Modeling physiological and environmental factors regulating relative fruit set and final fruit numbers in apple trees

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Chemical thinning of apple has been practiced for 50 years but it remains an unpredictable part of apple production with large variations from year to year and within years. Carbohydrate availability to support young fruitlet growth may play a significant role in apple tree response to chemical thinners, especially when the carbohydrate supply is the limiting factor for fruit growth. To address the carbohydrate component, we have tested the MaluSim simplified apple tree carbon balance model that integrates many environmental and tree physiological factors as a tool to predict chemical thinner response in field trials from 2000-2011. The model suggests that carbon supply-to-demand variations may explain some of the great variation in thinning spray response. Relative fruit set and final fruit number per tree were affected by the carbohydrate balance within two days before the spray and up to five days after. There was a period, 15-29 days after bloom that thinners showed higher action. The greater the carbohydrate supply relative to demand, the greater the relative set and the final fruit number. This suggested that carbohydrate supply-demand balance may be a baseline for thinner responses, and that integrative modeling of these balances can be useful in understanding variation in thinning responses. Apple relative fruit set and final fruit number per tree could be modeled relatively well with consideration of initial flower density, the carbohydrate balance model, and cumulative growing degree days since bloom.

Keywords: fruit drop; carbohydrate supply; carbohydrate demand; temperature; light; simulation model; thinning

Introduction

Management of crop load is a balance between reducing flower and fruit numbers sufficiently to achieve optimum fruit size without reducing yield excessively and without compromising return bloom in the following spring. For the past 50 years chemical thinning sprays have been the primary method growers use to reduce fruit numbers, but despite over 50 years of experience with chemical thinning, it remains an unpredictable part of apple production with large variations from year to year and within years due to weather variables such as temperature and radiation (Robinson et al., 2017; Robinson and Lakso, 2004; Robinson et al., 2012). There have been many studies that have attempted to understand better the roles of individual factors, with experimental manipulation of cultivar, tree vigor, bloom density, environmental conditions or chemical used (Lakso and Goffinet, 2017; Lordan et al., 2019). Yet, more than 30 years of field trials (Dennis, 2000; Greene, 2002; Greene and Costa, 2012; Greene and Lakso, 2013; Robinson and Lakso, 2011; Williams, 1979) have provided only general guidelines on the effects of weather conditions and timing of application, but have not been able to clarify regulatory processes or provide quantitative rules for prediction of apple chemical thinning response.

Conditions that lead to low carbohydrate balance are associated with heavy natural fruit drop (Lordan et al., 2019) and easier chemical thinning (Robinson and Lakso, 2011). These include hot temperatures, cloudy, heavy initial set on many weak spurs and stressed trees. Manipulation of carbohydrate balance by the use of inhibitors of photosynthesis, imposed low light periods, and high night temperatures all cause or enhance fruit abscission (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). Greater susceptibility to chemical thinners and increasing fruit abscission has been shown by the use of shading intensity treatments at different stages of fruit development (Byers, 2003; Mcartney et al., 2004; Zibordi et al., 2009). Therefore, it appears that the carbohydrate availability during cell division (when shoots have priority over the fruit), may play a significant role in apple tree response to chemical thinners, especially when the carbohydrate supply is the limiting factor for fruit growth (Corelli-Grappadelli et al., 1994; Lakso and Goffinet, 2017).

Carbohydrate demand of the crop depends on the number of actively growing fruits and shoots. In spring, the initial growth of shoots and flowers at budbreak is supported by carbohydrate reserves (Lakso and Goffinet, 2017). Conditions leading to poor carbohydrate balance during the previous summer, fall or winter may affect natural fruit set the following spring (Francesconi et al., 1996; Jackson and Hamer, 1980; Jackson et al., 1983; Lakso, 1987; Lordan et al., 2019). Carbohydrate support for fruit growth comes primarily from spur leaves and small ‘spur-like’ short lateral shoots on last year’s long shoots (Hansen, 1971; Lakso and Goffinet, 2017; Priestley, 1960; Wunsche et al., 1996). Under limiting radiation and limited photosynthesis early in the season, the tree appears to give priority to extending shoots, presumably to intercept more of the limiting light (Corelli-Grappadelli et al., 1994; Lakso and Goffinet, 2017; Lakso and Goffinet, 2013). In addition, high temperatures drive up demand for carbohydrates for growth and respiration of all organs while reducing the supply due to supra-optimal effects on photosynthesis, which may lead to carbohydrate limitations (Lakso and Goffinet, 2017).

The carbohydrate supply available to each fruit at each point in the season depends on both the carbohydrate supply as well as crop demand, which is determined by the number of fruit and stage of development. Although many factors affect the carbohydrate supply:demand balance, this is a process that is relatively well understood quantitatively and can be modeled (Lakso and Johnson, 1990; Le Roux et al., 2001). A practical and simple model of apple tree carbohydrate supply and demand balance, named MaluSim was developed by Alan Lakso, that can integrate several of the environment and tree factors that are known to affect thinner response (Lakso and Johnson, 1990; Lakso et al., 2001). The model was developed to: (1) integrate daily measurement data to obtain estimates of seasonal integrals of carbon that is fixed by photosynthesis, its allocation to various plant organs and carbon lost by respiration, (2) elucidate seasonal patterns of growth and carbon partitioning to different parts of the plant, (3) evaluate the effects of environmental variables and cultural practices, and (4) determine if there are periods of likely carbon deficits or surpluses that may affect orchard performance. The model identified the post-bloom thinning period as the most critical time for carbon deficits (Lakso and Robinson, 2014). We have previously used the MaluSim model to explain natural fruit drop over an 18 year period (Lordan et al., 2019).

Observed experimental responses to chemical thinners applied at different times after bloom and their correlations to carbohydrate balance have been noted in various previous studies (Lakso et al., 2006; Robinson and Lakso, 2011), but have not been subject to detailed statistical analysis of correlation and timing between carbon deficits or excesses and chemical thinning responses.

The goal of this study was to use key environmental data (temperature and radiation) to predict tree carbon balance at the time of chemical thinner application to make more precise predictions of thinning response and to allow growers to make appropriate real-time adjustments in chemical treatment frequency or concentration 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’. 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 average annual precipitation for Geneva NY is 889 mm and the plot was not irrigated. Water stress is not a problem in early spring in Geneva NY due to winter snow and spring rainfall, thus water stress in our study was unlikely to affect fruit set response.

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. From 2000-2011, individual trees were assigned to one of three spray treatments: 1) unthinned control, 2) a single application spray of a tank mix of 7.5 $mg \cdot L^{-1}$ of Naphthalene acetic acid (NAA) (formulation Fruitone N) plus 600 $mg \cdot L^{-1}$ of Carbaryl (formulation Sevin XLR Plus) or 3) a single application spray of a tank mix of 75 $mg \cdot L^{-1}$ of 6-benzlyadenine (BA) (formulation VBC- 30001) plus 600 $mg \cdot L^{-1}$ of Carbaryl. Different individual trees were treated with either of the two spray treatments at 3 or 4 day intervals beginning at petal fall (PF) until 21 days after petal fall (PF+21) for a total of 7 timings. Sprayed trees were sprayed only once each season. Untreated control trees (UTC) did not receive any chemical thinning spray whatsoever. The total of 2 spray treatments × 7 timings and an untreated control resulted in 15 total treatments. Each year new trees in each rep were selected for treatment which had substantial and similar bloom each year and return bloom was evaluated from the trees used the previous season. Each year the experiment was designed as a randomized complete block experiment with 5 single tree replications. All treatment trees were bounded by guard trees on either side. Trees were sprayed with a tunnel sprayer, which limited chemical drift onto the adjacent trees. Spray volume was 935 $L \cdot ha^{-1}$ using a 2X concentration of chemicals.

Calculated tree row volume was 1,870 L·ha^{-1}. No mechanical or hand thinning was performed whatsoever.

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 (2000-2011) 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. Relative fruit set was calculated as treatment fruit set in relation to the UTC fruit set [(fruit # / flower cluster #)/ UTC set]. Total fruit number per tree and yield (kg) were also recorded at harvest for every tree. Mean fruit weight (g) was then calculated. An estimate of initial flower cluster number per tree was calculated from the final fruit number using the percent fruit set calculated from the tagged branches.

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 a slender spindle 'Empire'/'M.9' tree at 1280 trees/ha with 600 fruits/tree (Lordan et al., 2019). 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 cumulative growing degree days (base 4°C) from bud break to full bloom (170 DD). Thus, the yearly variations of carbon balance were due only to the varying weather inputs after bloom.

Days from January 1st to bud break, from bud break to bloom, and from bloom to petal fall (when 90% of the petals had fallen) 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. Phenological ranges and variation over the 12 years of this study were published previously (Lordan et al., 2019).

MaluSim model description

A simple daily time step apple dry matter production model was initially developed (Lakso and Johnson, 1990) with daily estimations leaf area development based on cumulative growing degree-days base 4 °C and daily estimations of carbon production using the concept of a "big leaf" canopy light response curve from Charles-Edwards (1982). The model estimated carbon demands of daily growth and respiration of fruits, leaves, and the 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 empirically estimated competitiveness coefficients if the carbon supply was deficient. The model was used in this study to calculate daily carbon supply, total carbon demand (crop and vegetative), and estimated daily carbon balance available to support fruit growth.

Data analysis

Response variables were modeled using linear mixed effect models. Mixed models including each combination of treatment as a fixed factor, and block, year, and block × year as random factors were built to separate treatment effects for fruit set, relative fruit set, fruit number, fruit weight, and cluster number for each cultivar. Mixed models excluding UTC and including each combination of active ingredient × time of application as fixed factors, and block, year, and block × year as random factors were built to compare treatment effects for fruit set, relative set, fruit number, fruit weight, and cluster number for each cultivar. Relative fruit set and fruit number data were square root transformed, whereas cluster number data was log transformed to normalize data distribution. All mean separations were made by Tukey's HSD (P=0.05).

Scatter plots were generated to identify relationships between relative 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 relative 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). Relative fruit set and final 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

Fruit set, flower cluster and fruit number

There were no significant differences among treatments regarding the initial number of flower clusters per tree (Table 1). Using data from all the 12 years of the study we found no significant differences for fruit set, relative fruit set, and fruit number when comparing the active ingredients (BA *vs* NAA) for ‘Delicious’ and ‘Gala’ but there was a significant difference of active ingredient for ‘McIntosh’. There was no significant interaction of active ingredient × timing for all three cultivars. On the other hand, significant differences in relative fruit set and final fruit number were observed when comparing different timings of application (Table 1, Figure 1). The greatest thinning efficacy occurred at 200-250 DD after bloom. At earlier timings between 75 and 125 DD (petal fall to PF+4 days) and at later timings when DD was greater than 300 (>PF+18 days) thinning efficacy was significantly less than at the optimum timing.

Effects of timing of thinning sprays

When considering each year separately but pooling together all three cultivars some year to year variation was noted in the “U” shaped pattern of the curve for relative fruit set over the time period that thinning sprays were applied (Figure 2). Timing was expressed in DD after bloom as fruit developmental stages are closely related to heat accumulations at that time. In four of the 12 years (2001, 2002, 2008 and 2009) the curve simply had a negative slope with the relative set at petal fall the highest and declining continuously until the last spray timing. In the other 8 years the relative set at the later timings was significantly greater than at the optimum timing. The optimum timing (minimum relative set values ~0.4-0.6) varied from about 150 DD (2006-2007) to 250 DD (2001-2002, 2008 & 2011). King fruit diameters were found to be linearly correlated to DD from bloom to 25 mm with a slope for about 7 mm/100 DD. At 200 DD king diameters were about 12 mm (data not shown).

Modeling relative fruit set and fruit number

The final multiple regression model to explain the variation in relative fruit set and final fruit number per tree for ‘Delicious’ that we built through the iterative process explained in the Materials and Methods section had a final R^2 value of 0.41 (Figure 3). The significant regressor variables included initial number of flower clusters per tree, cumulative DD after bloom, carbohydrate net balance on the spray day, average carbohydrate net balance for the period comprised from one day after the spray through four days after (Ave1+4Da), DD from November to December, and DD from bloom to petal fall (PF). (For the calculations of carbon balance the MaluSim model was set with 600 fruits per tree). Looking at 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 relative fruit set and the initial number of flower clusters per tree. There was a quadratic correlation between relative fruit set and cumulative DD after bloom, with a minimum value around 200-250 DD. Carbohydrate net balance showed a positive correlation. Relative fruit set was ~0.7 when carbohydrate net balance was 0, and rose up to 0.85 when carbohydrate net balance over the 4 days after spraying was +43 g. Cumulative DD from November-December showed a positive correlation with relative fruit set. DD from bloom to PF were highly significant in predicting fruit set; with a higher positive relationship than DD from November-December. Relative fruit set varied from 0.6 when DD from bloom to PF were 60, and rose up to 0.91 when DD were 155.

The regression model to predict final fruit number had a higher R^2 value (0.57) than the model to predict relative fruit set (Figure 4). When predicting final fruit number, the significant regressor variables included number of initial flower clusters per tree, cumulative DD after bloom, carbohydrate net balance two days before the spray day (D-2), average carbohydrate net balance for the period of five days after spraying (Ave1+5Da), DD from January 1st to bud break, and DD from bud break to bloom. When looking at the prediction profiler for this model, fruit number per tree was positively related to the initial number of flower clusters per tree. There was a quadratic correlation between fruit number per tree and cumulative DD from bloom, with a minimum value around 200-250 DD. The effect of carbohydrate balance was positive. Fruit number varied from 115 when the average carbohydrate net balance for the period comprised from one day after the spray through five days after was -65 g up to 293 fruit/tree when it was +41 g. The effect of cumulative DD from January 1st through bud break was negative. On the other hand, DD from bud break to bloom was positively related to final fruit number per tree.

For ‘Gala’, the model to predict relative fruit set had an R^2 value of 0.36 (Figure 5). The significant regressor variables included number of flower clusters per tree, cumulative DD after bloom, carbohydrate net balance two days before the spray day (D-2), average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da), and DD from January 1st to bud break. Relative fruit set was negatively related to the initial number of flower clusters per tree. Cumulative DD after bloom had a quadratic shaped curve, where relative fruit set decreased when DD increased until reaching 200-250 DD, after which relative fruit set increased with increasing DD. The average carbohydrate net balance, had a positive relationship with relative fruit set, whereas the DD from January 1st to bud break had a negative relationship.

When modeling the final fruit number per tree for ‘Gala’ (R^2=0.38, Figure 6), significant regressor variables included initial number of flower clusters per tree, cumulative DD after bloom, carbohydrate net balance two days before the spray day (D-2), average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da), DD from January 1st to bud break, and DD from bud break to bloom. The prediction profiler, showed there was a positive relationship for fruit number and the initial number of flower clusters per tree while there was a quadratic relationship between fruit number and cumulative DD after bloom, with a minimum value around 200-250 DD. Carbohydrate net balance had a positive relationship, with final fruit number which varied from 414 when the average carbohydrate net balance for the period comprised from one day after the spray through five days after was -65 g up to 520 fruit/tree when it was +41 g. DD from bud break to bloom had a positive relationship with final fruit number whereas DD from January 1st to bud break had negative relationship.

The model that was built to predict relative fruit set for ‘McIntosh’ had an R^2 value of 0.49 (Figure 7). For this model, the significant regressor variables included initial number of flower clusters per tree, cumulative DD after bloom, average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da), average carbohydrate net balance for the period comprised from the spray day through two days before (Ave0+2Db), DD from January 1st to bud break, DD from bud break to bloom, and DD from bloom to petal fall. The correlation was negative for number of flower clusters per tree and was also negative for DD from January 1st to bud break. Carbohydrate net balance and DD from bud break to petal fall were positively related to relative fruit set. There was a quadratic correlation between relative fruit set and cumulative DD after bloom, with a minimum value around 200-250 DD. Relative fruit set varied from 0.5 when DD after bloom to petal fall was 60 to up to 1.2 when DD was 155.

The model to predict final fruit number per tree with ‘McIntosh’ had a higher R^2 values (0.59) compared to the model for relative fruit set (Figure 8). In this case the significant regressor variables included initial number of flower clusters per tree, cumulative DD after bloom, carbohydrate net balance two days before the spray day (D-2) and average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da), DD from January 1st to bud break, and DD from BB to bloom. The prediction profiler showed that fruit number per tree was positively related to the initial number of flower clusters per tree. There was a quadratic correlation between fruit number per tree and cumulative DD from bloom, with a minimum value around 200-250 DD. The carbohydrate balance was positively correlated to final fruit number. Fruit number varied from 205 when the average carbohydrate net balance for the period comprised from one day after the spray through five days after was -65 g up to 265 fruit/tree when it was +41 g. Cumulative DD from January 1st through bud break was negatively correlated with final fruit number while DD from bud break to bloom was positively related to final fruit number per tree.

Further regression analysis of the effect of carbohydrate balance (average of -2 days through 5 days after spraying) on thinning efficacy at different timings of spray application showed that the effect on thinning efficacy was different depending on the time of application. When thinning sprays were applied at PF there was no significant relationship of carbohydrate balance with thinning efficacy (Table 2, Figure 9). At PF+4 days only ‘Delicious’ showed a significant relationship of carbon balance and relative fruit set. At PF+7, PF+11 and PF+14 days all three cultivars showed a significant positive relationship between carbon balance and thinning efficacy. At PF+18 days all three cultivars showed a positive relationship between carbohydrate balance and final fruit number, while at PF+21 days ‘Delicious’ and ‘McIntosh’ also showed a positive relationship. In general the period between 7 and 14 days after petal fall is when thinning was most related to carbohydrate balance. The slopes of the significant regressions varied among the timings but averaged 2.52, 3.19 and 1.90 fruits/g of carbohydrate available for fruit growth of ‘Delicious’, ‘Gala’ and ‘McIntosh’, respectively (Table 2, Figure 9).

Discussion

Our goal in this study was to explain relative fruit set and final fruit number per tree using various tree, weather and simulated carbohydrate status variables before and after bloom. Relative fruit set and final fruit number per tree are both tree response variables related to thinning but they differ in an important characteristic. Relative fruit set in our study is an estimate of the effect of the chemical thinner independent of natural thinning that can be caused by climate, tree physiology and pollinator efficacy. Relative fruit set resulting from a chemical treatment is normalized by the natural fruit set of the untreated controls, whereas final fruit number is a measure of the combined effects of natural drop and drop induced by the chemical thinner. Relative fruit set is a useful response variable to isolate factors that influence tree response to chemical thinners. However, final fruit number per tree that integrates both natural drop and chemically induced drop is a very practical response variable since a fruit grower desires a target number of fruit on the tree after natural and chemically induced drop to maximize economic returns. Thus, similar final fruit numbers can be reached by high natural set and strong thinner response or viceversa.

The most important variable affecting relative fruit set was initial flower number per tree, which was negatively correlated to relative fruit set with all three cultivars, but positively correlated to final fruit number per tree. With more flowers there were always more final fruits on the tree regardless of thinning treatment, timing, or other climatic factors. This result coincides with a primary result of our previous paper where we showed that natural drop of unthinned trees over 18 years increased when the initial flower cluster number also increased (Lordan et al., 2019). Probably, this is because the large number of initial fruitlets compete for resources at the same period that the carbohydrate support for fruit growth mainly comes from the spur leaves (Byers, 2002; Byers et al., 1991; Corelli-Grappadelli et al., 1994; Lakso and Goffinet, 2017). During the thinning window (5-20 mm of fruit size) carbohydrate supply and demand 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) and with a high number of initial flowers the early fruitlet demand is often more than the tree can support.

A second important variable in explaining relative fruit set of chemical thinners was the time after bloom measured in DD that the chemical thinner was applied. This is likely an expression of the stage of development. Both BA and NAA applied at petal fall had the least effect on relative fruit set (0.9), whereas the greatest reduction in relative fruit set occurred when chemicals were applied at about 200-250 DD after bloom (~14 days after petal fall in most years). This result also coincides with the results of our previous paper where we showed that natural drop of unthinned trees over 18 years was greatest at 200-250 DD after bloom (Lordan et al., 2019). When looking at yearly patterns in our current work, there was some variation from the 200-250 DD optimum obtained by combining the data from all 12 years. At that time of the year, long-term weather averages at Geneva, NY show that each day contributes on average about 10 DD, which relates to about 0.6 mm fruit growth resulting in a fruit size of 11-12 mm, when fruitlets are most susceptible to chemical thinners.

However the patterns of thinner response varied considerably by year. In some years the minimum relative set induced by chemical thinners occurred when sprays were applied as early as 150 to 200 DD (2009 and 2010) and in other years when sprays were applied much later at 250-275 DD (2001, 2002, and 2008). Thus, in any given year there seemed to be natural drop reaching a maximum at 200-250 DD (Lordan et al., 2019) but also drop induced by chemicals could occur earlier or later than that time. In addition in some years like 2004 or 2009, relative set varied little (1-0.8) compared to the unthinned control trees and in response to chemical thinner applications over the entire thinning period from 100-350 DD. This illustrates that other factors in addition to initial flower number and DD from bloom are affecting chemical thinning efficacy.

When the data from all 12 years was considered, carbohydrate balance was an important factor in explaining relative fruit set. There was a positive linear relationship for the carbohydrate net balance for the period comprised between 2 days before the chemical application and up to 5 days after. However, the effect of carbon balance was greatest at 200-250

DD after bloom and was much less at earlier or later timings. This indicates that considering carbon balance using the MaluSim model can add important predictive power to models to predict thinning but carbon balance will be most helpful in predicting thinning efficacy at the PF+7 to the PF+18 time period. Carbon balance was not only important in predicting relative fruit set of a chemical thinning spray but our earlier work (Lordan et al., 2019) showed that it is also important in predicting natural fruit drop.

Several other less important factors had a significant effect on relative fruit set. DD from November through December was a significant variable but only for ‘Delicious’. There was a negative effect of DD from January 1st to bud break on relative fruit set for ‘Gala’ and ‘McIntosh’. DD from bloom to petal fall also had a significant impact on relative fruit set for ‘Delicious’ and ‘McIntosh’ with a positive relationship.

Interestingly when modeling final fruit number per tree (the most practical response variable), similar factors were found to be significant as when modeling relative fruit set despite the fact that final fruit number per tree integrates natural drop and chemically induced drop. In the case of final fruit number, the number of initial number of flower clusters per tree showed a positive relationship. Carbohydrate net balance for the period comprised between 2 days before the chemical application and up to 5 days, and DD after bloom had the same effect as well, with the lowest number of fruit per tree when thinners were applied at 200-250 DD after bloom. The other minor factors such as DD from January 1st through bud break showed a significant negative relationship and DD from bud break to bloom showed a positive relationship with final fruit number for all the three cultivars. Conversely, DD from bloom to petal fall had a positive relationship to final fruit number for ‘Delicious’ and ‘McIntosh’.

Relationships for the different regressor variables and cultivars have been summarized in Figure 10. In general, all the cultivars showed higher action of the thinners when they were applied at 200-250 DD from bloom. This period corresponds to 15-29 days after bloom, which coincides with a predicted period of carbohydrate deficit in relation to the needs of developing fruitlets (Lakso and Johnson, 1990; Lakso et al., 1999). This also is the same time when the fruits are in an exponential fruit growth rate (Lakso et al., 1995; Lakso et al., 1999). Corelli-Grappadelli et al. (1994) and Lakso et al. (1999) reported that the rapid fruit growth at that stage requires large carbohydrate supply. Thus we conclude that this is why fruitlets are more susceptible to chemical thinning at this stage, since chemical applications such as BA (Zhou et al., 2017) and NAA are likely to create a temporary carbohydrate deficit, triggering substantial fruit abscission. The effect of carbohydrate deficits on cell production at that stage has been reported in previous studies (Dash et al., 2012; Dash et al., 2013; Zhou et al., 2008).

Our results confirm that both relative fruit set caused by chemical thinning sprays and final fruit number per tree affected by both natural and chemical induced drop are affected by the carbohydrate balance two days before the spray and up to five days after. Zhou et al. (2017) have shown that at least for BA sprays, there is a down regulation of genes involved in carbon production and utilization. Thus, we theorize that chemical thinning sprays operate by inducing a carbohydrate deficit relative to fruit demand which causes reduced relative fruit set. This action by the chemical thinners is modified and modulated by climate induced carbohydrate deficits or surpluses. Thus, naturally induced carbohydrate surpluses available to support fruit growth could negate the chemically induced reduction in carbon supply and be the cause of higher relative fruit set and higher final fruit number in some years when chemical thinners do not work very well (Lakso et al., 2006; Robinson and Lakso, 2011). However in other years with a large climate created carbohydrate deficit coinciding with a chemical spray induced carbon deficit could be the cause of excessive thinning in some years.

Our data also support predicted carbon balances by the MaluSim model (Lakso and Johnson, 1990; Lakso et al., 1999). The model predicts that near petal fall the demand for carbon by the very small fruitlets is relatively low since fruitlets are small and not growing rapidly (Lakso and Robinson, 2014; Lakso et al., 2006; Lakso et al., 2001; Lakso et al., 1999). Even with a significant carbohydrate deficit at that time our field data indicate there was little impact of thinning chemicals at this timing since the slope of the relationship is almost zero. However, at later timings when fruit growth is more rapid and fruit demand for carbohydrate is high, our data showed large effects of carbon deficits on thinning efficacy when thinning chemicals were applied. The slopes of the relationship of carbohydrate balance and final fruit number at the time of maximum effect of carbon balance on final fruit number (12-14 days after petal fall) was 4 fruits, 3 fruits and 1.5 fruits per g of carbon for 'Gala', 'Delicious' and 'McIntosh', respectively (Figure 10). Thus efforts to model final fruit number must consider: 1) the initial flower number per tree, 2) the time after bloom (DD) when the spray is applied, and 3) the carbohydrate balance for 2 days before the spray through 5 days after the spray.

The other significant factor that impacted thinning efficacy was cumulative DD at different periods in the year which coincides with observations by various researchers in a qualitative way (Francesconi et al., 1996; Greene, 2002; Williams, 1979; Williams and Edgerton, 1981). These studies have indicated that final fruit number per tree and relative fruit set are affected by weather the previous summer, fall or winter, carbohydrate relations from the previous year, and temperature and sunlight from bud break to bloom or post bloom. Our study is the first to quantitatively evaluate these variables although our previous paper (Lordan et al.,

2019) seems to indicate that DD is a poor model of plant development during ecodormancy. Nevertheless DD from January 1st to bud break did have a significant relationship with thinning efficacy in the present study. In our study, high values of DD from the previous fall were related to higher relative fruit set the following season for ‘Delicious’. This period is known to be important for root development, storage of nutrient reserves and for flower bud development in late-developing buds for the next year (Lakso, 1987; Williams et al., 1980). Thus warm autumn temperatures may help these processes, leaving trees with a positive carbohydrate balance before the next season starts.

Cumulative DD from January 1st to bud break similarly affected relative fruit set and final fruit number per tree but with a negative relationship. In previous studies, warmer temperatures for that period have been related to lower yields (Jackson and Hamer, 1980; Jackson et al., 1983; Lakso, 1987). The actual mechanism of response is not clear, but it is possible that warmer temperatures in the late winter after the completion of endodormancy may cause the tree to use more carbohydrate reserves resulting in less carbohydrate available during the bloom period. It is also possible that warmer temperatures in that period might advance bloom, which can be significantly damaged if spring frosts occur.

Our results with DD from bud break to petal fall coincide with the results of Jackson and Hamer (1980), who showed a positive relationship between temperatures from bud break through petal fall. This might be explained by better conditions for pollination and fruit growth with warmer temperatures. Higher radiation may accompany higher temperatures which may stimulate leaf photosynthesis development, which may help carbon balance later. However, extremely high temperatures at that time might also have the opposite effect.

Conclusions

For 12 years, quantitative estimates of effects of daily carbohydrate balance were evaluated during the thinning period. We saw a correlation between carbohydrate balance and relative fruit set and final fruit number per tree with 3 cultivars. These correlations have been noted in various other studies, but have not been subjected to detailed statistical analysis of correlation and optimal timing between carbon deficits or excesses and chemical thinning responses. The detailed statistical analysis showed both relative fruit set and final fruit number per tree were affected by the carbohydrate balance within two days before the spray and up to five days after, but the magnitude of the effect depended on the time after bloom. There was a period, 200-250 DD from bloom, (15-29 days after bloom) that thinners showed higher action. The greater the carbohydrate supply relative to demand, the greater the relative set and the final fruit number. In addition, other factors such as initial flower density, temperatures of the previous fall, and from January to bud break, and from bud break to petal fall also had a significant impacts on natural fruit set and final fruit number.

In summary, in spite of the dozens of factors reported to affect relative apple fruit set and final number of fruits, over the 12 years of our study in a variable climate, both relative fruit set and final fruit numbers could be relatively well modeled with primarily flower density, representing the tree’s physiological history, an estimate of carbohydrate balance via a model representing carbon availability to support fruit growth, and DD over the season, representing season weather effects. This suggested that carbohydrate supply-demand balance may be a baseline for thinner responses, and that integrative modeling of these balances can be useful in understanding variation in thinning responses.

Acknowledgements

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Table 1. Fruit set (final fruit number/flower cluster), relative fruit set to untreated control (fruit set/UTC fruit set), final fruit number per tree, mean fruit weight (g), and number of flower clusters per tree of chemically thinned with 6-benzyladenine (BA) and Naphthalene acetic acid (NAA) at 3 or 4 day intervals beginning at petal fall (PF) until 21 days after petal fall (PF+21), and UTC for cultivars 'Delicious', 'Gala', and 'McIntosh' at Geneva, NY over 12 years (2000-2011). Grey bars represent variable value. Means followed by different letters within each column denotes significant differences (Tukey's honestly significant difference, $P \leq 0.05$).

Cultivar	**Treatment**	**Fruit set**	**Relative fruit set**	**Fruit number per tree**	**Fruit weight (g)**	**Number of flower clusters per tree**
'Delicious'	BA,PF	0.6 ab	0.9 a	241 bcde	209 abcd	445
	BA,PF+4	0.5 abcd	0.8 abc	238 abcd	207 bcd	492
	BA,PF+7	0.4 de	0.6 de	204 cde	221 abc	515
	BA,PF+11	0.5 cde	0.7 bcde	196 cde	223 abc	512
	BA,PF+14	0.4 e	0.6 e	198 de	234 ab	541
	BA,PF+18	0.6 abcd	0.8 abcd	242 abcd	208 bcd	487
	BA,PF+21	0.5 bcde	0.8 abcde	248 abc	208 abcd	532
	NAA,PF	0.6 abc	0.9 ab	260 ab	199 cd	499
	NAA,PF+4	0.5 bcde	0.8 abc	231 bcde	214 abc	499
	NAA,PF+7	0.5 bcde	0.7 bcde	215 bcde	218 abc	544
	NAA,PF+11	0.4 de	0.7 cde	189 e	225 ab	497
	NAA,PF+14	0.4 de	0.6 e	214 bcde	216 abc	570
	NAA,PF+18	0.5 bcde	0.8 abcde	212 bcde	218 abc	454
	NAA,PF+21	0.5 bcde	0.8 abcde	220 bcde	210 abcd	494
	UTC	0.7 a	.	302 a	187 d	503
	P	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**NS**
(Excluding UTC)	**Active ingredient (AI)**	**NS**	**NS**	**NS**	**NS**	**NS**
	Timing	**<0.0001**	**<0.0001**	**<0.0001**	**0.0002**	**0.0251**
	AI*timing	**NS**	**NS**	**NS**	**NS**	**NS**
'Gala'	BA,PF	0.7 bcd	0.8 ab	541 abc	139 bc	805
	BA,PF+4	0.7 bcd	0.7 b	515 bc	142 abc	861
	BA,PF+7	0.6 cd	0.7 b	435 c	152 a	803
	BA,PF+11	0.6 d	0.6 b	466 c	148 abc	889
	BA,PF+14	0.7 bcd	0.7 b	467 c	146 abc	751
	BA,PF+18	0.7 bcd	0.8 ab	494 bc	142 abc	799
	BA,PF+21	0.7 bcd	0.8 ab	543 abc	136 cd	820
	NAA,PF	0.8 ab	0.9 a	589 ab	136 cd	798
	NAA,PF+4	0.7 bc	0.8 ab	523 bc	141 abc	813
	NAA,PF+7	0.7 bcd	0.7 ab	465 c	150 ab	796
	NAA,PF+11	0.6 cd	0.7 b	467 c	146 abc	797
	NAA,PF+14	0.6 cd	0.7 b	472 c	145 abc	829
	NAA,PF+18	0.6 cd	0.7 b	481 c	144 abc	835
	NAA,PF+21	0.7 bcd	0.8 ab	508 bc	141 bc	799
	UTC	0.9 a	.	656 a	125 d	766
	P	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**NS**
(Excluding UTC)	**Active ingredient (AI)**	**NS**	**NS**	**NS**	**NS**	**NS**
	Timing	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**NS**
	AI*timing	**NS**	**NS**	**NS**	**NS**	**NS**
'McIntosh'	BA,PF	0.5 abc	0.8 abc	302 abc	159 abc	693
	BA,PF+4	0.5 abc	0.8 abc	261 bcde	163 ab	613
	BA,PF+7	0.4 cd	0.6 c	221 ef	168 a	657
	BA,PF+11	0.4 d	0.6 c	211 f	170 a	663
	BA,PF+14	0.4 cd	0.7 bc	233 def	168 a	710
	BA,PF+18	0.5 bcd	0.8 abc	249 cdef	169 a	605
	BA,PF+21	0.5 abc	0.9 ab	278 bcd	159 abc	617
	NAA,PF	0.6 ab	1.0 a	305 ab	152 bc	560
	NAA,PF+4	0.5 ab	0.9 a	292 abc	159 abc	607
	NAA,PF+7	0.5 abc	0.9 ab	251 cdef	163 ab	580
	NAA,PF+11	0.5 abcd	0.8 abc	245 cdef	162 ab	606
	NAA,PF+14	0.5 abcd	0.8 abc	254 bcdef	160 abc	606
	NAA,PF+18	0.5 abcd	0.8 abc	266 bcde	164 ab	633
	NAA,PF+21	0.6 ab	0.9 a	295 abc	153 bc	567
	UTC	0.6 a	.	350 a	149 c	614
	P	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	NS
(Excluding UTC)	**Active ingredient (AI)**	**<0.0001**	**<0.0001**	**0.0002**	**<0.0001**	**0.0059**
	Timing	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**NS**
	AI*timing	**NS**	**NS**	**NS**	**NS**	**NS**
Cultivar		**<0.0001**	**0.0046**	**<0.0001**	**<0.0001**	**<0.0001**

Table 2. Regression analysis of the relationship of average carbohydrate balance (CHO) and either relative fruit set (fruit set/untreated control fruit set) or final fruit number (Fruit #) at each of seven timings beginning at petal fall (PF) through PF+21 days when trees are sprayed with chemical thinning agents. Green highlighted values had a significant positive slope of fruit set or fruit number as a function of carbohydrate balance. Gray highlighted values had an unexpected negative slope.

Prediction variable and cultivar	Regression statistics	Timing of chemical spray						
		PF	PF+4	PF+7	PF+11	PF+14	PF+18	PF+21
Relative fruit set ‘Delicious’	R^2	0.16	0.38	0.43	0.25	0.21	0.08	0.01
	P value	NS	<0.0001	<0.0001	<0.0001	0.0001	0.031	NS
	CHO slope estimate	0.0045	0.0115	0.0094	0.0061	0.0042	-0.0035	-0.0016
Relative fruit set ‘Gala’	R^2	0.18	0.27	0.24	0.28	0.34	0.08	0.22
	P value	NS	NS	NS	0.0001	<0.0001	NS	0.006
	CHO slope estimate	-0.0021	0.0010	0.0007	0.0047	0.0039	0.0018	0.0029
Relative fruit set ‘McIntosh’	R^2	0.11	0.21	0.27	0.44	0.08	0.05	0.08
	P value	NS	NS	0.0017	<0.0001	NS	NS	NS
	CHO slope estimate	0.0013	0.0029	0.0072	0.0079	0.0026	-0.0001	-0.0036
Fruit # ‘Delicious’	R^2	0.24	0.15	0.23	0.38	0.46	0.38	0.42
	P value	NS	NS	0.0021	<0.0001	<0.0001	0.0003	<0.0001
	CHO slope estimate	-0.58	1.36	2.34	3.10	2.89	2.08	2.21
Fruit # ‘Gala’	R^2	0.004	0.22	0.14	0.14	0.39	0.12	0.05
	P value	NS	NS	0.0037	0.0008	<0.0001	0.0217	NS
	CHO slope estimate	-1.67	1.39	2.77	3.35	4.37	2.26	0.51
Fruit # ‘McIntosh’	R^2	0.17	0.11	0.31	0.39	0.39	0.41	0.31
	P value	0.0006	NS	NS	0.0009	0.0013	0.0022	0.0005
	CHO slope estimate	-5.26	-1.03	-0.63	1.64	1.47	2.09	2.39

Figure 1

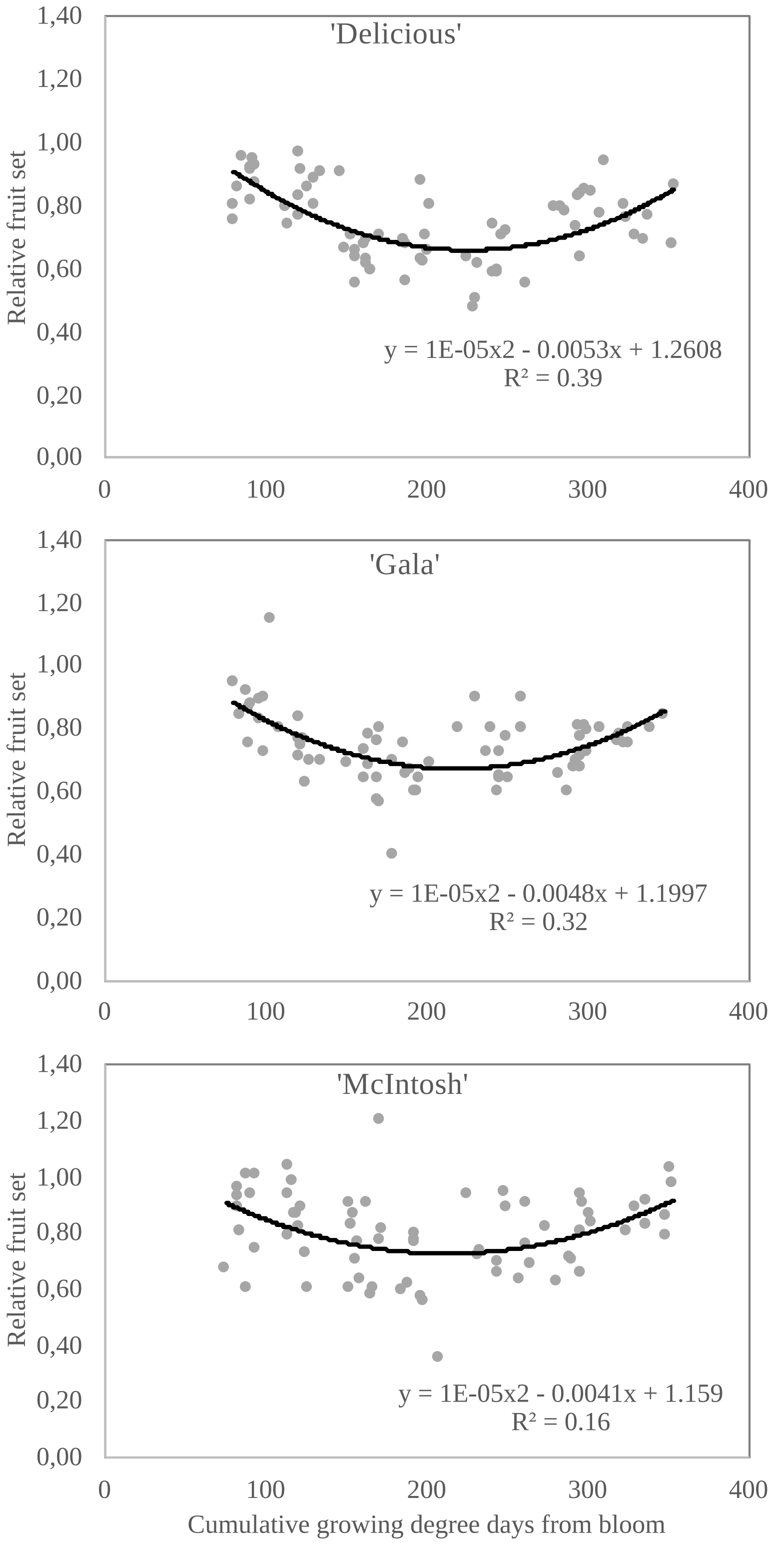

'Delicious'
y = 1E-05x2 - 0.0053x + 1.2608
R² = 0.39
'Gala'
y = 1E-05x2 - 0.0048x + 1.1997
R² = 0.32
'McIntosh'
y = 1E-05x2 - 0.0041x + 1.159
R² = 0.16
Relative fruit set
1,40
1,20
1,00
0,80
0,60
0,40
0,20
0,00
0
100
200
300
400
Cumulative growing degree days from bloom

Figure 2

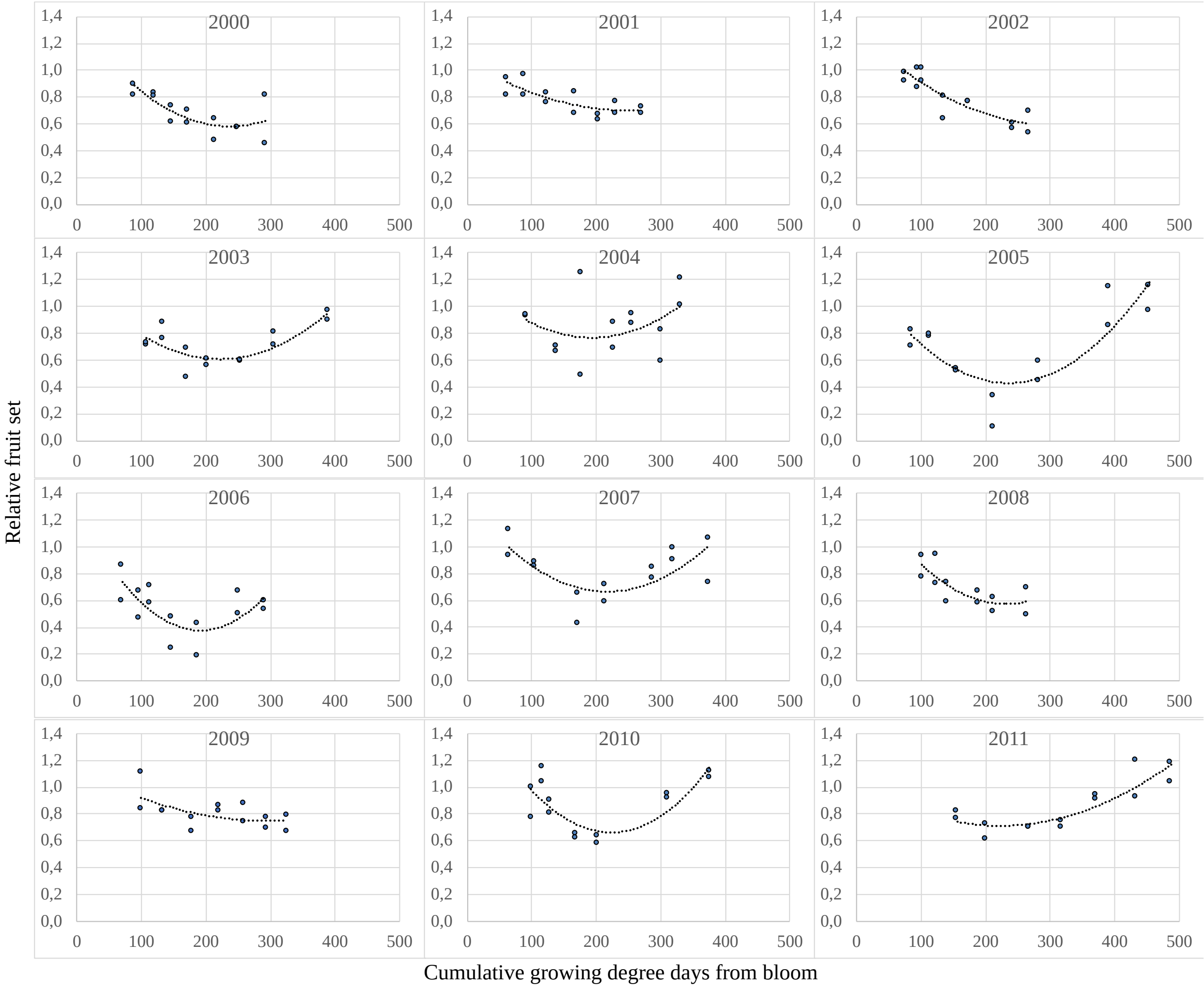

2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0,0
0
100
200
300
400
500
Relative fruit set
Cumulative growing degree days from bloom

Figure 3

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

Analysis of Variance

RSquare	0.422097			
RSquare Adj	0.412668			
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**
Model	7	18.788203	2.68403	44.7628
Error	429	25.723331	0.05996	**Prob > F**
C. Total	436	44.511533		<0.0001*

Parameter Estimates

Term	**Estimate**	**Prob>|t|**
Intercept	0.7648248	<0.0001*
Cluster#	-0.000714	<0.0001*
Cum DDBloom	-0.000544	0.0001*
(Cum DDBloom-210.911)*(Cum DDBloom-210.911)	1.0485e-5	<0.0001*
D0(600)	0.0008307	0.0169*
Ave1+4Da(600)	0.0032695	<0.0001*
DD Nov-Dec	0.000843	0.0231*
DD bloom-PF	0.0036272	<0.0001*

Prediction Profiler

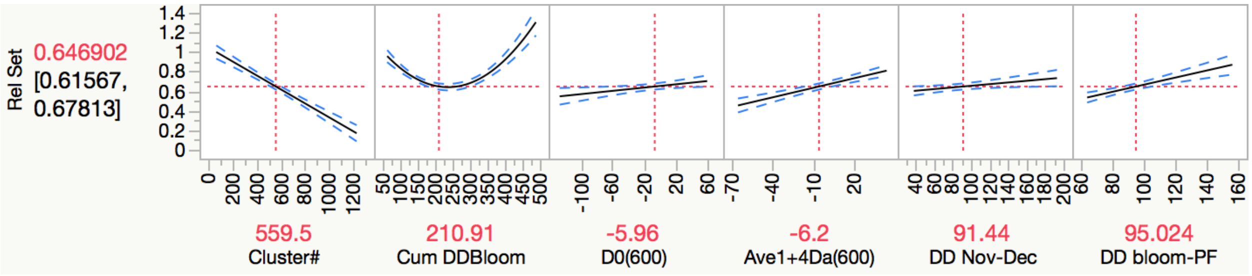


Figure 4

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

Analysis of Variance

RSquare	0.579325
RSquare Adj	0.573505

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	7	4059415.5	579917	99.5470
Error	506	2947731.4	5826	**Prob > F**
C. Total	513	7007146.9		<.0001*

Parameter Estimates

Term	Estimate	Prob>|t|
Intercept	122.98735	<0.0001*
Cluster#	0.1041769	<0.0001*
Cum DDBloom	-0.233663	<0.0001*
(Cum DDBloom-203.758)*(Cum DDBloom-203.758)	0.0027301	<0.0001*
D-2(600)	0.4099502	0.0001*
Ave1+5Da(600)	1.4120727	<0.0001*
DD Jan-BB	-2.599109	<0.0001*
DD BB-B	1.8613391	<0.0001*

Prediction Profiler

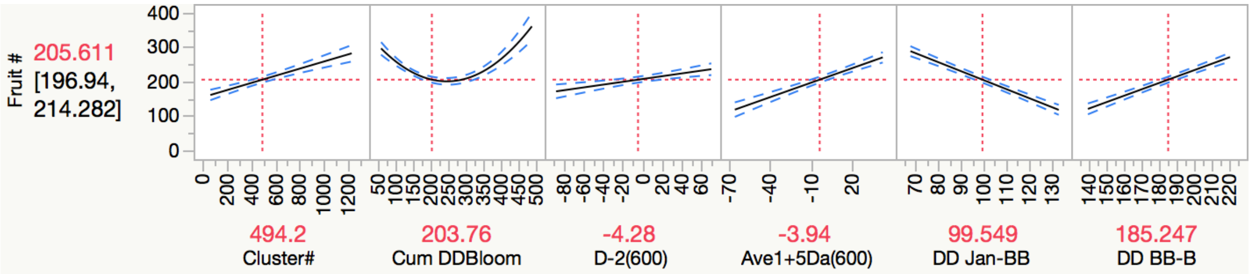


Figure 5

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

Analysis of Variance

RSquare	0.366633			
RSquare Adj	0.359748			
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**
Model	6	13.044301	2.17405	53.2553
Error	552	22.534375	0.04082	**Prob > F**
C. Total	558	35.578676		<.0001*

Parameter Estimates

Term	**Estimate**	**Prob>|t|**
Intercept	1.1692738	<0.0001*
Cluster#	-0.000376	<0.0001*
Cum DDBloom	-0.000495	<0.0001*
(Cum DDBloom-207.97)*(Cum DDBloom-207.97)	1.0223e-5	<0.0001*
D-2(600)	0.0013737	<0.0001*
Ave1+5Da(600)	0.0015578	<0.0001*
DD Jan-BB	-0.001096	0.0130*

Prediction Profiler

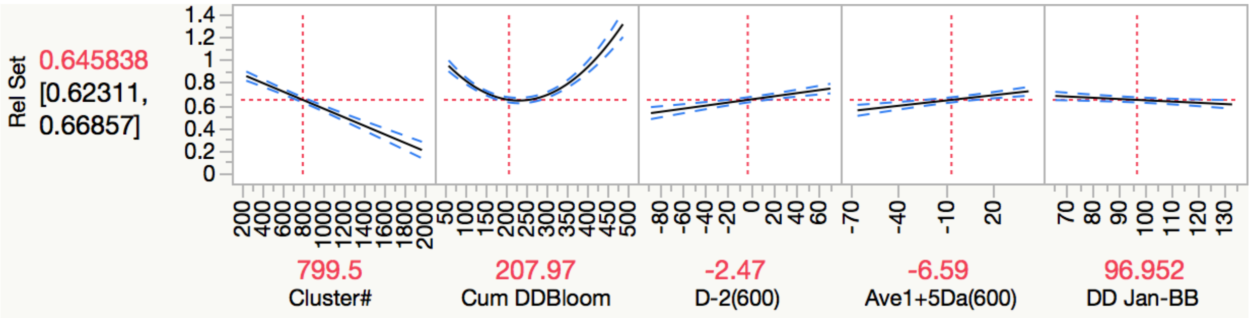


Figure 6

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

Analysis of Variance

RSquare	0.384652			
RSquare Adj	0.376255			
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**
Model	7	5956428	850918	45.8106
Error	513	9528815	18575	**Prob > F**
C. Total	520	15485242		<.0001*

Parameter Estimates

Term	**Estimate**	**Prob>|t|**
Intercept	346.16808	<0.0001*
Cluster#	0.1803534	<0.0001*
Cum DDBloom	-0.360477	<0.0001*
(Cum DDBloom-207.756)*(Cum DDBloom-207.756)	0.0051637	<0.0001*
D-2(600)	1.0475291	<0.0001*
Ave1+5Da(600)	0.9997799	<0.0001*
DD Jan-BB	-2.85099	<0.0001*
DD BB-B	1.8871055	<0.0001*

Prediction Profiler

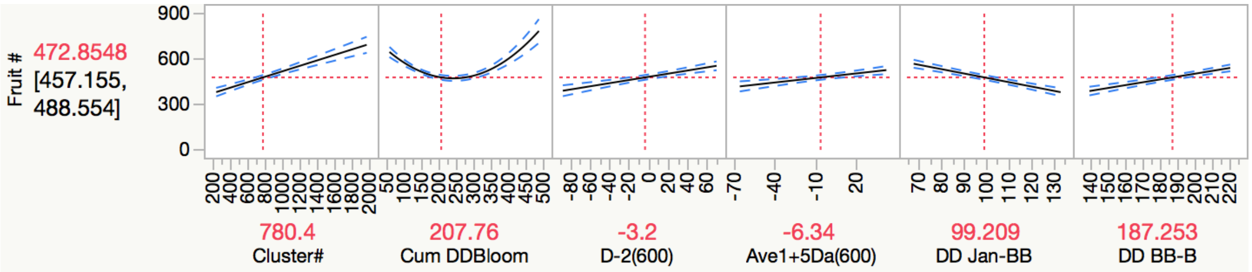


Figure 7

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

Analysis of Variance

RSquare	0.495563			
RSquare Adj	0.487156			
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	25.448243	3.18103	58.9445
Error	480	25.903945	0.05397	Prob > F
C. Total	488	51.352188		<.0001*

Parameter Estimates

Term	Estimate	Prob>|t|
Intercept	0.7395765	<0.0001*
Cluster#	-0.000558	<0.0001*
Cum DDBloom	-0.000473	0.0004*
(Cum DDBloom-204.135)*(Cum DDBloom-204.135)	9.6049e-6	<0.0001*
Ave1+5Da(600)	0.0015704	0.0027*
Ave0+2Db(600)	0.0013225	0.0028*
DD Jan-BB	-0.003197	<0.0001*
DD BB-B	0.0006701	0.0846
DD bloom-PF	0.0066709	<0.0001*

Prediction Profiler

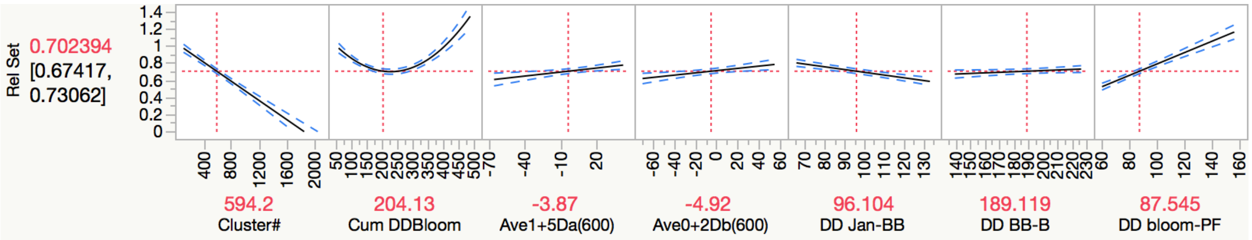


Figure 8

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

Analysis of Variance

RSquare	0.600754			
RSquare Adj	0.594359			
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**
Model	7	4534669.2	647810	93.9377
Error	437	3013625.1	6896	**Prob > F**
C. Total	444	7548294.3		<.0001*

Parameter Estimates

Term	Estimate	Prob>|t|
Intercept	-97.10789	0.0040*
Cluster#	0.1113945	<0.0001*
Cum DDBloom	-0.220869	<0.0001*
(Cum DDBloom-204.622)*(Cum DDBloom-204.622)	0.0030965	<0.0001*
D-2(600)	0.3632399	0.0049*
Ave1+5Da(600)	0.5698059	0.0022*
DD Jan-BB	-1.744141	<0.0001*
DD BB-B	2.6553929	<0.0001*

Prediction Profiler

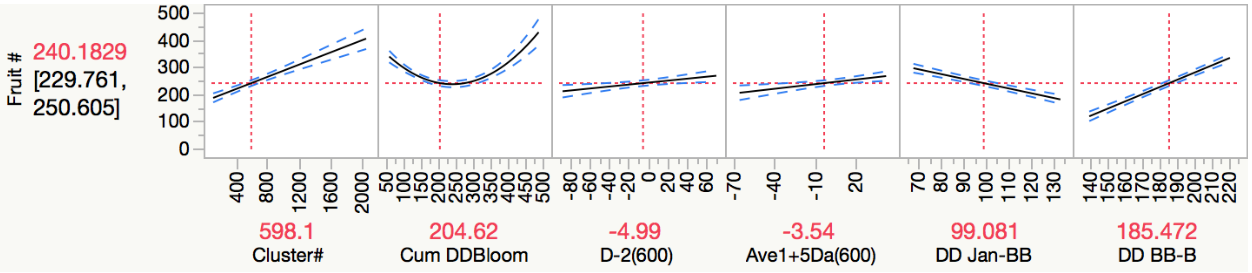
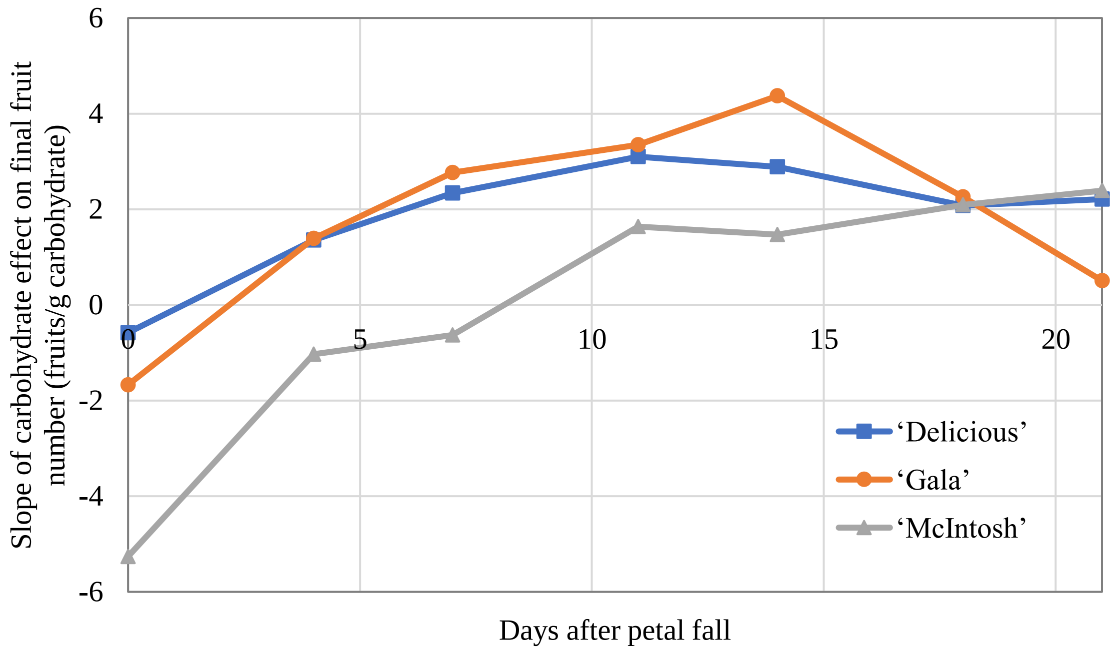
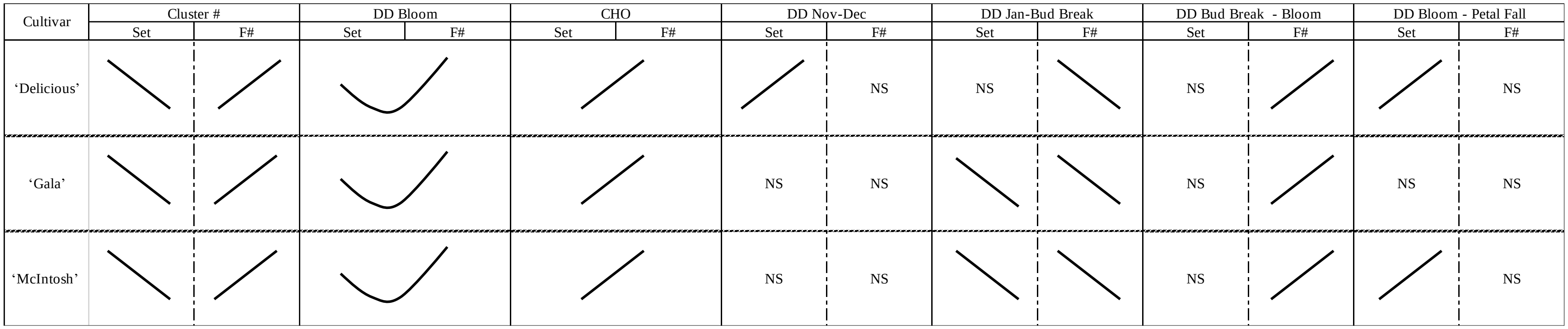


Figure 9



Slope of carbohydrate effect on final fruit number (fruits/g carbohydrate)
6
4
2
0
-2
-4
-6
0
5
10
15
20
Days after petal fall
‘Delicious’
‘Gala’
‘McIntosh’

Figure 10



Cultivar	Cluster #		DD Bloom		CHO		DD Nov-Dec		DD Jan-Bud Break		DD Bud Break - Bloom		DD Bloom - Petal Fall	
	Set	F#	Set	F#	Set	F#	Set	F#	Set	F#	Set	F#	Set	F#
‘Delicious’	↘	↗	∪		↗		↗	NS	NS	↘	NS	↗	↗	NS
‘Gala’	↘	↗	∪		↗		NS	NS	↘	↘	NS	↗	NS	NS
‘McIntosh’	↘	↗	∪		↗		NS	NS	↘	↘	NS	↗	↗	NS

Figure captions

Figure 1. Relationship of cumulative growing degree days from bloom and relative fruit set (fruit set/untreated control fruit set) for ‘Delicious’, ‘Gala’ and ‘McIntosh’ apple trees over 12 years when sprayed with a chemical thinning spray at Geneva, NY.

Figure 2. Relationship of cumulative growing degree days from bloom and relative fruit set (fruit set/untreated control fruit set) for each year at Geneva NY, pooling together the three cultivars ‘Delicious’, ‘Gala’ and ‘McIntosh’ and both thinners 6-benzlyadenine and Naphthalene acetic acid (BA and NAA).

Figure 3. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Delicious’ model built to predict relative fruit set (fruit set/untreated control fruit set) using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, carbohydrate net balance on the spray day (g), average carbohydrate net balance for the period comprised from one day after the spray through four days after (Ave1+4Da) (g), DD from November to December, and DD from bloom to petal fall (PF).

Figure 4. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Delicious’ model built to predict final fruit number per tree using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, carbohydrate net balance two days before the spray day (D-2) (g), average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da) (g), DD from January 1st to bud break (BB), and DD from BB to bloom (B).

Figure 5. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Gala’ model built to predict relative fruit set (fruit set/untreated control fruit set) using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, carbohydrate net balance two days before the spray day (D-2) (g), average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da) (g), and DD from January 1st to bud break (BB).

Figure 6. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘Gala’ model built to predict final fruit number per tree using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, carbohydrate net balance two days before the spray day (D-2) (g), average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da) (g), DD from January 1st to bud break (BB), and DD from BB to bloom (B).

Figure 7. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘McIntosh’ model built to predict relative fruit set (fruit set/untreated control fruit set) using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da) (g), average carbohydrate net balance for the period comprised from the spray day through two days before (Ave0+2Db) (g), DD from January 1st to bud break (BB), DD from BB to bloom (B), and DD from bloom to petal fall (PF).

Figure 8. Summary of fit, analysis of variance, parameter estimates, and prediction profiler of ‘McIntosh’ model built to predict final fruit number per tree using MaluSim with 600 fruit/tree. Model coefficients are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, carbohydrate net balance two days before the spray day (D-2) (g), average carbohydrate net balance for the period comprised from one day after the spray through five days after (Ave1+5Da) (g), DD from January 1st to bud break (BB), and DD from BB to bloom (B).

Figure 10. Change in slope of regression line between carbohydrate balance and final fruit number for three cultivars averaged over 12 years at Geneva, NY, USA. At petal fall there is a very small effect of carbohydrate balance on thinning results. At later times the effect varied from 1 fruit to 4 fruits per g of carbon.

Figure 10. Relation of regressor variables to predict fruit set and final fruit number per tree for ‘Delicious’, ‘Gala’, and ‘McIntosh’. Variables are initial number of flower clusters per tree, cumulative growing degree-days (DD) from bloom, carbohydrate net balance (CHO), DD from November to December, DD from January 1st to bud break, DD

from bud break to bloom, and DD from bloom to petal fall. NS indicates no significant variable for that prediction model.