georgiou, 2002) but not in another experiment (Smith eta l., 2004). Barritt et al. (1997) combined data from two apple rootstock trials with three cultivars and found a positive or negative relationship between trunk cross-sectional area (TCA) and the biennial index (Hoblyn et al., 1936), depending on cultivar. The index can have values from 0 (no alternate bearing) to 1.0 (complete alternate bearing); where biennial bearing index (I) = (year 1 yield) – (year 2 yield)/year 1 yield + year 2 yield (Hoblyn et al., 1936). After reviewing the literature, Forshey and Elfving (1989) and Jonkers (1979) concluded that, in general, there is a negative relationship between vegetative and reproductive growth in apple. Because rootstock can influence vegetative vigor, it is possible that rootstock may also influence return bloom. The NC-140 apple physiology trial was initially established to study the relationship between crop density and fruit weight as affected by rootstock and growing regions (Marini et al., 2012). In some seasons, cooperators also collected

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data on bloom and this unique data set provided an unusual opportunity to evaluate the individual and the interrelated effects of previous season's crop density, rootstock and growing region on return bloom.

Materials and Methods

In spring 2003 a rootstock trial was established at 13 locations, but the data for bloom was reported for only 11 locations (Table 1). At each location, 10 'Gibson Golden Delicious' trees budded on G.16, M.26 EMLA and M.9 NAKBT337 rootstocks were planted in a completely randomized design. All trees were propagated by TRECO, Inc., Woodburn, OR. Trees were planted at a spacing of 2.5 m x 4.5 m and were trained to the Vertical Axis system. Trees were defruited in 2004 and some cooperators allowed trees to carry a light crop (<3.0 fruit/cm^2 trunk cross-sectional area, TCA) in 2005. In 2006, where trees cropped adequately, crop loads were adjusted by hand thinning to achieve five crop densities (CD, number of fruit/cm^2 of TCA). Two trees per rootstock were thinned to target CDs of 3, 5, 8, 11 and 14 fruit/cm^2. Trees were not treated with chemical thinners. Because fruit set could not be evaluated until completion of June-drop, the timing of hand-thinning varied with year and location, but was usually completed within 45 days after bloom. Data on initial fruit set, before thinning were not recorded. To obtain the desired CD, the number of fruit retained per cluster varied. For example, on heavy blooming trees an average of less than one fruit per cluster was retained to obtain a CD of 3.0 fruit/cm^2, whereas two fruit per cluster may have been retained on moderately blooming trees to obtain a CD of 11.0 fruit/cm^2. The year following crop load adjustment, the trees were thinned to CDs of <3.0 to ensure adequate return bloom to repeat crop adjustments the following year. For various reasons, crop adjustment was not possible at every location in 2006 and again in 2008 as planned. Therefore, in years when trees bloomed adequately to require thinning, the cooperators adjusted the CDs appropriately. Treatments were re-randomized each year.

Data collection and analyses. Each fall TCA and number of fruit harvested per tree were recorded and CD was calculated. In 2005 and 2006, all the blossom clusters on each tree were counted and flower density (FD, flower clusters/cm^2 TCA) was calculated. In subsequent years, two or three of the largest scaffold branches per tree were selected and FD was calculated as the number of flower clusters/cm^2 branch cross-sectional area (BCA). Because variances were not similar for all years and locations, and the range of the covariate was not similar for all years, data were analyzed by year and location. Each data set was subjected to an analysis of cova-

Table 1. Locations and cooperators participating in the 2003 NC-140 apple physiology trial.

Location	Cooperator	Planting location
(BC) British Columbia	Cheryl Hampson	Summerland, Canada
(CHIH) Chihuahua	Rafael Parra Quezada	Cuauhtémoc, Mexico
(IA) Iowa	Paul Domoto	Ames
(KY) Kentucky	Joseph Masabni, Dwight Wolfe	Princeton
(MA) Massachusetts	Wesley Autio	Belchertown
(ME) Maine	Renae Moran	Monmouth
(NJ) New Jersey	Winfred Cowgill, Jr., Daniel Ward	Pittstown
(NY) New York	Terence Robinson	Geneva
(ONT) Ontario	John Cline	Simcoe, Canada
(PA) Pennsylvania	Robert Crassweller	Rock Springs
(UT) Utah	Brent Black	Kaysville

riance (ANCOVA), using SAS's Mixed procedure (Littell et al., 2006), where FD was the response variable, the previous season's CD (CD_{ps}) was the covariate, and rootstock was the indicator (class) variable. The model selection criteria suggested by Milliken and Johnson (2002) and Littell et al. (2006) were used to identify the appropriate model for each data set. Details for the ANCOVA were explained in detail by Marini and Ward (2012). Because the rootstock x CD_{ps} interaction was never significant, data were analyzed with a normal ANCOVA when the covariate (CD_{ps}) was significant. Data were analyzed with ANOVA when the covariate was not significant.

Results

For most data sets, the covariate, CD_{ps}, was not significant, so LSmeans were estimated with ANOVA. When the covariate was significant, the slopes were generally between -1.0 and -3.0, meaning that for each fruit/cm^2 TCA, there were 1.0 to 3.0 fewer flower clusters per cm^2 BCA the following year. Table 2 shows data for New Jersey and Pennsylvania, where return bloom was never influenced by rootstock or CD_{ps}. New Jersey had relatively low FD for the two years when data were reported, whereas Pennsylvania reported relatively high FD for three consecutive years.

Table 3 shows data for four locations where FD was affected by rootstock or CD_{ps}, for at least one season, but never both in the same season. In Kentucky, an alternate bearing pattern was apparent with high FD in 2006, 2008 and 2010 (Table 3), following years of low CD in 2005, 2007 and 2009. FD was negatively related to the CD_{ps} in the "off years" of 2007 and 2009 when FD was relatively low. In 2007, FD was greater for trees

Table 2. Flower density (FD, flower clusters/cm^2 branch cross-sectional area) of 'Golden Delicious' apple trees on three rootstocks in Pennsylvania and New Jersey, as affected by the previous season's crop density (CD_{ps}). Flower density was not significantly affected by rootstock or CD_{ps}.

Rootstock	2006	2007	2008
		New Jersey	
		CD_{ps} [z]	
	0.0	1.8 - 11.5	
		FD [x]	
G.16	7.6	1.0	- - -
M.26 EMLA	8.5	0.6	- - -
M.9 NAKBT337	4.9	0.9	- - -
		P-values from ANCOVA	
Rootstock	0.470	0.337	- - -
CD_{ps}	0.522	0.819	- - -
		Pennsylvania	
		CD_{ps}	
	0.0	1.3 - 12.5	4.3 - 8.1[z]
		FD	
G.16	28.1	13.3	19.1
M.26 EMLA	27.8	13.0	19.3
M.9NAKBT337	32.7	15.7	19.6
		P-values from ANCOVA	
Rootstock	0.181	0.259	0.606
CD_{ps}	0.094	0.280	0.064

[z] Previous season crop density (minimum - maximum).

[x] Least-squares means within location and year not significant, by ANOVA.

Table 3. Flower density (flower clusters/cm[2] branch cross-section area) of 'Golden Delicious' apple trees on three rootstocks in five locations as affected by the previous season's crop density (CD_{ps}). Flower density was significantly affected by rootstock or CD_{ps} in at least one season at these locations.

Rootstock	2006	2007	2008	2009	2010
			Kentucky		
			CD_{ps} [z]		
	0.0[y]	1.2 – 12.4	0.0	3.2 – 14.5	0.3 – 3.6
			FD		
G.16	42.7	4.8 a [x]	12.8	0.9	23.0
M.26 EMLA	31.3	2.3 ab	13.5	0.4	24.7
M.9NAKBT337	42.7	2.2 b	12.7	0.4	29.0
			P-value from ANCOVA [y]		
Rootstock	0.091	0.064	0.830	0.120	0.078
CD_{ps}	0.264	0.002	0.338	0.002	0.648
			New York		
			CD_{ps}		
	0.0	2.3 – 9.2	5.5 – 7.6	3.1 – 15.9	1.0 – 11.7
			FD		
G.16	1.2	- - -	10.9	10.8	- - -
M.26 EMLA	1.8	- - -	10.9	13.7	- - -
M.9NAKBT337	2.0	- - -	10.5	12.9	- - -
			P-value from ANCOVA		
Rootstock	0.148	- - -	0.886	0.477	- - -
CD_{ps}	0.721	- - -	0.528	0.005	- - -
			Ontario		
			CD_{ps}		
	0.0	1.7 – 8.8	0.1 – 4.2	1.1 – 5.2	1.3 – 4.5
			FD		
G.16	- - -	1.1	1.1 ab	4.8	- - -
M.26 EMLA	- - -	1.2	1.3 a	4.8	- - -
M.9NAKBT337	- - -	1.0	0.9 b	5.5	- - -
			P-value from ANCOVA		
Rootstock	- - -	0.380	0.042	0.713	- - -
CD_{ps}	- - -	0.920	0.682	0.016	- - -
			Utah		
			CD_{sp}		
	0.0	1.3 – 12.0			
			FD		
G.16	7.8 ab	- - -	- - -	- - -	- - -
M.26 EMLA	6.7 b	- - -	- - -	- - -	- - -
M.9NAKBT337	9.3 a	- - -	- - -	- - -	- - -
			P-value from ANCOVA		
Rootstock	0.050	- - -	- - -	- - -	- - -
CD_{ps}	0.752	- - -	- - -	- - -	- - -

[z] Previous season crop density (minimum - maximum).
[y] Least-squares means within locations and years not followed by a common letter differ at the 5% level of significance, by diff.
[x] When the P-value for CD_{ps} from the previous season, used as a covariate, was ≥ 0.05 an ANOVA was performed to generate the LSmeans. When the P-value was ≤ 0.05, an ANCOVA was performed to estimate means at the average value of the covariate.

on G.16 than trees on M.9 NAKBT337 (P = 0.064). New York had high FD in 2008 and 2009, but in all years FD was not influenced by rootstock and it was negatively related to CD_{ps} in only 2009. In Ontario, FD was fairly low in all three years when data were reported (Table 3). FD in 2009 was related CD_{ps} and FD was affected by rootstock in 2008 when trees on M.26 EMLA had the highest FD and trees on M.9 NAKBT337 had the lowest FD. Utah reported data for only one season, and trees on M.9 NAKBT337 had the highest FD and trees on M.26 EMLA had the lowest FD.

Table 4 shows data from the five locations where FD was affected by both rootstock and CD_{ps} for at least one season. In British Columbia, data were available for four consecutive seasons: FD was moderate in 2007, and FD was low the other three years (Table 4). Both rootstock and CD_{ps} were significant all four years, and trees on M.26 EMLA consistently had the highest FD. In Chihuahua, FD was linearly related to the CD_{ps} in 2008 and after adjusting for CD_{ps}, FD was higher for trees on M.26 EMLA and G.16 than for trees on M.9 NAKBT337. Massachusetts had high FD in 2005 and 2009 (Table 4). Both rootstock and CD_{ps} influenced FD in 2008 when FD was highest for trees on M.9 NAKBT337. Trees in Iowa had FD > 6.8 for five consecutive years. FD was affected by rootstock in three of five years, and FD was linearly related to the CD_{ps} in 2007 and 2008. FD was significantly higher for trees on G.16 than for trees on M.26 EMLA in all three years. In Maine, FD was high in 2006, 2007, and 2009 (Table 4). FD was related to the CD_{ps} in only 2008, but FD was significantly affected by rootstock in all four years. Trees on M26 EMLA had the lowest FD in three of the four years.

Discussion

Data were available for 37 location-year combinations in this study and rootstock and/or CD_{ps} were significant 28 times or 76% of the time. FD was significantly affected by rootstock 16 times or 43% of the time. Both rootstock and CD_{ps} were significant only 12 times or 32% of the time. The interaction of CD_{ps} and rootstock was never significant, so the relationship between FD and CD_{ps} did not depend on the rootstock and the effect of rootstock on FD was independent of CD_{ps}.

The effect of rootstock on return bloom seemed to depend on location. Of the 16 cases where rootstock affected return bloom, G.16 had the highest FD 5 times, and three of those cases occurred in Iowa. Trees on M.26 EMLA had the highest FD 6 times and 4 of those cases occurred in British Columbia. Trees on M.9 NAKBT337 had the highest FD 5 times and 3 of those cases occurred in Maine. Rootstock did not significantly affect bloom in New Jersey, Pennsylvania, New York, or Chihuahua. Therefore, the effect of rootstock on return bloom may be highly dependent on location.

The influence of rootstock on biennial bearing in apple has not been well studied, probably because crop loads are managed to avoid biennial bearing in most rootstock trials. In a rootstock trial where trees were thinned to encourage annual cropping, Ferree et al. (1995) calculated the biennial bearing index for three apple cultivars on 22 dwarfing rootstocks and they reported that some of the rootstocks with relatively high biennality included CG.10, M.9 and M.9EMLA and rootstocks with low bienniality included P.2, P.22 and Mark. Barritt et al. (1997) used data from experiments involving three cultivars with varying growth habits and 40 rootstocks with a very wide range of vigor to evaluate the relationship between TCA and biennial bearing index. For ‘Golden Delicious’ and ‘Granny Smith’ there was a positive linear relationship and the slope was most steep for ‘Golden Delicious’, meaning that biennial bearing was most severe for trees on vigorous rootstocks. However, there was a negative relationship for the weak-growing cultivar ‘Redchief Delicious’. Since there is a balance between vegetative and reproductive growth, it appears that rootstock vigor may influence biennial bearing by altering the balance of the two types of growth. Our data support those of Costes and Garcia-Villanueva (2007), who grew two apple cultivars with different growth habits on own their own roots or grafted onto M.9 Pajam2 rootstock. They found that grafted trees had fewer shoots, a higher percentage of long shoots, more flowers, and a higher return bloom.

Table 4. Flower density (flower clusters/cm^2 branch cross-sectional area) of 'Golden Delicious' apple trees on three rootstocks in four locations as affected by the previous season's crop density (CD_{ps}) for six years. Flower density was affected by both rootstock and CD_{ps} for at least one season at these locations.

Rootstock	2005	2006	2007	2008	2009	2010
			British Columbia			
			CD_{ps} [z]			
	0.0	0.0	1.5 – 14.0	0.1 – 4.5	1.7 – 10.1	0.1 – 5.3
			FD			
G.16	- - -	- - -	5.8 b [y]	3.2 b	3.7 b	2.9 ab
M.26 EMLA	- - -	- - -	7.8 a	4.9 a	7.9 a	3.5 a
M.9NAKBT337	- - -	- - -	6.4 b	3.6 ab	5.3 b	2.4 b
			P-value from ANCOVA [x]			
Rootstock	- - -	- - -	0.001	0.001	0.001	0.001
CD_{ps}	- - -	- - -	0.001	0.008	0.032	0.032
			Chihuahua			
			CD_{ps}			
	0.0	0.0	1.4 – 13.4	0.1 – 1.1	0.6 – 3.1	1.4 – 7.8
			FD			
G.16	- - -	- - -	8.2	7.1 a	5.2	9.7
M.26 EMLA	- - -	- - -	9.6	7.6 a	3.6	12.1
M.9NAKBT337	- - -	- - -	6.3	1.9 b	1.0	3.0
			P-value from ANCOVA			
Rootstock	- - -	- - -	0.181	0.003	0.098	0.151
CD_{ps}	- - -	- - -	0.320	0.036	0.241	0.130
			Massachusetts			
			CD_{ps}			
	0.0	0.0	0.5 – 5.0	2.6 – 14.6	0.1 – 3.5	4.6 – 21.9
			FD			
G.16	27.3	- - -	- - -	4.3 b	14.3	0.3
M.26 EMLA	33.6	- - -	- - -	3.7 b	14.6	0.1
M.9NAKBT337	34.1	- - -	- - -	9.7 a	12.7	1.2
			P-value from ANCOVA			
Rootstock	0.103	- - -	- - -	0.006	0.195	0.362
CD_{ps}	0.261	- - -	- - -	0.001	0.511	0.459
			Iowa			
			CD_{ps}			
	0.0	0.0	1.0 – 12.6	0.1 – 3.1	1.6 – 4.4	0.4 – 4.5
			FD			
G.16	- - -	32.0 a	17.8 a	24.5 a	11.1	17.3
M.26 EMLA	- - -	13.9 c	7.0 b	15.2 b	6.9	16.7
M.9NAKBT337	- - -	23.2 b	7.9 b	23.6 a	9.3	18.3
			P-value from ANCOVA			
Rootstock	- - -	0.001	0.001	0.001	0.060	0.566
CD_{ps}	- - -	0.441	0.001	0.015	0.550	0.789
			Maine			
		CD_{ps}				
0.0	0.0	0.0	0.9 – 11.7	0.0	0.1 – 12.8	
	FD				G.16	- - -
29.4 a	21.9 a	5.1 b	16.8 b	- - -	M.26 EMLA	- - -
17.1 b	17.5 b	3.0 c	17.9 ab	- - -	M.9NAKBT337	- - -
24.8 a	23.4 a	7.6 a	20.7 a	- - -		
			P-value from ANCOVA			
Rootstock	- - -	0.002	0.020	0.001	0.043	- - -
CD_{ps}	- - -	0.247	0.517	0.009	0.116	- - -

[z] Previous season crop density (minimum - maximum).
[y] Lsmeans within locations and years followed by a common letter do not differ at the 5% level of significance, by diff.
[x] When the P-value for CD_{ps} from the previous season, used as a covariate, was ≥ 0.05 an ANOVA was performed to generate the LSmeans. When the P-value was ≤ 0.05, an ANCOVA was performed to estimate means at the average value of the covariate.

Although data from previous rootstock trials were used to evaluate the influence of apple rootstock on return bloom (Ferree et al., 1995; Barritt et al., 1997), we believe that the current experiment is the first that was designed specifically to study the relationship between cropping and various aspects of tree physiology as affected by dwarfing rootstocks. Data from the current study, where trees were thinned to a range of CDs, provide the first indication that rootstocks with similar vigor control may affect return bloom differently after adjusting for CD_{ps}. It is well known that return bloom tends to be poor the year following a heavy crop, however, our data show that return bloom was sometimes influenced by rootstock following years of heavy as well as light crop loads, indicating that the effect of rootstock on flower bud initiation may not be entirely related to the previous season crop load.

Guitton et al. (2012) studied biennial bearing in a segregating apple progeny resulting from a cross of 'Starkrimson Delicious' and 'Granny Smith' that were grafted onto M.9 Pajam 1 rootstock. They found a moderate negative relationship between flowering in a given year and the number of fruit harvested the previous season (r = -0.18 to -0.54) and they hypothesized that biennial bearing is controlled by flowering genes regulated by hormones. They also stated that flower genes are less likely to be responsible for biennial bearing than hormone-related genes. Jensen et al. (2003) found that trees grafted on M.9 rootstock had increased expression of an APETALA2-like gene which is involved in flowering in *Arabidopsis* (Weigel, 1995). Therefore, it is likely that rootstock can influence flowering of the scion independent of previous season CD.

Several undesirable factors inherent in multi-location multi-year studies may have inadvertently affected our data. (1) Obtaining the desired CDs was difficult due to the inability of cooperators to see young fruit on the trees while hand-thinning; (2) For various reasons, the timing of hand-thinning was not uniform for all locations or all years. Since early thinning is more beneficial than late thinning for return bloom (Jonkers, 1979; Monselise and Goldschmidt, 1982), it is likely that our data were affected by time of thinning. (3) The number of fruit retained per flower cluster was not uniform for all treatments and may have affected return bloom. Davis (2002) thinned limbs to varying numbers of fruit per spur and reported that the percentage of spurs that bloomed the following year was about 80, 66 and <10%, respectively for spurs thinned to 0, 1 and 2 fruit per spur. (4) FD calculated on the basis of branch cross-sectional area may not always provide accurate estimates of the entire tree (Marini, 2004) because flowering and fruit set on individual limbs is sometimes quite variable. However, counting all the flower clusters on entire trees is not reasonable for 8-yr-old trees, and limb estimates are commonly reported (Byers and Carbaugh, 1991; Greene and Autio, 1994; Williams, 1993).

The fact that rootstock and previous season's CD influenced return bloom about 35% and 26% of the time, respectively suggests that the influence of rootstock on return bloom is at least partly independent of previous season's crop and other factors likely influence flower bud initiation.

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