Natural fruitlet abscission as related to apple tree carbon balance estimated with the MaluSim model

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Abstract

Apple trees produce many more flower clusters than needed for a full crop, but natural early season flower and fruitlet abscission drastically reduce the final fruit number. Natural fruit abscission varies significantly year to year. There have been attempts to try to model apple fruit abscission in the past. However, due to the great complexity of a perennial crop system in a dynamic environment with significant plant manipulations, regulatory processes and controlling environmental variables have been difficult to elucidate. In 1995, a field trial was planted at the New York State Agricultural Experiment Station in Geneva, New York with 3 apple cultivars (‘Delicious’, ‘Gala’, and ‘McIntosh’). Beginning in 2000 and for 18 years thereafter, we recorded the natural whole-season fruit abscission of untreated trees that received no chemical or hand thinning. We also estimated early season patterns of carbohydrate supply-to-demand each year with a carbon balance model. These data were used to correlate tree carbon balance status and other environmental variables with natural fruit abscission responses. In general terms, natural set, defined as final fruit/flower cluster, of ‘Gala’ averaged ~1 fruit for each flower cluster (fruit set = 0.9), whereas fewer fruits were set on ‘Delicious’ and ‘McIntosh’ (fruit set = 0.7 and 0.6, respectively). Fruit set of ‘Gala’ was less variable than of ‘Delicious’ or ‘McIntosh’, and there was a clear pattern for decreasing fruit set when the number of initial flower clusters per tree increased. Fruit weight was less dependent on fruit number for ‘Delicious’ and ‘McIntosh’ than for ‘Gala’. Multiple regression models indicated that number of flower clusters per tree and average carbohydrate balance between 0-60 degree days (DD) after bloom and 300-360 DD after bloom were the main significant variables that explained 60-80% of the variability in natural fruit set or final fruit number. For ‘Delicious’, temperatures of the previous fall also explained a significant amount of variation in final fruit set and final fruit number. For ‘Gala’, carbon balance from bloom to shortly after petal fall and when fruits were about 18 mm were the two main periods, which were more sensible to carbohydrate deficiency triggering fruit abscission. A later susceptible period was also observed for ‘McIntosh’, suggesting a larger thinning window for this cultivar.

Introduction

Apple trees produce many more flower clusters than needed for a full crop but natural early season flower and fruitlet abscission drastically reduce the final fruit number. In addition, hand and chemical flower or fruit thinning reduce fruit numbers even more to achieve commercial fruit size and quality. However, fruit thinning is the single most important, yet difficult management strategy that determines the annual profitability of apple orchards (Dennis, 2000; Greene and Costa, 2012; Robinson et al., 2013). If thinning is inadequate and too many fruits remain on the tree, fruit size will be small, fruit quality will be poor and flower bud initiation for the following year's crop may be either reduced or eliminated.

Natural fruit abscission varies significantly year to year. There have been attempts to try to model apple fruit abscission and thinning in the past. Rogoyski et al. (1989) and Crassweller et al. (1992) simplified the continuous biological process of fruit set and abscission after flowering in the form of a sum of intervals of tree and environmental factors with some variable weighting to qualitatively simulate apple fruit abscission throughout the growing season. However, the models were quite site-specific since they were not based on tree physiology, and were not widely adopted. Years of field trials of post-bloom apple thinning have provided general guidelines for growers (Dennis, 2000; Fallahi and Greene, 2010; Greene, 2002; Greene and Lakso, 2013; Robinson and Lakso, 2011; Williams, 1979). But empirical trials have not been able to elucidate regulatory processes and adequately control apple thinning. This is due to the great complexity of a perennial crop system in a dynamic environment with significant plant manipulation. There are probably dozens of interacting factors that are difficult to integrate.

Conditions that favor good carbohydrate status are associated with less natural fruit abscission and more difficult chemical thinning response (Robinson and Lakso, 2011). These conditions are cool temperatures, sunny days, light initial fruit set on a moderate number of spurs on healthy trees with good leaf area. The opposite conditions are associated with greater natural fruit abscission. Therefore, the carbohydrate balance plays a significant role in apple tree response to fruit abscission when the carbohydrate supply is the limiting factor for fruit growth. However, if the carbohydrate supply is abundant, then other factors may ultimately limit fruit development and abscission.

In relation to crop development, the carbohydrate supply: demand balance depends on both the carbohydrate supply available to the fruit as well as crop demand, determined by the number of fruit and stage of development (affecting growth and respiration). Although many factors affect the carbohydrate supply: demand balance, this is a process that is relatively well understood quantitatively and can be modeled (Le Roux et al., 2001).

Thus, we have developed a model of apple tree carbohydrate supply and demand balance, named MaluSim, that can integrate many of the environment and tree factors that are known to affect thinning response (Lakso and Johnson, 1990; Lakso et al., 2001). The model was developed to: (1) integrate instantaneous measurement data to obtain estimates of seasonal integrals of fixed carbon and respiratory costs, and resultant dry matter production (2) elucidate seasonal patterns of tree and fruit growth and carbon exchange among parts of the plant, (3) evaluate the effects of environmental changes and cultural practices, and (4) determine if there are periods of likely carbon deficits or surpluses that may affect orchard performance.

For the purpose of determining if carbon balance relates to natural fruit abscission, we focused on comparing the simulated early season patterns of carbohydrate supply-to-demand to the observed experimental fruit abscission responses of untreated control trees that had no hand or chemical fruit thinning. The annual variation carbon balance due to the environment was emphasized by simulating the carbon balance of a “standard” slender spindle tree, with constant tree parameters, but varying the weather inputs each year. The correlation of carbon balance and fruit abscission have been noted in various studies (Lakso et al., 2006; Robinson and Lakso, 2011), but have not been subject to detailed statistical analysis of correlation and optimal timing between carbon deficits or excesses and natural fruit abscission responses.

The goal of this project was to determine if the MaluSim physiological model that integrates key environmental data to estimate carbon supply: demand balance may explain year-to-year variation in natural drop of apples. If so, it may help explain the observed correlations of carbon balance to response to chemical thinners. An online application of the MaluSim model (http://newa.nrcc.cornell.edu/newaTools/apple_thin) is currently used by growers to help make appropriate real-time adjustments in treatments for more consistent thinning.

Materials and methods

Trial site, design, and agronomic assessments

In 1995, a field trial was planted at the New York State Agricultural Experiment Station in Geneva, New York (lat. 42.5°N, long. 77.2°W), with 3 apple (*Malus* × *domestica* Borkh.) cultivars (‘Ace Delicious’, ‘Royal Gala’, and ‘Marshall McIntosh’) trained to a vertical axis system. ‘Delicious’ trees were grafted on M.26 EMLA rootstocks, whereas ‘Gala’ and ‘McIntosh’ trees were grafted on M.9T337 rootstocks. The site previously had been planted with vegetables and the soil was a sandy clay loam with good water holding capacity, well drained and fertile with about 3% organic matter content. The plot was not irrigated.

The experimental plot had 252 trees of each cultivar planted in 4 rows of each cultivar with 63 trees of a single cultivar in each row. Trees were spaced 2.1 m × 4.2 m. The 252 trees were divided into 5 sections of row (blocks) of 50 trees each. Each year starting in 2000 (when trees were in their 6th leaf) and continuing for the next 18 years (2017), 1 tree from each block which had high flower bud load was selected for this study. Since selected trees were not thinned (either by chemical, mechanical or by hand) the trees were almost always over cropped which resulted in low bloom density the following year, thus different trees in each rep (block) were selected each year of the study. All treatment trees were bounded by guard trees on either side, and although other trees in the orchard were sprayed with chemical thinners, the selected trees were protected from chemical drift by the use of a tunnel sprayer which limited chemical drift.

The trees were trained and pruned in the vertical axis system which included a permanent bottom tier of branches and temporary upper branches. Annually we removed 1-3 of the largest branches on the tree at their point of origin leaving a stub with a beveled cut to promote the regrowth of a replacement branch. Since the orchard was sprayed with a tunnel sprayer, the trees were pruned to the same physical dimensions each year (3.8 m tall and 2.8 m diameter). The number of spurs on each tree after pruning each year was not measured but in the pruning process we pruned to approximately the same number of branches and spurs each year (~1000 spurs).

Each year (2000-2017) at pink bud stage, two branches on opposite sides of each test tree, one lower tier scaffold and one upper tier scaffold, were selected and the number of flower clusters per branch was recorded. At harvest, the number of fruits on each branch was recorded. Fruit set was defined and calculated as the ratio of fruits harvested on both branches to the number of flower clusters on both branches. Total fruit number per tree and yield (kg) were also recorded at harvest for every tree. Fruit weight (g) was then calculated. Initial flower cluster number per tree was estimated from the final fruit number and the percent fruit set calculated from the tagged branches. Flower buds were significantly damaged by a spring frost in 2012, thus, no data was recorded that year.

Daily maximum and minimum temperatures and total daily solar radiation were recorded at a reference weather station within 1 km of the experimental orchard. Radiation data was measured by an Eppley pyranometer. This weather data was inputted into a simplified daily growth, photosynthesis and respiration apple tree model (MaluSim) (Lakso and Johnson, 1990; Lakso et al., 2001) to calculate carbon balance on a “standard” tree that had constant tree parameters representing slender spindle ‘Empire’/M9 trees at 1280 trees/ha. Thus, the yearly variations were due only to the varying weather inputs. To run the model, weather data until bloom was standardized, using for all the years the same number of days from bud break to full bloom.

Days from January 1st to bud break, from bud break to bloom, and from bloom to petal fall were recorded each year and cumulative growing degree days (DD) were calculated using the Baskerville and Emin (1969) formula from January 1st to bud break and from bud break to bloom and after bloom using 4 °C as the base temperature (Johnson and Lakso, 1986; Lakso, 1984; Lakso et al., 2001). Bud break, bloom, and petal fall were assessed according to Fleckinger (1964) with visual assessments every three days. Bud break and full bloom were similar for the 3 cultivars. Bud break was defined as green tip for spurs and full bloom was defined as 80% of the flowers open on the north side of the tree. DD from September to December the previous season and from November-December of the previous season were also calculated as related preliminary studies found that the previous Fall temperatures had some effects on spring phenology and natural drop.

MaluSim model description

A simple daily time step apple dry matter production model was initially developed (Lakso and Johnson, 1990) using an estimated leaf area development using the concept of a “big leaf” canopy light response curve from Charles-Edwards (1982), minus simulated respiration of fruits, leaf area, and woody structure. Over the years the model has been gradually extended, improved and partially validated. A carbon partitioning sub model was added (Lakso et al., 2001) based on summing organ carbon demands, comparing to supply, and partitioning via competitiveness coefficients if the carbon supply was deficient. From the estimated carbon balance available to support fruit growth, a fruit growth and abscission sub model was developed. For this study the model calculated a daily carbon supply to total demand (crop and vegetative) balance as a general index of tree carbon balance.

Data analysis

Scatter plots were generated to identify relationships between natural fruit set, and weather and carbon balance variables. Linear, quadratic, and cubic terms for days and DD after bloom, DD from September to December the previous season, November-December the previous season, DD from January 1st to bud break, DD from bud break to bloom, average running and cumulative carbon net balance for different periods of days, and flower cluster number per tree were considered regressor variables in a multiple regression model to explain variability observed in fruit set and final fruit number per tree.

The multiple regression model was run iteratively with the most complex interaction term with the highest *P* value deleted from the model and the model was run again. This manual backward elimination continued until only significant ($P = 0.05$) terms remained in the model (Milliken and Johnson, 2001). Fruit set and fruit number data for all years were pooled together for the analysis. Data were analyzed using the JMP statistical software package (Version 12; SAS Institute Inc., Cary, North Carolina) and Infostat 2006p.2 software (UNCO, Córdoba, Argentina).

Results

Phenology, fruit set, bloom density, and fruit weight

Over the 18 years of the study, bud break at Geneva, New York State was on April 11th on average, and in years 2016, 2017, and in 2010, bud break was in late March, being the earliest recorded date March 21, 2016 (Table 1). The latest recorded date for bud break was on April 19, 2007. On average, bloom occurred the second week of May, the earliest date was on April 30, 2010, whereas the latest one was on May 20, 2014. Bloom lasted 9 days on average; the shortest period was 5 days in 2013, whereas the longest was 13 days in 2011.

Cumulative degree-days base 4°C (DD) from the previous September 1st through December 31st were fairly consistent over the years with 704 DD on average (Table 1). The lowest total was 618 DD in 2010, whereas the highest total was 818 DD in 2016. More variability was observed when degree-days were accumulated from November 1st through December 31st. For that period, the average was 93 DD, with the lowest total of 39 DD in 2008, and the highest total of 192 DD in 2002. No data was available for 2000 and 2001.

DD totals from January 1st to bud break averaged 90 DD (Table 1). The lowest total was 61 in 2015, whereas in 2000 there was a much higher total of 133 DD. From bud break to full bloom there were on average 209 DD, with the lowest total of 140 DD in 2001, and the highest total of 284 DD in 2014. The highest total of degree-days from bloom to petal fall, 156 DD, was in 2011, coinciding with the longest bloom length of 13 days. On the other hand, the lowest total was 52 DD in 2013, coinciding with the shortest bloom length (5 days). The highest cumulative degree-days from bloom to 21 days after petal fall (PF) was 487 DD in 2011, whereas the lowest value was 268 DD in 2002. The average total of cumulative degree-days from bloom to up to 41 days after PF was 509 DD, the highest total was 590 DD in 2011, whereas the lowest total was 414 DD in 2002.

For all the three cultivars, there was a trend where fruit set decreased with increasing number of flower clusters per tree (Figure 1 and Table 2). ‘McIntosh’ reached the highest number of flower clusters per tree (~1400 in 2011), followed by ‘Gala’ (~1100 in 2006), and then ‘Delicious’ (~1000 in 2008). Overall, ‘Gala’ had the highest average number of flower clusters per tree (776), followed by ‘McIntosh’ (648), and then ‘Delicious’ with the lowest value (503). Fruit number per tree was very similar among years for ‘Gala’ (Figure 1 and Table 2). In this figure, fruit number is represented by the size of the bubble. Greater differences in fruit number were observed for ‘Delicious’ and ‘McIntosh’ between years.

For ‘Delicious’, fruit set was ~0.4-0.6 when flower clusters per tree were greater than 800 (Figure 1 and Table 2). When flower cluster number per tree was lower (200-500), fruit set varied from 0.2-1.3. The average fruit set value for all years was 0.7.

For ‘McIntosh’, fruit set decreased from 0.6 when flower clusters per tree were 800, to 0.2 when flower clusters per tree were 1400 (Figure 1 and Table 2). Fruit set varied from 0.3-1.3 when the number of flower clusters per tree was 300-600. The average fruit set value for all years was 0.6.

Conversely to what happened with ‘Delicious’ and ‘McIntosh’, for ‘Gala’ there was less variability of fruit set when the number of flower clusters per tree was lower, but variability increased when the number of flower clusters per tree increased (Figure 1 and Table 2). The highest fruit set value was 1.7 for ~400 flower clusters per tree, and decreased down to ~0.6 when the number of flower clusters per tree was ~1000. The average fruit set value for all years was 0.9.

Fruit weight for all cultivars over a span of years was related to fruit number per tree as a negative linear relationship (Figure 2). The correlation of fruit weight and fruit number had greater R^2 values for ‘Gala’ (0.43), followed by ‘McIntosh’ (0.36), and then ‘Delicious’ (0.30).

On average, fruit weight for ‘Delicious’ was 185 g, 124 g for ‘Gala’, and 148 g for ‘McIntosh’ (Figure 2 and Table 2). For ‘Delicious’, fruit weight declined by about 17 grams for every additional 100 fruit (Figure 2). For ‘Gala’, fruit weight decline was 10 g/100 fruit, and was 11 g/100 fruit for ‘McIntosh’ (Figure 2).

Net carbon balance with different number of fruits

To determine the optimum fruit number to use with the carbon balance model when predicting fruit set we compared the output of the model using fruit numbers ranging from 300 to 800 fruits per tree. The number of fruits per tree had little effect on carbon balance at bloom and petal fall, but there was a large effect on the daily net carbon balance after 300 DD from bloom, which is approximately fruit diameter of 12-15 mm (Figure 3). This effect was apparent in all years, with a similar pattern for different crop loads (from 300 to 800 fruit/tree), with the higher the number of fruit per tree increasing demand, the more negative the carbon balance during this period. For some years, differences in carbon balance among different number of fruits became apparent as early as 200 DD from bloom, whereas in other years like 2013, differences started after 400 DD. The largest deficit (-250 g) was in 2013 for 800 fruits at ~550 DD. The best predictive response of the model output for fruit set was with 600 fruits per tree.

Modeling fruit set and fruit number

A multiple regression model using 600 fruits per tree was built to predict fruit set for 'Delicious' (Figure 4). The final model had relatively high R^2 values (0.55) and the significant regressor variables included number of flower clusters per tree, degree-days from bud break to bloom, and the average daily carbohydrate balance from bloom to 60 DD, from 60 DD to 120 DD, and from 240 DD to 300 DD. The prediction profiler interactively explains how each factor impacts the response as well as the other factors in the model. There was a negative linear correlation for fruit set and the initial number of flower clusters per tree. On the other hand, cumulative degree-days from bud break to bloom had a positive linear correlation with fruit set. The average daily carbohydrate balance was highly significant in predicting fruit set; with a positive relation between 0-60 DD and 240-300 DD after bloom and a negative relation between 60-120 DD after bloom.

The regression model to predict final fruit number had greater R^2 values (0.86) than the model to predict fruit set (Figure 5). When predicting final fruit number, the significant regressor variables included number of flower clusters per tree, cumulative degree-days of the previous fall from November 1st through December 31st, and average daily carbohydrate balance for different DD periods after bloom: 180 to 240, 240 to 300, 300 to 360, 360 to 420, 420 to 480, and 540 to 600. When looking at the prediction profiler, fruit number per tree was positively related to the initial number of flower cluster per tree up to 600 clusters, then it leveled off. Cumulative degree-days from November through December were highly negatively correlated, whereas the carbohydrate balance was positively or negatively correlated depending on the period.

For 'Gala', the model to predict fruit set had higher R^2 values than the model to predict fruit number (0.79 *vs* 0.60) (Figure 6 & Figure 7). For the fruit set model, the significant variables included number of flower clusters per tree and the average daily carbohydrate balance from bloom to 60 DD, and from 300 DD to 360 DD. Number of flower clusters per tree for 'Gala' had a quadratic shaped curve (Figure 6), where fruit set decreased when increasing cluster number until 750 flower clusters/tree, then it leveled off. The average carbohydrate balance had a positive relation with fruit set for the periods of 0-60 DD and 300-360 DD after bloom. The same variables were significant when modeling the final fruit number per tree for 'Gala', but in this case the initial number of flower clusters per tree had a positive linear correlation instead of curvilinear (Figure 7).

The model that was built to predict fruit set for 'McIntosh' had high R^2 values as well (0.72) (Figure 8). For this model, the significant regressor variables included number of flower clusters per tree and the average daily carbohydrate balance from bloom to 60 DD, from 120 DD to 180 DD, and from 360 DD to 420 DD. All the variables had a linear correlation. The correlation was positive for number of flower cluster per tree, carbohydrate balance from 0-60 DD after bloom and 360-420 DD after bloom. The correlation was negative for the carbohydrate balance between 120-180 DD after bloom. The model to predict final fruit number per tree with ‘McIntosh’ had similar R^2 values (0.73) as the one for fruit set, but in this case the significant variables included number of flower clusters per tree and the average daily carbohydrate balance between 360 DD to 420 DD after bloom, both with a positive linear correlation (Figure 9).

Discussion

Over the 18 years of this study, there were large differences in the number of flower clusters per tree each year. With ‘Gala’ the number varied from 350 flower clusters per tree to 1100 clusters per tree, with ‘McIntosh’ the range was greater (300-1400), and with ‘Delicious’ the range was 200-1000. The significant annual variation in flower cluster number per tree was observed despite the fact that each year we selected the heaviest blooming trees for this study. The sources of the variability in flowering intensity were not investigated in this study but probably was related to crop-load the previous year and climate and weather variables the previous summer, fall, winter and early spring. Francesconi et al. (1996) showed that return bloom and return fruit numbers were well correlated to the tree carbon balance as canopy photosynthesis per fruit the previous summer. Our goal in this study was to explain the natural final fruit number and final fruit set when no thinning was done using various weather and carbohydrate status variables before and after bloom. The most important variable affecting fruit set was initial flower number per tree, which was negatively correlated to final fruit set for all three cultivars.

There was also an important difference in fruit set among the cultivars. In general terms, ‘Gala’ set ~1 fruit for each flower cluster (average fruit set = 0.9), whereas fewer fruits were set for ‘Delicious’ and ‘McIntosh’ (average fruit set = 0.7 and 0.6, respectively). A study done with

‘Royal Gala’ in New Zealand by Breen et al. (2015), reported a natural fruit set of 1-2 fruits per bud. However, that higher fruit set in NZ may be due to better conditions for photosynthesis, especially after harvest, leading to less bienniality.

The final fruit number per tree was generally positively related to initial flower cluster number per tree. ‘Gala’ had the highest final fruit number (675) and also the highest initial flower cluster number. ‘McIntosh’ had a lower final fruit number (351) and a lower initial flower cluster number. ‘Delicious’ had the lowest final fruit number (308) and the lowest initial flower cluster number. Final fruit number is likely a co-dependent variable of the initial number of flower clusters per tree. This makes sense that they are dependent thus we name this variable a dependent variable, because its value depends on the values of the predictor variables. Since initial flower numbers was the first and most important predictor variable, we consider it a covariate to assess the impact of the other variables. This allowed our model to normalize flowering intensity to an averaged initial flower number to assess the effect of the other variables we considered as predictor variables.

Because fruit set was negatively correlated with initial flower cluster numbers, the final fruit number per tree for ‘Gala’ was more similar than the large differences in initial flower number. With ‘Delicious’ and ‘McIntosh’ greater differences in final fruit number were observed.

The causes of this natural variability in final fruit number per tree have been ascribed to many factors including weather the previous summer, fall or winter, carbohydrate relations from the previous year, temperature and sunlight from bud break to bloom or post bloom, tree vigor, leaf area, or the sensitivity of the tree itself, which is related to the level of bloom (Francesconi et al., 1996; Greene, 2002; Williams, 1979; Williams and Edgerton, 1981). Many of these factors may be related to the balance of carbohydrate supply from tree photosynthesis in relation to the demand for carbohydrates from all of the competing organs of the tree (crop, shoots, roots, and woody structure). We have theorized that a naturally induced carbohydrate deficit relative to fruit growth demand could be the cause of reduced fruit set and final fruit number in some years, whereas naturally induced carbohydrate surplus available to support fruit growth could be the cause of higher fruit set and higher final fruit number in other years (Lakso et al., 2006; Robinson and Lakso, 2011).

Lakso et al. (2006) observed fruit abscission even when fruit numbers per tree were low (300), suggesting that in some seasons there may be periods where photosynthesis cannot supply carbon demand from developing organs even when flower density is low, or that the low flower density indicates a weakened physiological state of the tree. Fernandez et al. (2018) in almond, reported how fruiting spurs depend on fruitless spurs to withstand the high sink demand on their fruits, suggesting that fruit load in almond spurs define starch and total soluble carbohydrate concentration and therefore their survival and bloom probabilities in the next season.

Our prediction models for fruit set and final fruit number per tree showed that the number of flower clusters per tree and average carbohydrate balance from 0-60 DD after bloom (bloom and petal fall period) and the carbohydrate balance from 300-360 DD after bloom (fruit size 15~18mm) were the main significant variables that explained 60-80% of the variability in natural fruit set or natural final fruit number per tree.

Of the myriad of possible effectors, many of the factors related to the observed variations in fruit abscission response appear to be consistent with carbohydrate supply and demand. Post-bloom conditions that lead to poor carbohydrate status were associated with greater natural abscission. These conditions are hot temperatures, low light intensity from cloudy sky conditions, and heavy initial set with weak spurs that have small total leaf area (Byers, 2002; Greene, 2002; Kondo et al., 1987; Kondo and Takahashi, 1987; Lehman et al., 1987; Williams, 1979; Williams and Edgerton, 1981; Zibordi et al., 2009; Zibordi et al., 2014). Our modeling efforts showed that when the MaluSim model was run with a low fruit number per tree (300 fruits) the carbon balance deficits were smaller while with higher fruit numbers the simulations showed much greater deficits. The best prediction models of final fruit set and final fruit number were achieved with 600 fruits per tree for the simulated tree.

The severity of pruning may affect the result we obtained. Robinson and Dominguez (2015) have suggested a more aggressive form of precision pruning to reduce flower bud load to 1.5 times the desired final fruit number. In our study the ratio was much higher ~2-2.5. With the more aggressive precision pruning target of 1.5 flower cluster per final fruit number, the demand for carbon by fruitlets in the period after bloom would be less than in our study. In addition, more aggressive modern chemical thinning based on repeated chemical sprays starting at full bloom to rapidly reduce fruit number after bloom, would also reduce the demand for carbohydrate by the fruitlets and result in smaller carbohydrate deficits. A related study found that hand thinning at 8 mm to a moderate final fruit number led to essentially no later fruit drop (Lakso unpublished data). This may be why anecdotally we see less “June drop” on precision managed crop load trees than in un-thinned trees.

Our field study results indicating that carbon balance is an important factor in determining fruit set and final fruit number with un-thinned trees are also supported by recent detailed studies of carbon flows to fruit and gene expression related to environmental effects and chemical thinners. Low light that causes abscission has been found to reduce phloem flows of carbon to the fruit supporting the connection of photosynthesis reduction to fruit carbon supply (Morandi et al., 2011; Zibordi et al., 2009; Zibordi et al., 2014). The initial gene expression effects of very low light and benzyladenine treatment were mostly related to carbon metabolism in the fruit, consistent with carbon starvation and reduction of cell division processes (Dash et al., 2012; Dash et al., 2013; Zhou et al., 2008; Zhou et al., 2017). This suggests that a carbon supply limitation to the fruit may be an important trigger for the fruitlet abscission process.

Ethylene gene responses appeared to follow later at 72 hours after shading began. Any major change in the physiology of an organ, such as transitioning from active growth to abscission of the fruit, would be expected to affect many processes. As expected, many genes related to hormones in the fruit are affected during abscission (Eccher et al., 2015; Ferrero et al., 2015; Kolarič et al., 2011). However, Botton et al. (2011) based on a broad gene expression analysis proposed a model of induction of fruit abscission consistent with initiation by carbon starvation and a cascade of events including reduction of auxin transport that induces the formation of an abscission zone.

Other factors that had a lesser influence on final fruit set and final fruit number were temperatures of the previous fall. However, these variables were only significant with ‘Delicious’. The higher the temperatures during this period which resulted in lower the fruit set and final fruit number could be due to carbohydrate depletion. Lakso (1987) found that regional yields were correlated to the average temperatures from January 1st to bud break (negative relationship: warmer=lower yields), previous fall average temperatures (positive relationship, higher fall temperatures equals to greater carbon fixation and better stored balance for the following season) and temperatures from bud break to bloom or somewhat after (positive relationship). This is also in accordance with observations made in the UK and the US, that yield in the “light” year was correlated to the warmth of the previous fall and the mid-to-late winter temperatures (Jackson and Hamer, 1980; Jackson et al., 1983; Lakso, 1987). Jackson et al. (1983) also showed that artificially cooling potted trees in February-April led to higher fruit set.

When comparing the three cultivars of our study, ‘Gala’, had higher number of flower clusters per tree than ‘Delicious’ and ‘McIntosh’. Hence, there was an extremely large number of initial fruitlets with ‘Gala’, up to 1100 clusters or 6600 fruitlets, competing for resources shortly after bloom. According to previous studies, right at this period the carbohydrate support for fruit growth mainly comes from the spur leaves, which is highly associated with the level of light and temperature (Byers, 2002; Byers et al., 1991; Corelli-Grappadelli et al., 1994; Lakso and Goffinet, 2017). Perhaps this is why there was a positive correlation with the average carbohydrate balance and fruit set or final fruit number in the early period from bloom to 0-60 DD after bloom which is the period from bloom to shortly after petal fall.

The later period from 300-360 DD after bloom when carbohydrate balance was positively correlated with final fruit set and final fruit number is about 21 days after petal fall, or when fruit weight is ~2-2.5 g (~15-18 mm fruit diameter). Corelli-Grappadelli et al. (1994) and Lakso et al. (1999) reported rapid fruit growth about that stage, which requires large carbohydrate demand. Therefore, carbohydrate deficits at this stage may trigger substantial fruit abscission, especially on ‘Gala’. Similar behavior was observed for ‘McIntosh’; however, for this cultivar, there was and even later period (360-420 DD) when carbohydrate balance significantly affected fruit set and final fruit number. This suggests that ‘McIntosh’ could be susceptible to carbohydrate deficits later in the season, even later than the usual thinning window, which suggests an extended period in which growers may perform chemical thinning for this cultivar. ‘McIntosh’ is noted as a variety that is easy to thin and may not even require chemical thinning.

The data we collected also allowed us to correlate final fruit number and final fruit size. The negative slope of final fruit size for increasing fruit number was expected and is the basis of why growers reduce fruit number to achieve larger fruit size (Robinson et al., 2013). The differences we observed in the final fruit number per tree as a result of final fruit set being affected by initial number of flower clusters per tree help to explain the different linear relationships of the 3 cultivars that correlate fruit weight and fruit number. The correlation between fruit number and fruit size was relatively poor. This may be due to the lack of irrigation in our research orchard which affected the relationship in years when drought occurred.

Breen et al. (2015) suggested that fruit set could be improved by early removal of the competing floral sinks. While fruit size is largely determined by cell number, cell division can also be limited when there is competition for resources early in the season (Lakso et al., 1995). For instance, Breen et al. (2015) reported a 10–30 g increase in mean fruit weight when crop load was reduced from 6 to 4 fruit/cm^2 of trunk cross-sectional area. Crop load has been reported to affect leaf assimilation in mid-season but we have not seen this phenomenon in the early season. For instance, Palmer et al. (1997) observed leaf assimilation to be reduced ~65% when comparing deflowered *vs* high crop load trees. With 'Gala' the relationship indicate the much greater need to reduce crop load to achieve fruit size but there are limits to the size improvement that could limit the economic gain from thinning too much (Francescatto et al., 2018). This appears to be truer with 'Gala' than with either 'McIntosh' or 'Delicious'.

In addition to the factors we considered, previous season crop load is known to affect flower bud density (return bloom) the following year (Dennis, 2000; Williams, 1979). Since initial fruit number was a highly significant factor in explaining fruit set and final fruit number, it is logical that the previous season crop load also would have explained significant variation in fruit set and final number. A related but different variable is photosynthetic supply the previous season which is affected by crop load (Fernandez et al., 2018), but also by insect damage to the leaves during the previous season (Francesconi et al., 1996). In the study by Francesconi, they showed that the fruit numbers per tree the following year was better correlated than flower numbers to the carbon availability.

Another factor which could affect fruit set and final fruit number, which we did not attempt to model, is the effect of temperature and rainfall on the activity of pollinators. If cool rainy conditions limited bee activity perhaps that could account for some of the variation in fruit set and fruit number that our multiple regression model did not explain.

A final consideration is the relatively large variation in DD recorded over the 18 years to move the trees from endodormancy to bud break (61 to 133 DD from January 1st to bud break). In NY, climate chilling requirement is almost always met by January 1st. If bud break is largely temperature driven during ecodormancy, this large range suggests that the DD model we used is not an optimal model. It is possible that the base temperature that we used (4°C) is incorrect, the the period of DD accumulation should begin at rest completion, or perhaps the entire concept of DD is excessively simple to explain the progression from the end of endodormancy to bud break. The DD concept does not account the effect of Q10=~2. For each 10°C increase in temperature DD increase linearly but plant metabolism increases exponentially. Nevertheless, the variation in DD as we used it was a significant factor in explaining natural fruit set. It should also be noted that observations of bud break, bloom and petal fall included variations in observer's visual assessments as each stage consists of large populations of shoots or flowers to evaluate over a range of shoot or flower development in multiple trees. This variation is difficult to quantify, but must be acknowledged.

Conclusions

For 18 years, we assessed experimental responses of un-thinned apple trees in relation to flower intensity and early season patterns of carbohydrate supply-to-demand to better understand natural fruit abscission. Fruit set for ‘Gala’ was generally greater and had less variability than for ‘Delicious’ or ‘McIntosh’. But in all cultivars, there was a clear pattern for fruit set to decrease when the number of flower clusters per tree was high. Multiple regression models were built to predict final fruit set and final fruit number per tree. Number of flower clusters per tree was the variable that had the greatest impact on final fruit set and fruit number, but average carbohydrate balance for the periods of 0-60 DD and 300-360 DD after bloom also were important variables which explained natural fruit set and final fruit number. The greater the carbohydrate supply to demand, the greater the set. The best models using these variables explained 60-80% of the variability in natural fruit set and final fruit number of un-thinned trees. For ‘Delicious’, temperatures of the previous fall also had a significant impact on natural fruit set and final fruit number. For ‘Gala’, carbohydrate balance from bloom to shortly after petal fall and when fruit size was about 18 mm diameter were related to triggering fruitlet abscission. A later susceptible period was also observed for ‘McIntosh’, suggesting a larger thinning window for this cultivar.

In summary, in spite of the dozens of factors reported to affect set, apple fruit set and final numbers over 18 years in a variable climate could be relatively well modeled with primarily flower density, representing the tree’s physiological history, and a carbohydrate model, representing early season weather effects.

Acknowledgements

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Tables

Table 1. Bud break (BB), bloom (B), and petal fall (PF) dates, bloom length (days), and degree days (DD) with base temperature of 4°C from September 1st - December 31st (previous fall), November 1st – December 31st (previous fall), January 1st to bud break, bud break to bloom, bloom to PF, bloom to PF+21 days, and from bloom to up to 41 days for each recorded year (2000-2017) at Geneva NY. Grey bars represent variable value.

Year	Bud break	Bloom	Petal fall	Bloom length (days)	DD previous fall (Sep1-Dec31)	DD previous fall (Nov1-Dec31)	DD Jan1 - BB	DD BB-B	DD B-PF	DD B-PF+21d	DD B+41d
2000	10-Apr	7-May	13-May	6	.	.	133	172	88	293	479
2001	14-Apr	10-May	16-May	6	.	.	68	140	61	270	492
2002	14-Apr	6-May	16-May	10	812	192	126	179	75	268	414
2003	16-Apr	16-May	27-May	11	683	51	90	220	108	348	478
2004	18-Apr	11-May	17-May	6	649	91	105	205	91	331	540
2005	18-Apr	12-May	23-May	11	702	75	104	154	84	391	528
2006	11-Apr	10-May	17-May	7	774	122	106	215	70	313	493
2007	19-Apr	14-May	21-May	7	651	136	93	218	65	361	567
2008	17-Apr	5-May	17-May	12	786	39	111	184	101	313	474
2009	14-Apr	7-May	18-May	11	638	77	79	193	100	325	450
2010	31-Mar	30-Apr	7-May	7	618	81	66	226	99	309	509
2011	18-Apr	12-May	25-May	13	648	53	86	171	156	487	590
2013	14-Apr	15-May	20-May	5	694	72	66	258	52	328	543
2014	14-Apr	20-May	26-May	6	662	63	71	284	70	369	594
2015	16-Apr	12-May	19-May	7	669	61	61	249	77	309	503
2016	21-Mar	15-May	23-May	8	818	185	70	231	60	377	548
2017	30-Mar	7-May	19-May	12	760	94	89	255	79	315	453

Table 2. Number of flower clusters per tree, fruit set (final fruit number/flower cluster), final fruit number per tree, and mean fruit weight (g) of un-thinned 'Delicious', 'Gala', and 'McIntosh' apple trees over 18 seasons at Geneva, NY. Grey bars represent variable value.

Cultivar	Year	Number of flower clusters per tree	Fruit set	Fruit number per tree	Fruit weight (g)
Delicious	2000	230	0.7	161	250
	2001	222	1.1	235	175
	2002	526	0.3	132	199
	2003	538	0.5	269	179
	2004	589	0.8	366	173
	2005	334	0.4	132	212
	2006	306	1.3	333	180
	2007	428	1.0	385	96
	2008	983	0.5	505	175
	2009	500	1.1	551	140
	2010	513	0.6	305	220
	2011	869	0.4	325	224
Gala	2000	668	0.7	433	157
	2001	525	1.1	586	119
	2002	577	1.2	663	94
	2003	362	1.7	616	123
	2004	998	0.7	633	151
	2005	754	0.5	391	124
	2006	1063	0.8	827	125
	2007	890	1.2	989	64
	2008	806	1.0	804	120
	2009	756	1.0	782	134
	2010	930	0.5	432	174
	2011	854	0.8	719	132
	2013	982	0.7	701	122
	2014	457	1.4	562	137
	2015	699	0.9	594	146
	2016	1049	0.9	950	77
	2017	829	1.0	796	110
McIntosh	2000	318	0.7	210	202
	2001	338	0.6	196	177
	2002	632	0.3	173	128
	2003	504	0.6	279	126
	2004	816	0.6	513	140
	2005	384	0.5	196	155
	2006	450	1.3	563	137
	2007	530	1.1	566	101
	2009	1027	0.5	544	127
	2010	444	0.4	150	204
	2011	1417	0.3	503	136
	2013	915	0.4	324	144

Figure 1

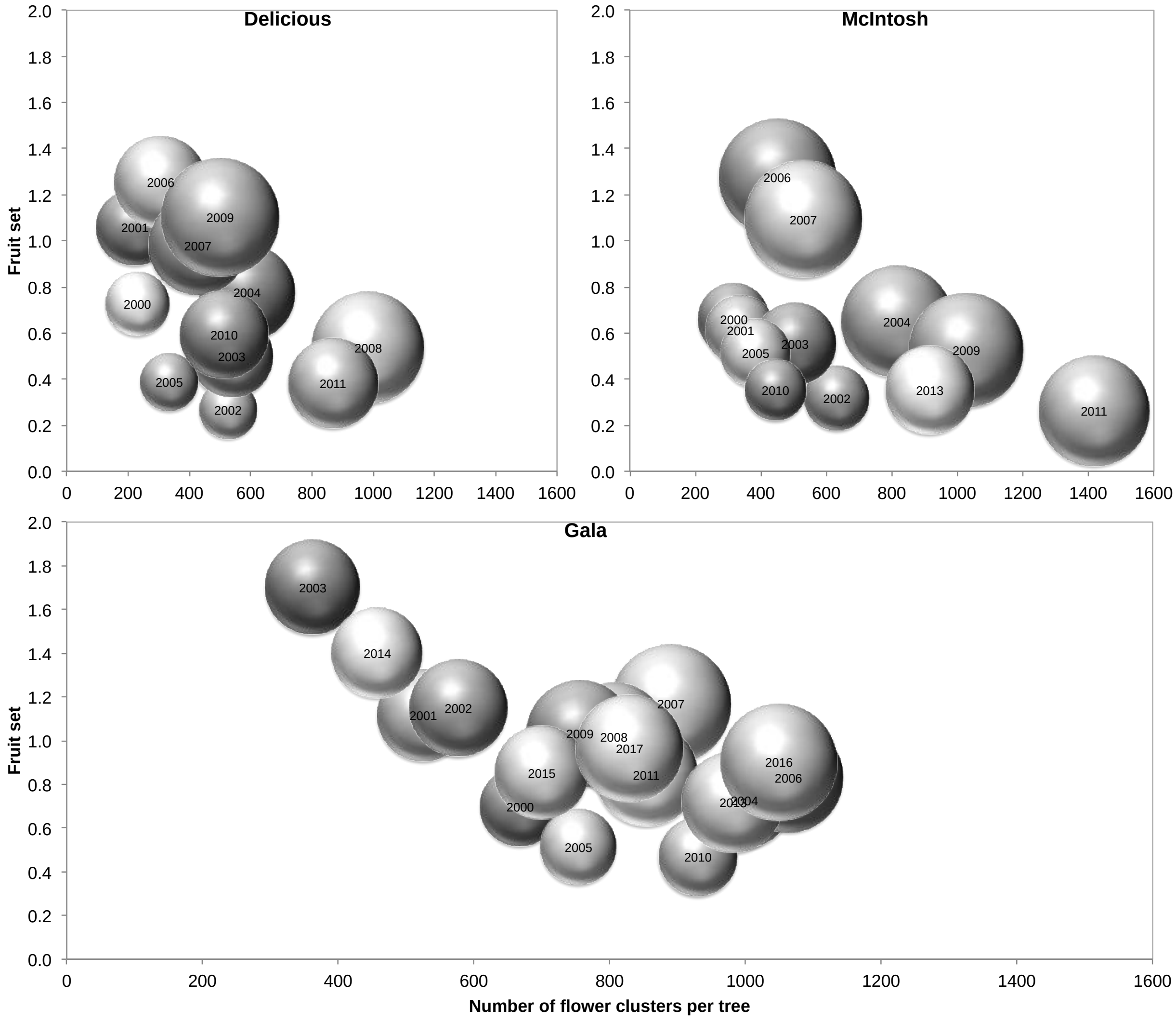
Delicious
McIntosh
Gala
Fruit set
Number of flower clusters per tree
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
0
200
400
600
800
1000
1200
1400
1600
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2013
2014
2015
2016
2017

Figure 2

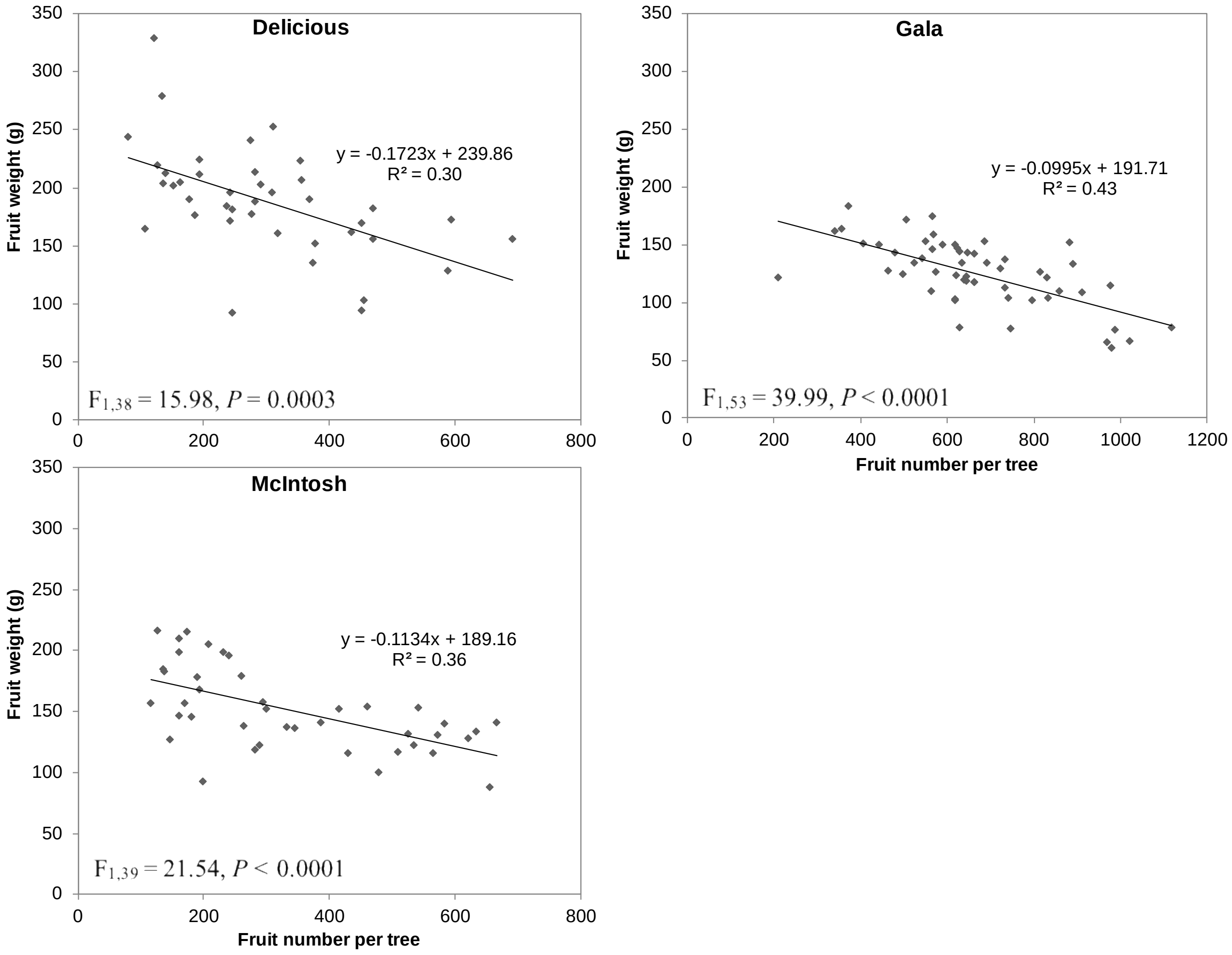
Delicious
Fruit weight (g)
350
300
250
200
150
100
50
0
0
200
400
600
800
y = -0.1723x + 239.86
R² = 0.30
$F_{1,38} = 15.98$, $P = 0.0003$
Gala
Fruit weight (g)
0
200
400
600
800
1000
1200
Fruit number per tree
y = -0.0995x + 191.71
R² = 0.43
$F_{1,53} = 39.99$, $P < 0.0001$
McIntosh
Fruit weight (g)
Fruit number per tree
y = -0.1134x + 189.16
R² = 0.36
$F_{1,39} = 21.54$, $P < 0.0001$

Figure 3

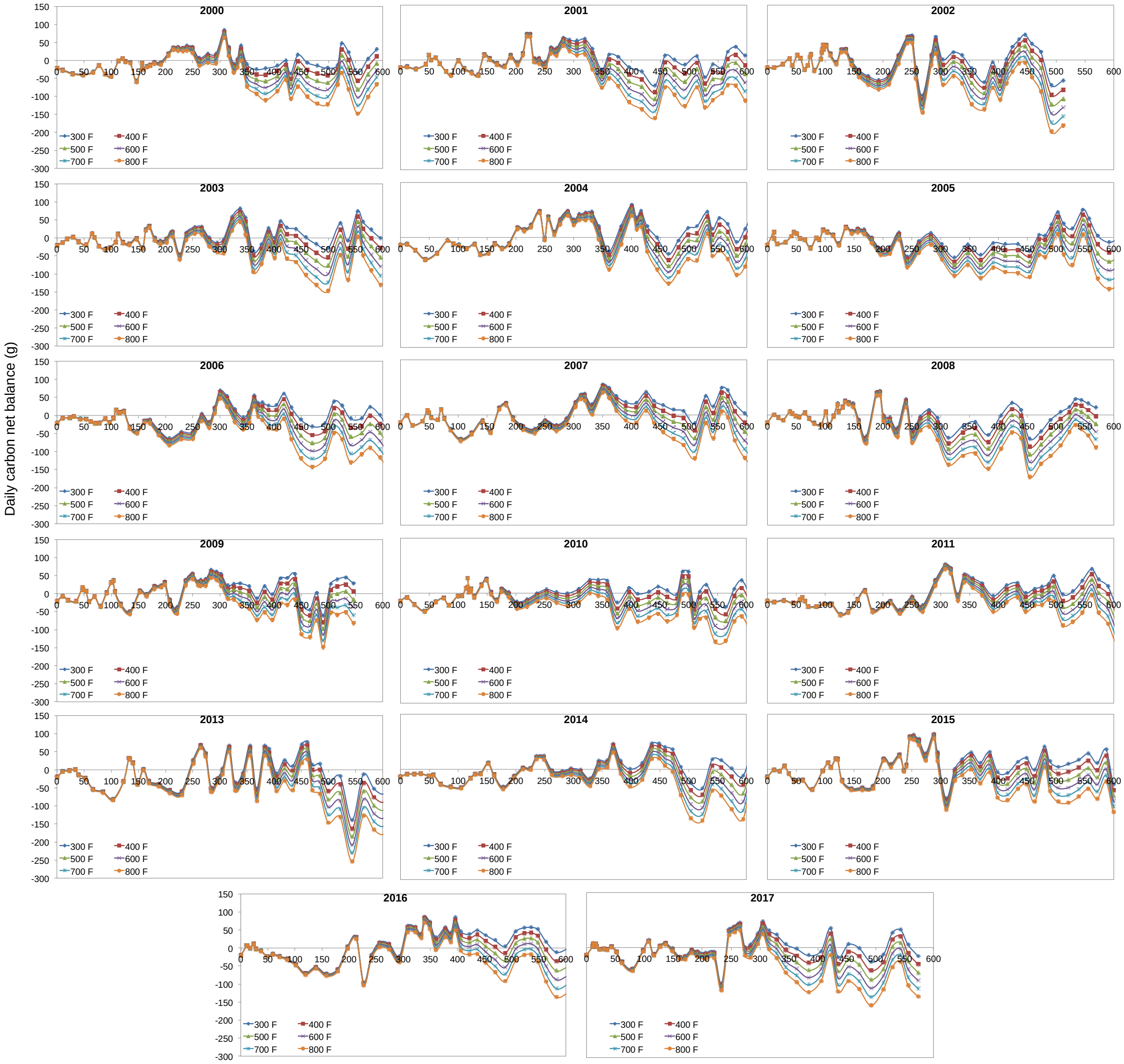
Daily carbon net balance (g)
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2013
2014
2015
2016
2017
150
100
50
0
-50
-100
-150
-200
-250
-300
0
50
100
150
200
250
300
350
400
450
500
550
600
300 F
400 F
500 F
600 F
700 F
800 F

Figure 4

Delicious model for fruit set (using MaluSim with 600 fruit/tree)

Summary of Fit

RSquare	0.606217
RSquare Adj	0.546553
Root Mean Square Error	0.211013
Mean of Response	0.678036

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	5	2.2620584	0.452412	10.1605
Error	33	1.4693740	0.044526	**Prob > F**
C. Total	38	3.7314324		<0.0001*

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.2255926	0.258696	0.87	0.3895
Cluster#	-0.000588	0.000133	-4.43	<0.0001*
DD BB-B	0.0044689	0.001423	3.14	0.0035*
0_60 DD (600)	0.0163641	0.004317	3.79	0.0006*
60_120 DD (600)	-0.014217	0.003567	-3.99	0.0004*
240_300 DD (600)	0.0061196	0.001594	3.84	0.0005*

Prediction Profiler

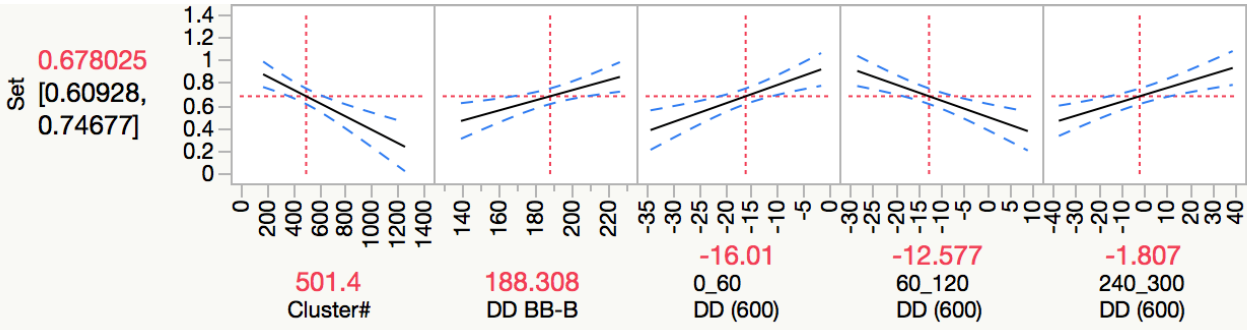

Figure 5

Delicious model for fruit number (using MaluSim with 600 fruit/tree)

Summary of Fit

RSquare	0.899765
RSquare Adj	0.856808
Root Mean Square Error	57.0372
Mean of Response	328

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	9	613263.91	68140.4	20.9454
Error	21	68318.09	3253.2	**Prob > F**
C. Total	30	681582.00		<0.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	959.44768	113.8896	8.42	<0.0001
Cluster#	0.2548787	0.058308	4.37	0.0003
DD Nov-Dec	-6.360102	0.801655	-7.93	<0.0001
180_240 DD (600)	5.409963	0.93469	5.79	<0.0001
240_300 DD (600)	-5.146798	1.144903	-4.50	0.0002
300_360 DD (600)	-5.690113	1.033115	-5.51	<0.0001
360_420 DD (600)	12.517007	1.332041	9.40	<0.0001
420_480 DD (600)	3.3631736	0.87453	3.85	0.0009
540_600 DD (600)	-8.129323	1.123879	-7.23	<0.0001
(Cluster#-572.178)*(Cluster#-572.178)	-0.0006	0.000148	-4.06	0.0006

Prediction Profiler

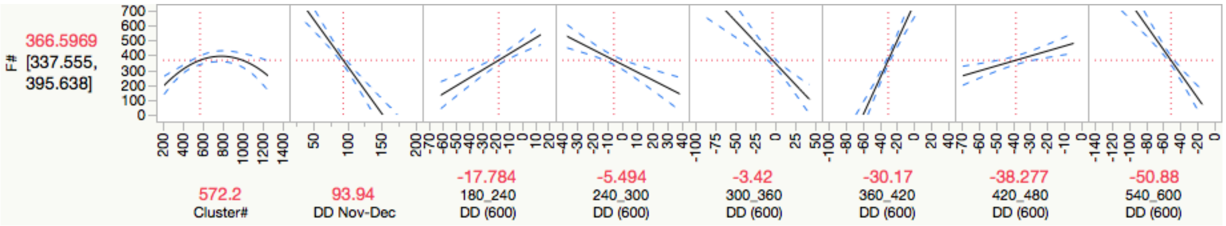

Figure 6

Gala model for fruit set (using MaluSim with 600 fruit/tree)

Summary of Fit

RSquare	0.813942
RSquare Adj	0.798754
Root Mean Square Error	0.160179
Mean of Response	0.967292

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	4	5.4998931	1.37497	53.5898
Error	49	1.2572114	0.02566	**Prob > F**
C. Total	53	6.7571044		<0.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	1.9534283	0.076044	25.69	<0.0001
Cluster#	-0.001129	0.000085	-13.30	<0.0001
0_60 DD (600)	0.0163423	0.002438	6.70	<0.0001
300_360 DD (600)	0.0026586	0.000722	3.68	0.0006
(Cluster#-767.273)*(Cluster#-767.273)	1.416e-6	2.411e-7	5.87	<0.0001

Prediction Profiler

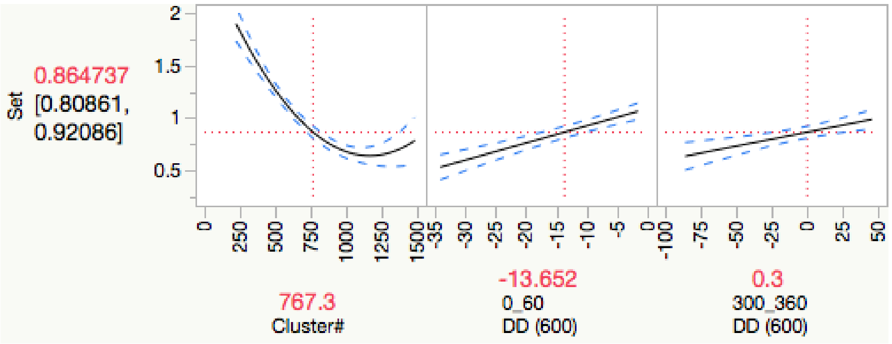

Figure 7

Gala model for fruit number (using MaluSim with 600 fruit/tree)

Summary of Fit

RSquare	0.627577
RSquare Adj	0.605231
Root Mean Square Error	111.9717
Mean of Response	673.5185

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1056370.8	352124	28.0853
Error	50	626882.7	12538	**Prob > F**
C. Total	53	1683253.5		<0.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	635.07816	53.14025	11.95	<0.0001
Cluster#	0.2659519	0.057783	4.60	<0.0001
0_60 DD (600)	12.177239	1.689067	7.21	<0.0001
300_360 DD (600)	2.1369848	0.498208	4.29	<0.0001

Prediction Profiler

Figure 8

McIntosh model for fruit set (using MaluSim with 600 fruit/tree)

Summary of Fit

RSquare	0.751239
RSquare Adj	0.721974
Root Mean Square Error	0.139257
Mean of Response	0.577813

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	4	1.9911635	0.497791	25.6694
Error	34	0.6593408	0.019392	**Prob > F**
C. Total	38	2.6505043		<0.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	1.0785044	0.080953	13.32	<0.0001
Cluster#	-0.000592	7.729e-5	-7.66	<0.0001
0_60 DD (600)	0.006516	0.002147	3.03	0.0046
120_180 DD (600)	-0.009503	0.002375	-4.00	0.0003
360_420 DD (600)	0.0045658	0.000884	5.16	<0.0001

Prediction Profiler

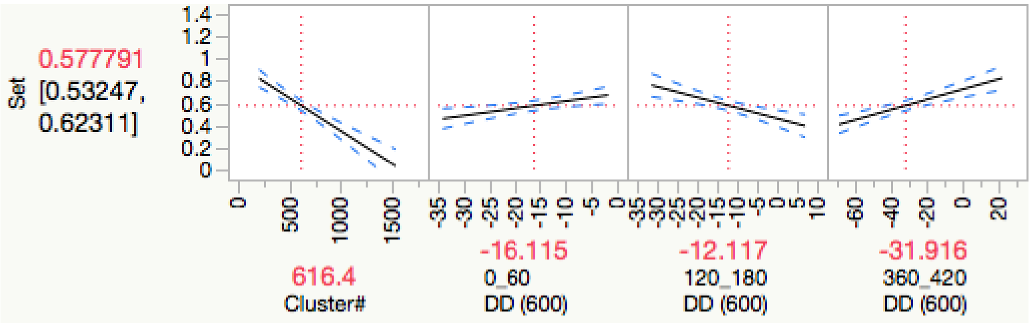

Figure 9

McIntosh model for fruit number (using MaluSim with 600 fruit/tree)

Summary of Fit

RSquare	0.74423
RSquare Adj	0.730021
Root Mean Square Error	89.46741
Mean of Response	327.1026

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	2	838474.5	419237	52.3757
Error	36	288159.0	8004	**Prob > F**
C. Total	38	1126633.6		<0.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	338.12929	41.87531	8.07	<0.0001
Cluster#	0.165495	0.04915	3.37	0.0018
360_420 DD (600)	3.5415344	0.482366	7.34	<0.0001

Prediction Profiler

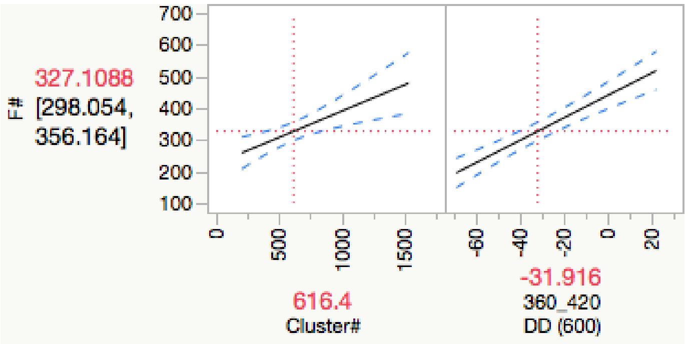

Figure captions

Figure 1. Bubble plots showing the three dimensional relationship between fruit set (final fruit number/initial flower cluster number) and number of flower clusters per tree and number of harvested fruits per tree for each cultivar (‘Delicious’, ‘McIntosh’, and ‘Gala’) at Geneva NY. The size of the circles is proportional to the number of harvested fruits per tree and the numbers in the circles indicate the year (2000-2017).

Figure 2. Scatter plot showing the relationship between fruit weight (g) and fruit number per tree for ‘Delicious’ (2000-2011), ‘McIntosh’ (2000-2013), and ‘Gala’ (2000-2017) at Geneva NY. Each symbol represents 1 tree in 1 year. For each year there were 3-5 trees.

Figure 3. Daily carbon net balance (g) running the MaluSim model with different number of fruits per tree (300, 400, 500, 600, 700, and 800) along cumulated degree days from bloom for each year (2000-2017) at Geneva NY. For each year, data represents 48 days. Daily C net balance is total C production – total vegetative and fruit demand in g CO_2 equivalents.

Figure 4. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Delicious’ model built to predict fruit set using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, degree-days (DD) from from BB to bloom (B), average carbohydrate net balance from bloom to 60 DD after (0_60 DD (600)), average carbohydrate net balance from 60 DD to 120 DD from bloom (60_120 DD (600)), and average carbohydrate net balance from 240 DD to 300 DD from bloom (240_300 DD (600)).

Figure 5. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Delicious’ model built to predict fruit number using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, degree-days (DD) from November to December of previous fall, average carbohydrate net balance for different DD periods from bloom: 180 to 240, 240 to 300, 300 to 360, 360 to 420, 420 to 480, and 540 to 600.

Figure 6. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Gala’ model built to predict fruit set using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, average carbohydrate net balance from bloom to 60 DD after (0_60 DD (600)), average carbohydrate net balance from 300 DD to 360 DD from bloom (300_360 DD (600)).

Figure 7. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Gala’ model built to predict fruit number using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, average carbohydrate net balance from bloom to 60 DD (0_60 DD (600)), and average carbohydrate net balance from 300 DD to 360 DD from bloom (300_360 DD (600)).

Figure 8. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘McIntosh’ model built to predict fruit set using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, average carbohydrate net balance from bloom to 60 DD after (0_60 DD (600)), average carbohydrate net balance from 120 DD to 180 DD from bloom (120_180 DD (600)), and average carbohydrate net balance from 360 DD to 420 DD from bloom (360_420 DD (600)).

Figure 9. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘McIntosh’ model built to predict fruit number using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree and average carbohydrate net balance from 360 DD to 420 DD from bloom (360_420 DD (600)).