Final Report  
Project AH-01-63  

Title: Development and Testing of a Model of Carbohydrate Production and Distribution That Supports Fruit Set, Abscission and Thinning in Apples  

Submitted by: Alan N. Lakso  
Cornell University, Dept. Hort. Sciences, Geneva, NY  

Co-PI's  
Duane Greene, University of Massachusetts (2000-02)  
L. Lombardini & Jim McFerson, WTFRC, Wenatchee (2000-02)  

Objectives  
The overall objectives of the proposed research during the past 3 years were to improve the apple carbohydrate balance model for fruit growth and set by (a) experimental research on the key data needed to construct and (b) improvements in the model and model testing:  

Experimental Research Objectives  
(1) To evaluate the effects of common postbloom thinners (NAA, carbaryl and Accel) on the carbon production by apple trees in relation to effects on fruit thinning.  
(2) Determining the effects of differing levels of light on the relative growth of interior and exterior fruits versus shoots and trunks and fruit set at several times after bloom.  
(3) Determining the patterns of interior and exterior apple fruit carbon reserve development after bloom and determine if the reserves smooth out variations in fruit growth caused by variations in current photosynthesis.  
(4) To document the patterns of fruit growth and seed development in the first half of the growing season for Delicious and Gala apples in WA and NY to relate specific seed to fruit developmental shifts and see if climate affects these processes.  
(5) To evaluate the respiration rates of Delicious and Gala apples at intervals over a season to develop comparative estimates of apple carbohydrate demand over the season.  

Model Development and Testing Objectives  
(1) To test the recently-developed carbon balance model to determine if it can explain and predict the effects of environment (temperature and light) on response to thinners.  
(2) To improve the model by adding a component to model chemical and hand thinning on set and fruit sizing.  
(3) Testing the model simulations using Washington State weather and tree inputs versus whole canopy photosynthesis measurements made in Washington orchards.  
(4) To improve the fruit growth and abscission submodel in the carbohydrate balance model of the apple tree, and to develop a quantitative submodel of fruit growth and abscission response to chemical thinners.  

Significant Findings  
Since there were several aspects to the work over 3 years, the significant findings will be organized first by experimental results then by the modeling work.
Experimental Research Results

Post-bloom Thinner Effects on Photosynthesis and Thinning.
The effects of NAA, BA and Carbaryl on leaf and canopy photosynthesis was relatively minor and short-lived. The effects of these thinners on photosynthesis are inconsistent, but generally mild. The thinning effect of NAA, BA and Carbaryl was not fully explained by their effects in leaf and canopy photosynthesis although it may play a secondary role (Fig. 1).

Fig. 1. Comparative effects of chemical thinners on apple leaf photosynthesis and final crop load.

Effects of Shade on Fruit vs Shoot Competition
The effects of changing light levels to apple trees at the 17 mm fruit diameter stage showed that although shoot growth was not affected by shade to 12% of full sun, fruit growth was reduced markedly and in relation to the reduction in tree photosynthesis (as estimated by whole tree photosynthesis in balloon chambers in Wenatchee and in Geneva, and by the carbohydrate model) (Fig. 2). The 35% light caused significant fruit drop, but the 12% light completely defruited the trees. Clearly fruit growth and set was sacrificed at this time for shoot growth, but tree photosynthesis is a good indicator of carbohydrates available to the fruit at this critical fruit development stage.
Fig. 2. Effects of changes of available light by soil reflector or by shade to 35 or 12% of full light for 6 days on fruit and shoot growth relative to controls (lines). Individual points are estimates of relative tree photosynthesis determined by whole tree balloon chambers in WA or NY and by the carbohydrate model.

**Effects of Shade on Apple Fruit Growth and Fruit Carbohydrate Reserves**

This experiment led to several conclusions, some of them quite surprising:

• Starch accumulation in apple fruits began as soon as 10 mm diameter, but staining was not seen until about 20-25 mm in young fruitlets of Empire apples (or other varieties) (Fig. 3). The fruit contained as much as 5-7% starch by dry weight before staining occurred.

![Graph showing starch concentrations in developing Empire apple fruit.](image)

Fig. 3. Starch concentrations in developing Empire apple fruit. Fruit diameters were about 10 mm on 25 May, 20 mm on 10 June and 35 mm on 30 June.

• When heavy shade to 20% of full sun was applied, the fruit slowed or stopped growth at all stages tested between 10 and 35 mm. They stopped accumulating starch, but showed little starch usage even when the fruit fell (Fig. 4). In some cases fruit fell with over 10% starch contents still in them!

![Graph showing increase in fruit diameter in prior 3 days](image)
Fig. 4. Relationship of fruit growth rates of control fruits and shaded fruits of Empire apples at 35 mm diameter to their internal starch concentration.

• When trees were shaded at the common thinning stage of 12 mm fruit diameter, fruit growth rate was reduced and drop was related to the severity of growth reduction. This effect was aggravated by heavy cropping as predicted by the carbohydrate model (Fig.5).

![Graph showing fruit growth rate vs. days of shade for McIntosh apples at 12-17 mm diameter.](image)

Fig. 5. Reductions in apple fruit growth, expressed as % of low-cropped control trees. Note the combined effect of shade and heavy cropping.

• Interestingly, at 35 mm fruits could reduce their growth to near zero for several days, but not drop as strongly as normally occurs earlier during cell division (at 5-20 mm fruit diameter). This difference in response of drop to growth rate is being changed in the model although we do not fully understand the mechanism.

Physiological and Anatomical Development of Delicious and Gala

• We found that Delicious fruit showed similar dark respiration rates as Gala and Empire (similar to Gala; not shown for clarity) per gram of tissue or per fruit until about the 15 mm fruit diameter stage. Then Delicious fruits showed markedly higher respiration rates for the rest of the season expressed either way. The reason for this is not clear, as respiration normally is a function of growth, yet the growth rates in this study were not that different. Nonetheless, this suggests that Delicious may have a higher demand for carbohydrates over the season compared to other varieties like Gala or Empire.
Fig. 6. Dark respiration rates of Delicious and Gala fruits as respiration per fruit over the 2002 season. Measurements taken at similar temperatures.

• Fruit and Seed Development - Since key fruit development patterns, such as the duration of cell division, have been reported to be controlled by seed development, we began in 2002 an anatomical examination of the timing and duration of cell division flesh versus the patterns of seed development of fruits grown in New York and Washington. Many fruits were collected in NY and WA over the first 9 weeks after bloom. Unfortunately, most of the samples from WA were destroyed in shipment to NY, so the WA portion will be repeated in 2003. The detailed anatomical analyses are continuing. So far, our results supports findings in the older literature that the embryo does not develop to any degree until endosperm (a tissue that supports embryo development later) becomes cellular at about the time of the end of cell division. In the figures, it can be seen that at 4 weeks after bloom, the embryo itself is tiny and only beginning to develop (Fig. 7). After that time it grows rapidly. However, we cannot yet conclude that fruit cell division is tightly related to seed development in these cases until all analyses are complete.

Fig. 7. Embryo and endosperm development in Red Delicious apple. A. Embryo at 4 weeks post bloom is still at globular phase, while endosperm tissue enlarges in free-nuclear division within the
nucellus. B. Embryo initiating heart-shaped cotyledonary phase at 4 weeks, with endosperm progressing into its cellular phase. C. Embryo at 7 weeks showing two cotyledons and radicle, while endosperm enlarges and nucellus is crowded inside the integuments. D. Embryo at 8-1/2 weeks fills the seed, while remaining endosperm is absorbed. Abbreviations: E, embryo; En, endosperm; In, integuments; N, nucellus.

Carbohydrate Supply/Demand Model Development and Testing

Note - The modeling reported here deals with the carbohydrate supply/demand component of tree behavior. It does not model hormonal or nutritional effects that are likely also important in response to chemical thinners.

Modeling the effects of environment on natural fruit drop and response to thinners

• Model simulations of fruit abscission responses to low light or reduced photosynthesis at thinning time appear to give realistic responses of natural drop and greater thinner response due to poor light (Fig. 8). The results are promising; however, the fruit drop in the model appears to be more sensitive than it should be. This is being evaluated currently.

Fig. 8. Actual (from Byers, et al., 1991) and modeled effects of 1, 2 or 3 days of continuous low light or 2 or 3 days of low light alternated with sunny days on final fruit crop load or final fruit numbers/tree (simulations).

• Interacting effects of light and temperature have been reported (i.e. good set at cool night temps and high daily light, heavy drop with warm night temps and low light). These effects were modeled at 2 weeks after bloom by varying night temps that affect demand for carbohydrates at high and low light that affect supply of carbohydrates. The simulations indicate that if it is sunny, night temperatures do not make much difference until very warm as there is adequate supply. However, under low light conditions (equivalent to overcast), warming night temperatures have much stronger effects. Again this behavior is realistic and promising.
Fig. 9. Modeled interactions of night temperatures (4 nights) and daily light on natural fruit set at 2 weeks after bloom. Low light was set to be equivalent to heavily overcast skies for 2 days.

- Chemical thinners may have their effects by several mechanisms, including direct hormonal effects and effects due to the mild reduction of photosynthesis. To estimate the potential effect of reduction in tree photosynthesis on fruit drop, we modeled the effect for a heavily-cropping tree at 12 mm fruit diameter (Fig. 10). The simulation assumed the reduction in photosynthesis continued for 3 days. With this scenario, it appears with measured reductions of about 15%, we would expect about 10% crop reduction due only to reduced carbohydrate supply. So, based on experiments (Fig. 1) and modeling, it appears that photosynthetic reduction can account for a portion, but not all of chemical thinning effects.

Fig. 10. Modeled effects of a 3 day reduction in photosynthesis due to chemical thinners (or other factors that affect photosynthesis) to varying amounts on fruit set.

- Modeling Approaches to Chemical Thinners
  - Input a specified reduction in fruit growth rate due to thinner - This is based on the common observance that the growth rate of fruit that will drop is reduced by chemical thinners. This
can give realistic interactions with the environment and pre-thinning crop load. However, this approach does not include any mechanisms that may respond differently in different situations, so its generality may be limited. This is the initial approach until the following are possible.

- **Input the range of effects of thinners on important processes** - This approach would input effects of thinners on competing shoot growth, photosynthesis, respiration and other major components of carbohydrate balance that interact. With such a range of effects it may explain the common effect of thinners that have differing behavior (for example, one might affect mostly supply; another might mostly affect demand). The greatest problem is that we know so little quantitatively about these other effects of thinners. Need much more information on non-fruit effects of thinners, but we are exploring what can be done at this time.

- **Integrate carbohydrate model with hormonal model** - This will be a future approach as Dr. Fritz Bangerth in Germany and colleagues are developing better hormonal models. We hope to cooperate to integrate our models in the future. Also molecular genetic efforts should help clarify some of the hormonal mechanisms of action that have eluded us.

**Carbohydrate Modeling with Washington and New York Weather.** The major conclusions from the model comparisons were that the first 50-60 days or so after budbreak were quite similar in the two climates. This is due to the tree not beginning growth until the weather reaches a given temperature regardless of climate. Budbreak and bloom in WA occur about 3 weeks ahead of NY, but at similar temperatures. However, after about 50-60 days from budbreak (about 3 weeks after bloom), the higher light in WA leads to more potential canopy photosynthesis for the rest of the season. Also, the season in general is longer, so there is much better postharvest photosynthesis in WA which appears to be good for recovery and better final bud development for the next year. Overall the model suggests that similar trees in WA should produce about 25-28% more total carbohydrates over the season compared to NY. Of course, differences in training systems, leaf areas, photosynthesis rates or stress effects that may occur were not modeled in this comparison. These can be modeled, but need site-specific data.

![Fig. 11. Long-term growing season max and min temperatures at Wenatchee, WA and Geneva, NY. Budbreak dates used were 24 March for WA and 15 April for NY.](image-url)
Fig. 12. Seasonal daily light values (thin lines) and simulated daily tree photosynthesis of a "standard" dwarf tree using Wenatchee and Geneva weather inputs. Bloom occurs at about 30 days from budbreak.

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