Apple Fruit Growth

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The apple fruit goes through a complex developmental sequence over a growing season. Understanding the processes involved, what supports fruit growth and what limits it, helps to support good crop management. This article describes the basic processes of fruit growth and the factors that support or limit fruit growth.

> **"Apple flower opening in the spring is supported by tree carbohydrate reserves until bloom but post-bloom fruit growth is supported by the current photosynthesis of the leaves. Spurs support fruit growth in the first few critical weeks after bloom. Extension shoots do not support fruit initially as they support themselves until a few weeks after bloom. These results emphasize the importance of open canopies to get light to spurs, light pruning to have fewer vigorous shoots, and early thinning to allow maximum cell numbers to be produced."**

The apple fruit derives from the base of the apple flower after pollination and fertilization of the egg cells in each of the 10 ovules in the base of the flower (Figure 1). After petal fall the base ovary of the flower begins to expand to make the fruit we harvest, as the diagram shows.

Apple growth is properly measured in *weight* gain. Diameter can be measured but since it is only one dimension of a 3-dimensional fruit, diameter expansion can be deceiving. For example, a 1-mm increase in diameter very early in the season may represent only part of a gram while near harvest a 1-mm increase can mean several grams of weight growth. So, we use weight growth in this discussion.

Seasonal Growth Pattern of Apple Growth

Once the flower is fertilized, the fruitlet grows initially by exponential cell division; that is, cells divide to produce twice as many cells, then divide again to give 4 times as many, then 8 times, etc. This gives an ever-increasing rate of growth. For the first week or so growth is only by cell division as cells do not get bigger (Figure 2).

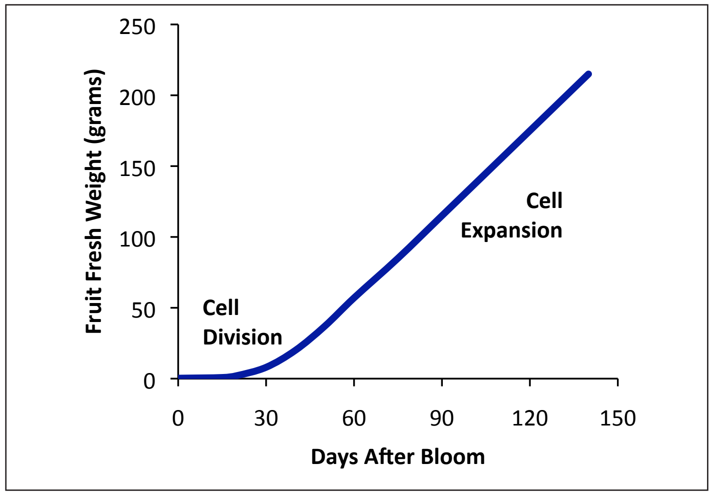
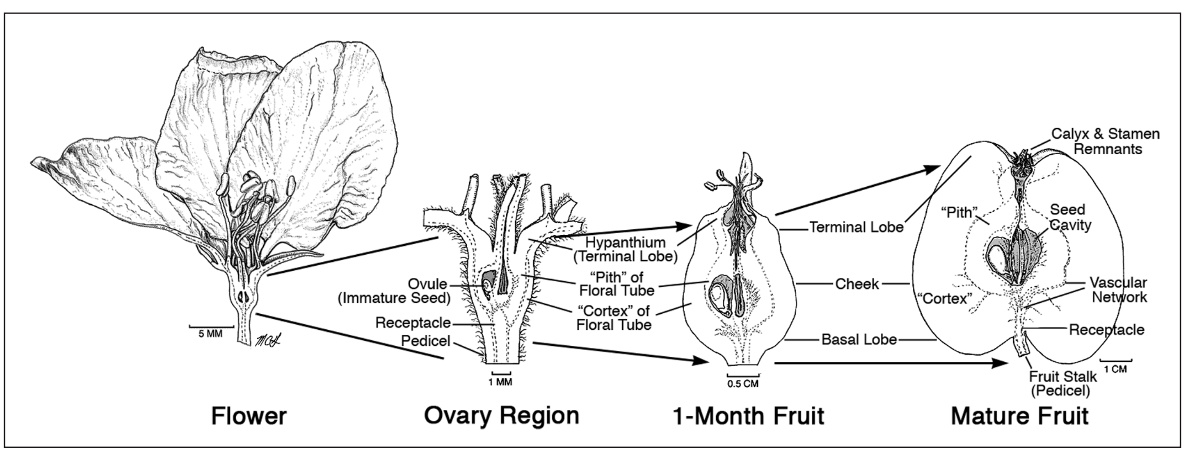


Figure 2. The inherent seasonal pattern of apple fruit growth by weight with no crop or environmental limitations. Note the initial curvilinear growth for 4-6 weeks is by cell division but later linear growth is by cell expansion.

Then from about 1 week after bloom until about 4 or 5 weeks after bloom, growth occurs by both cell division and cell expansion. Finally, growth for the rest of the season occurs essentially only by cells expanding. During this cell expansion period the fruit adds a similar amount of weight per day until harvest, although with very heavy crops or cold weather the rate of fruit growth may decline before harvest. We have found that large fruit have higher growth rates than smaller fruit (for example, 2



Figurere 1. Diagram of the apple flower and how it evolves into a fruit. Drawing by M. Goffinet.

grams per day versus 1.2 grams per day respectively). When we measured cell numbers per fruit, we found that the difference in growth rate was directly controlled by cell numbers, as each cell grew the same amount per day in all fruits.

Because the apple tree, with a heavy bloom, will produce 10-15 times more flowers and potential fruit than desirable at harvest, 90-95% of the fruits must fall off to avoid over cropping. If too many fruit compete for too long, cell division is curtailed. In a detailed anatomical study we found that fruit size variation at harvest from thinning trials was about 85% explained by cell numbers and only a small amount due to cell size variation.

The bottom line is that the final fruit size potential, and generally the actual size at harvest, depends primarily on the number of cells in the fruit. And since cell numbers are set in only the first few weeks after bloom, that is a critical time for the whole season. Fruit with low cell numbers from excess competition after bloom, due to late or inadequate thinning, can never catch up later to become large fruit.

Good fruit size requires a lot of cells. Since cell numbers are a result of cell division that occurs only in the first several weeks after bloom, the critical time to adjust fruit numbers by thinning is as early as possible after bloom. If thinning is done early, the retained fruit will have time for further cell division, thus improving size potential. However, if thinning is done late, the fruit will have suffered from competition for too long, have too few cells and have little to no time to catch up in cell numbers.

Additionally, next year's flower buds are already developing at the same time fruitlets are setting in the weeks after bloom. If thinning is delayed too long, not only is fruit size decreased, but return flowering and next year's crop potential will be reduced as well. Both these factors place an emphasis on early crop adjustment.

As fruit grow in weight, the apple fruit accumulates large amounts of starch during the season. We have found that the starch is not available to support fruit growth, but it appears that the starch is saved to be converted to sugars as harvest approaches. Presumably this was a natural selection for making fruits in the wild sweeter and more attractive to animals to increase seed dispersal. This change from starch to sugar provides a useful common indicator of fruit maturity.

Why Do Some Fruit Drop and Some Stay on the Tree?

Since often 90% or more of the young apple fruitlets need to fall, either naturally or by chemical or hand thinning, we wondered why some fruits drop but others stay on the tree? It turns out that *fruit that can maintain a continuously high growth rate stay on the tree. However, fruit that have a slow growth or slow their growth for several days will drop.*

We have monitored the growth of thousands of fruit over many years and find a consistent general relationship between fruit growth rate and drop (Figure 3). Although varying a bit, it is the same for many varieties as well as for fruit drop caused by different thinners, natural stresses of low light or just excess competition among fruits. A decrease in growth rate that leads to fruit drop can also occur for only a few days, but once it happens the fruit is destined to drop in the next week or so. *So the bottom line is that anything that reduces fruit growth will increase drop.* That seems to explain why so many different things (stresses, different chemical, cloudy or hot periods, etc.) can increase fruit drop.

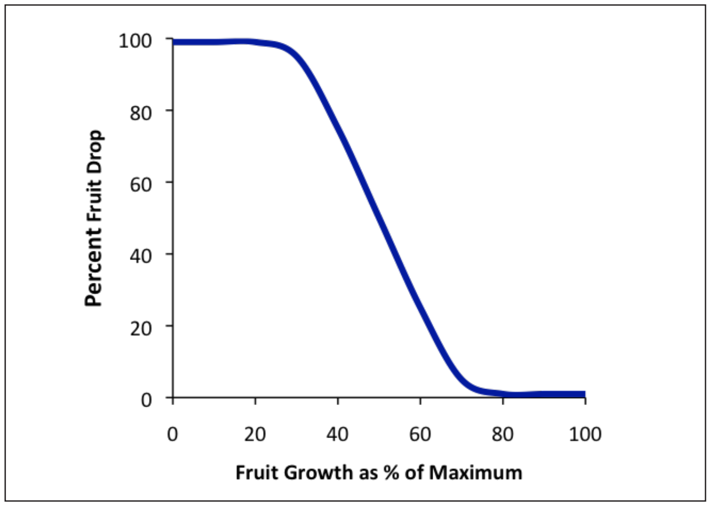


Figure 3. General relationship between apple fruit drop and growth rate showing that fruit have to retain a high growth rate to be able to stay on the tree.

Fruit Respiration and Mineral Uptake

Fruit respiration (that generates energy for growth) is very high early in the season, as cell division requires a lot of energy. As the fruit shifts more in mid and late season to cell expansion that requires less energy, the respiration rates decline. However, apple is what is called a "climacteric" fruit that has a marked increase in respiration and the production of ethylene just at harvest. This indicates a striking change in the metabolism of the apple fruit as it reaches maturity.

As well as accumulating carbohydrates and water, the fruit take up mineral nutrients during the season such as nitrogen, potassium and calcium that are needed for growth and cell function. Calcium is particularly critical for fruit quality and postharvest storability. Calcium is taken up more rapidly in the first half of the season, during the cell division period. As the fruit grows and a thicker waxy cuticle forms there is progressively less calcium uptake. This means that as the fruit is expanding but taking up less and less calcium, the calcium concentration in the fruit declines as harvest approaches. It has been found that uptake of calcium depends on the spur leaf area associated with the fruit. Again this focuses our attention on the early season activity. Early thinning removes fruit competition and therefore helps calcium uptake of the retained fruit.

The take-home message is again that the first few weeks after bloom are critical for fruit nutrition also. Good crop management requires early and effective thinning.

Support for Fruit Growth

The inherent growth pattern of the apple fruit is genetically determined. Fruit growth requires substantial support of carbohydrates, water and nutrients; however, it can be limited by lack of these resources.

Carbohydrate reserves - The initial growth of the shoots and flowers at bud break in the spring is supported by carbohydrate reserves in the roots and branches. Gradually, as leaves are produced, there is a transition from solely depending on reserves to obtaining greater support from current photosynthesis of the leaves. Several studies have found that the carbohydrate reserves bottom out just about bloom then begin to increase again, indicating that after bloom the fruit are not depending on reserves any

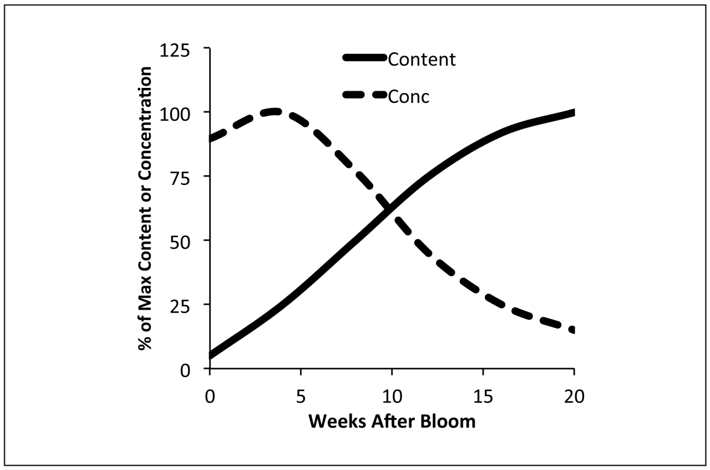


Figure 4. General diagram of seasonal apple fruit calcium content (amount per fruit) and concentration (% of weight) as percent of the seasonal maximum. The decline in concentration over the season is the result of continued fruit growth while Ca uptake gradually decreased.

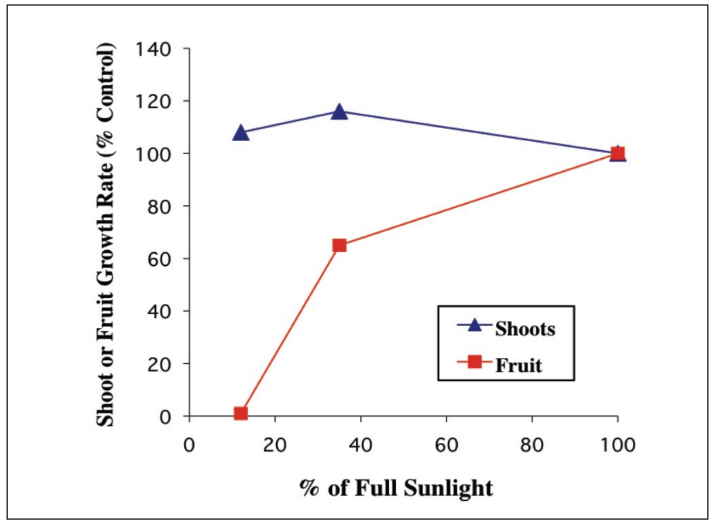


Figure 5. The effect of 6 days of varying light on the growth rate of extension shoots versus apple fruit at about 3 weeks after bloom (fruit diameter about 16 mm).

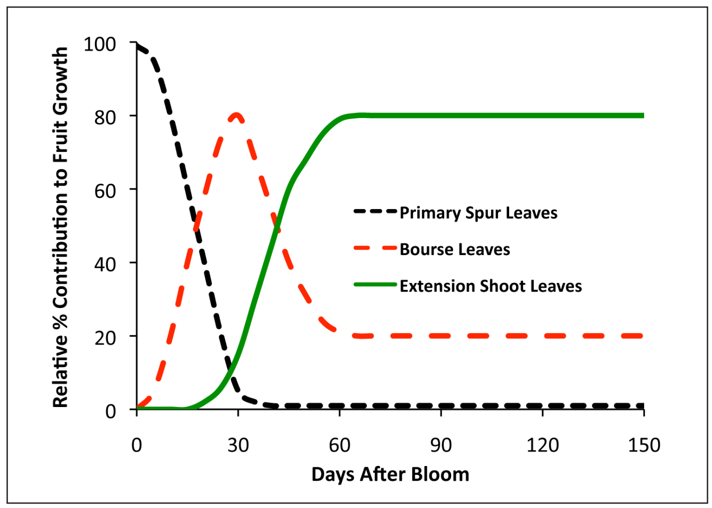


Figure 6. General diagram of the seasonal pattern of which leaves contribute to the support for fruit growth. Note that the extension shoot leaves generally contribute very little to the fruit until about 3-4 weeks after bloom.

more. Several other studies have shown that after bloom, fruit are almost entirely supported by current tree photosynthesis.

Current Photosynthesis. Do all leaves on the tree support the fruit or do some support other competing organs such as shoots and roots? We have done studies to determine which leaves on the trees support fruit development at different times over the season. These and studies of several other labs have clarified the picture.

Extension shoot leaves support the growth of the shoot with carbohydrates until at least 10-12 leaves have unfolded. After that, the most basal leaves on the shoot can export carbohydrates to the fruit. However, we have found that if the shoot is shaded, then as many as 20 leaves will send their carbohydrates to the shoot and not to the fruit. Eventually, when extension shoots stop growing, all the leaves can send their carbohydrates to the fruit. That is why very light pruning that gives a large number of shoots that stop growth quite early, will support fruit set and early fruit growth better than heavy heading cuts that give more long, vigorous extension shoots that compete with the fruit for longer times.

In the first few critical weeks after bloom the carbohydrate support for fruit growth comes from the spur leaves and small "spur like" leaves on the short lateral shoots off last years stems, not from the extension shoot leaves. This was very clearly seen when we shaded whole trees for 6 days when the fruit averaged about 16 mm diameter and then measured how much growth occurred in fruit versus extension shoots (Figure 5). Even down to 12% of full sunlight, shoots continued to grow at the same rate while fruits were reduced to essentially zero. This heavy shade to 12% of full sun led to complete de-fruiting of the trees while having no effect on shoot growth.

It appears that under limiting light, the tree puts its limited energy into extending shoots to obtain more light and survive till another year. This is also consistent with (1) the tree replenishing reserves after bloom even though the tree is supporting young fruitlet growth, and (2) the mechanism of juvenility for apple seedlings which is the tendency to not flower or set fruit for several years to allow the tree to get established and can support a crop.

The general pattern of support for fruit growth after bloom (Figure 6) is that primary spur leaves (those that come out before bloom) initially are important to support the fruit, but their importance gradually declines due to their small leaf area. Next, the leaves on the lateral ("bourse") shoots in the spur develop after bloom and support the fruit unless they are extremely vigorous. Finally, the leaves on the extension shoots with more than about 12 leaves begin to support the fruit. Gradually as shoots stop growing, all their leaves can support fruit growth. For the last 2/3 of the season both bourse leaves and shoot leaves support the fruit.

From these studies it seems clear that we need to expose spur canopy of leaves to sun as much as feasible the during the weeks just after bloom since they are the primarily supporting the fruit. Using a laser as an artificial sunbeam, we analyzed what percentage of the sun was captured by spur leaves versus shoot leaves 3 weeks post-bloom in several orchards. We related the sunlight capture to the yields of those orchards.

As expected from the discussion above, we found that:
(1) Orchard yields were positively related to sunlight capture by

the spur leaves. This combined the total sunlight capture of the whole orchard and the relative sunlight capture by the spurs versus extension shoots.

(2) Conversely, excessive sunlight capture by extension shoot leaves, by reducing the light available to the spurs in denser canopies, led to lower orchard yields.

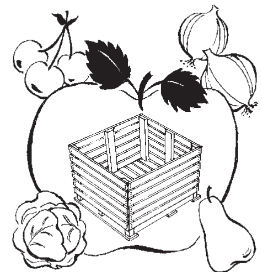
(3) By about a month after bloom, all or most shoot leaves can support fruit, the local effects of light seen earlier are much less important.

Summary

In summary, there are many aspects of apple development that have been learned. Many of the key points are:

- Fruits develop from the base of the apple flower after pollination and fertilization and the flower walls around the seed cavity expand to become the fruit flesh.
- The apple fruit grows initially by cell division for about a week, then by both cell division and cell expansion for 3-4 more weeks, then predominantly by cell expansion.
- Final potential fruit size depends primarily on cell numbers, which are produced shortly after bloom. So, for good fruit size thinning effectively and early is critical (that is, small fruits at 1 month after bloom will never make big fruit).
- Carbohydrate reserves support flower development but are apparently not supporting the fruit growth after bloom. Post-bloom fruit growth is supported by the current photosynthesis of the leaves.
- Spurs support fruit growth in the first few critical weeks after bloom. Extension shoots do not support fruit initially as they support themselves until a few weeks after bloom.
- If light is limited (cloudy, etc.), shoot growth seems to have priority and fruit growth and set will suffer if there are too many shoots to support.
- Yields of apple orchards depend strongly on the sunlight captured by the spurs in the critical weeks after bloom.
- All of these results emphasize the importance of open canopies to get light to spurs, light pruning to have fewer vigorous shoots, and early thinning to allow maximum cell numbers to be produced.

Alan Lakso is a research and teaching professor located at Cornell's Geneva campus who leads Cornell's program in apple and grape physiology. **Martin Goffinet** is a retired Senior Research associate who specializes in anatomy and morphology.



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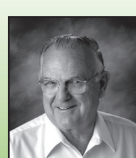
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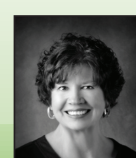
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