THE PHYSIOLOGY OF

CRANBERRY YIELD

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WHAT REALLY LIMITS YIELD?

In order to improve yield of cranberry beds it is important to understand what is currently limiting yields. This summer in a series of articles I will attempt to describe for you research from the scientific literature for cranberries that relates to this topic. There is a substantial body of material regarding yield in cranberries that has been published over a number of years. I will attempt to bring all of this together so that by September you will hopefully understand what is truly limiting to cranberry yields and possible approaches to increase yields and profits.

The first thing to do in situations like this is to define terms. What is yield? This question would be answered slightly differently by people from different backgrounds. An ecophysiologist would define yield as total biomass produced per unit ground area per year. A horticulturist might define yield as total fruit production per year. A grower might define yield as total fruit harvested from a bed, or fruit delivered to a handler. A handler might define yield as fruit processed and sold. For our purposes we'll define yield as either total biomass or as total fruit produced in one year.

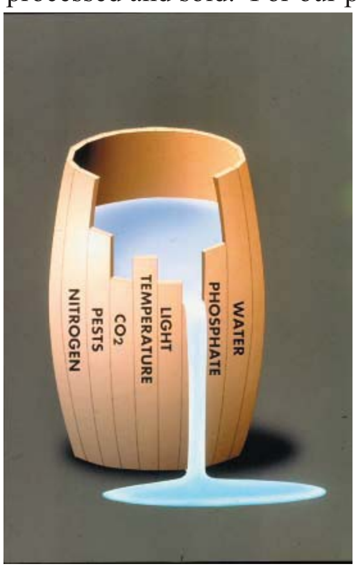

Fig 1. A rain barrel as a representation of yield potential.

Yield capacity can be thought of being similar to an old-fashioned barrel with wooden staves (Fig. 1). The volume of water that the barrel can hold is determined by the length of the shortest stave. If we make one of the long staves longer we do nothing to increase the capacity. Only when we identify and "lengthen" the short stave can we increase yield.

Ecologists track energy flow and nutrient flow through ecosystems. Farms are ecosystems. Energy arrives in the form of sunlight and stays as plant tissue or organic material. Energy and mineral nutrients are removed as the crop is harvested and as leaf litter, etc. Following the flow of energy through the system is very important when we want to determine what is limiting yields.

When asked what they farm, many growers would answer that they farm the soil. While there is a certain amount of truth there, I would answer that farmers don't farm the soil, they farm sunlight. Regardless of what we may do, crops grow primarily in response to sunlight, temperature, water availability, carbon dioxide availability, mineral nutrients and genetics. We'll discuss these in that order.

Without light plants won't grow. Light can be described in both qualitative and quantitative terms. Light quality would include wavelength or color. Plants are only able to use light with wavelengths between 400 and 700 nm. This is roughly coincident to the visible spectrum of light that you and I can see. Plants can't use light energy in the infrared or ultraviolet range. Light also has a quantitative value. Its energy content can be measured in moles of light received.

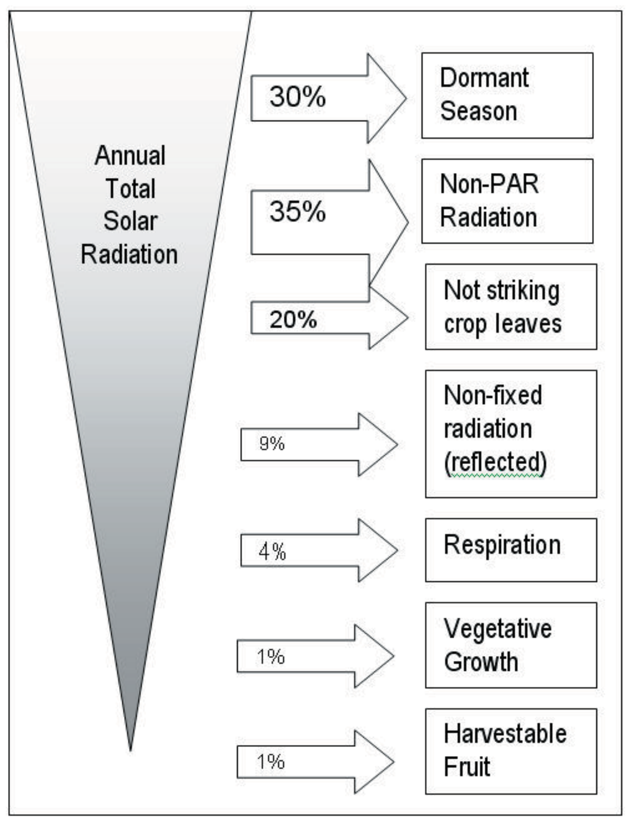

Figure 2. Estimate of the fate of energy that strikes the earth.

If we consider the total amount of light that is received by a given piece of ground during the course of a year only a small fraction of that light actually results in harvestable yield (Fig. 2). As you can see, much of the light arrives when the vines are dormant. Much is not of the correct wavelength for plants to utilize. Some light is reflected or given off as heat. Some of the products of photosynthesis are broken down in respiration, or are partitioned to vegetative growth or roots. Only about 1% of light that strikes a crop is utilized to produce harvestable yield.

Green plants receive light energy and through the process of photosynthesis convert that light energy into chemical energy that is stored as carbohydrates or sugars. These sugars can be linked together in complex ways to make cellulose, the structural component of plants; lipids, the primary constituent of cell membranes; or proteins, some of which are enzymes that facilitate biochemical reactions within cells. Sugars formed through photosynthesis also give fruit their inherent sweetness.

A primary limitation of photosynthesis is light. As light intensity or quantity increases the rate of photosynthesis also increases (Fig. 3).

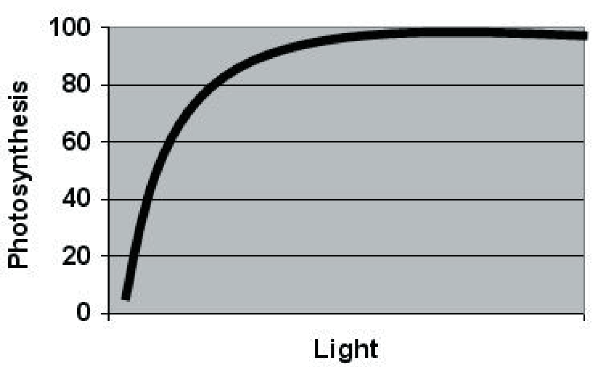

Figure 3. Light response curve for cranberry photosynthesis.

However, there comes a point where photosynthesis no longer increases as light intensity increases. This is called the light saturation point. In cranberries this point is about 700 µmol/m^2/s. In contrast, full sunlight in Wisconsin is about 2000 µmol/m^2/s. Incident light intensity usually does not limit photosynthesis except on very cloudy days and at night.

The limitations to crop yield by light are usually a result of either not having enough leaf canopy to capture all of the light striking cropland or with internal shading within a canopy so that

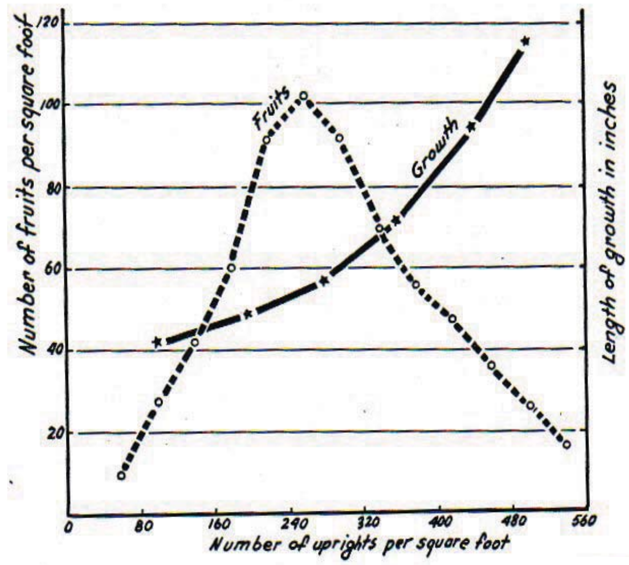

Figure 4. The relationship between upright density, crop yield and upright length in cranberries. From Roberts and Struckmeyer, 1941.

some of the leaves are shaded and unproductive. In the 1940's Roberts and Struckmeyer in Wisconsin examined the effect of upright density on yield of Searles cranberries. They found that as the number of uprights per square foot increased that the number of fruit also increased until they got to a certain point and then berry number declined (Fig 4). For Searles they found the optimum upright density was about 250 to 300 per square foot. The optimal number for hybrids such as Stevens is probably higher. The reason for the decline as upright density got too high was that uprights were shading one another, causing the uprights to elongate and more of the products of photosynthesis were spent making vines so less was available for making fruit. The importance of light for productivity is also demonstrated in weedy beds. Weeds block sunlight from striking cranberry leaves and by so doing reduce the amount of light available for photosynthesis in the vines. This is the primary form of competition for many of the most pernicious cranberry weed species.

Plants respond to temperature. When it is very cold out during the winter plants go dormant to protect themselves against the inhospitable conditions. Of course frost is a serious risk to most fruit crops and especially to cranberries since they are grown in low wet areas. Photosynthesis is also sensitive to temperatures. The optimal temperature for most crop plants is about 70-75°F. When temperatures are either above or below these the rate of photosynthesis declines. Cranberries are not particularly sensitive to temperatures between about

70 and 90°F (Vanden Heuvel and Davenport 2005). Grower experience also supports reduced yields during years with exceptionally cold or hot weather.

For many crops yield can be seriously limited by water availability. Because cranberries are grown in naturally wet areas and are irrigated water availability is rarely a limitation for yield in cranberries. Water quality may be an issue as water that contains high levels of nitrate may lead to vine overgrowth. Too much water can also be a problem leading to root roots and lack of oxygen in soils.

In the process of photosynthesis light energy is captured and then used to attach one molecule of CO_2 from the air onto a 5 carbon sugar which is immediately split to produce two 3 carbon sugars. When carbon dioxide is in short supply the photosynthetic rate is reduced. A carbon dioxide response curve looks very similar to the light response curve. At low concentrations of carbon dioxide photosynthesis is limited by CO_2. As the CO_2 concentration increases photosynthesis is limited by having enough 5 carbon sugars to act as acceptors of CO_2. As the concentration of CO_2 in the environment has increased rates of photosynthesis of many crop plants have increased.

In order to grow and reproduce plants need water, oxygen, carbon dioxide, and 13 mineral elements in sufficient supply. The plant nutrient guidelines that have been published for some years quantify the amount of these required mineral elements that should be found in plants so that they won't be a limitation to yield. Once these requirements are met adding additional nutrients won't increase yield. Data from the UW Soil and Plant Analysis Lab suggests that Wisconsin Cranberry Growers are doing a great job at providing sufficient nutrients so that these nutrients won't be limiting to growth. Virtually all samples were in the sufficient range for the important major (N, P, K) and minor nutrients (Ca, Mg, S) (Roper 2005, Roper and Combs 1992).

Genetics play a very important role in determining yield of crop plants. Crop yields in field crops have been greatly enhanced by exploiting changes in crop architecture or how much of the products of photosynthesis are partitioned to harvestable yield. Virtually all cranberry cultivars presently being grown are either selections from the wild or one generation from the wild. I believe that there are marvelous increases in yield that are available and that will be discovered as we improve the genetic resources of this crop.

Summary

In this chapter we learned:

- That yield can't be increased by improving non-limiting factors.
- Light is the energy source for plant life and that only a small fraction of incident sunlight is used by plants to make fruit.
- Temperature can limit plant productivity.
- CO_2 concentration can limit plant productivity, although rarely in nature.
- Plants need 13 mineral elements in addition to water, sunlight and CO_2 to grow and reproduce.

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Roberts R.H. and B.E. Struckmeyer. 1942. Growth and fruiting of the cranberry. Proc. Amer. Soc. Hort Sci. 40:373-379.

Roper, T. R. 2005. Tissue Test Summary. Proc. Wisconsin Cranberry School 13:20-23.

Roper, T.R. and S.M. Combs. 1992. Nutrient status of Wisconsin cranberries. Proc. Wisconsin Cranberry School 3:12-16.

Vanden Heuvel, J.E. and J.R. Davenport. 2005. Effects of light, temperature, defoliation, and fruiting on carbon assimilation and partitioning in potted cranberry. HortScience 40:1699-1704

YIELD COMPONENT ANALYSIS

In the first article in this series we explored environmental factors that can affect the rate of photosynthesis such as light, temperature, CO_2 concentration, mineral nutrients, and genetics. That sets the stage for this discussion of yield component analysis. Yield component analysis is a statistical procedure where various measurable or calculable factors can be assessed to see which have the greatest correlation with yield.

George Eaton and coworkers at the University of British Columbia performed yield component analysis of cranberry in the late 1970's (Eaton & Kyte 1978). In their study they collected all of the tissue growing in a square decimeter. This is about 4 x 4 inches or 16 square inches. Samples were collected from four properties in BC over two years. They counted the total number of uprights (U/dm2), the number of flowering uprights (Uf/dm2), number of flowers (F/dm2), number of berries (B/dm2), and the fresh weight of berries or yield (g/dm2). From these data they were further able to calculate floral induction (Uf/U), flowering (F/Uf), fruit set (B/F), and berry size (g/B). The resulting data were then subjected to statistical procedures to determine which factors were most important in determining yield.

They determined that two factors were most important in determining yield: floral induction (Uf/U) and fruit set (B/F). Floral induction is the proportion of fruiting uprights among the total number of uprights. The proportion of fruiting uprights was more important than the total upright density. Fruit set describes how many fruit set from the flowers that are present on a flowering upright. Since these two factors have been shown to be the most important factors determining yield researchers have spent much effort attempting to further describe them and to attempt to find ways to increase them. We'll deal first with floral induction.

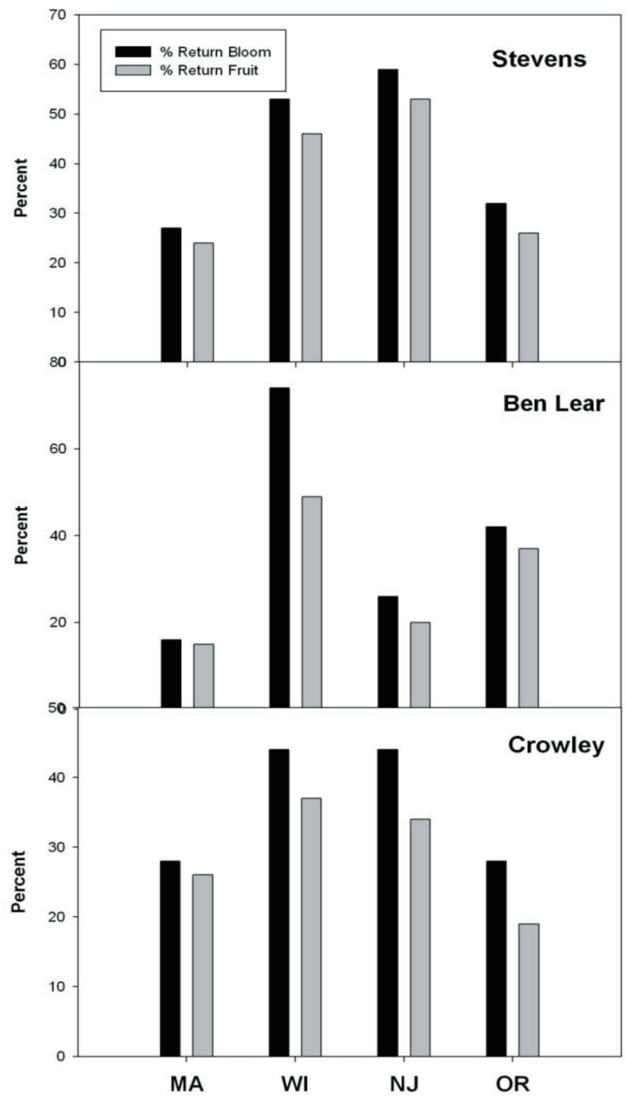

Figure 1. The effect of fruiting one year on subsequent year flowering and fruiting.

Individual uprights in cranberry beds tend to produce flowers and fruit in alternate years. However, since there are millions of uprights per acre total yields can be more uniform, but grower data also shows the trend to a large crop one year followed by a smaller crop the subsequent year. This phenomenon is very common in other temperate fruit crops. In an effort to document the extent of biennial bearing in cranberry uprights researchers from MA, WI, NJ, and OR cooperated in a research project. In beds of Stevens, Ben Lear, and Crowley in each state six-foot lines were set out in beds and 60 uprights that fruited in 1989 were tagged with vinyl tape after harvest but before the winter flood. Fruiting was determined by the presence of persistent pedicels from the fruit after harvest. In the late summer of 1990 fifty of the tagged uprights were cut and the presence of flowers and fruit was counted. The results of the study are shown in Figure 1.

For uprights that fruited in 1989 the percent return bloom ranged from 74% for Ben Lear in Wisconsin to 16% for Ben Lear in Massachusetts (Fig 1B). Percent return fruit ranged from 49% for Ben Lear in Wisconsin to 15% for Ben Lear in

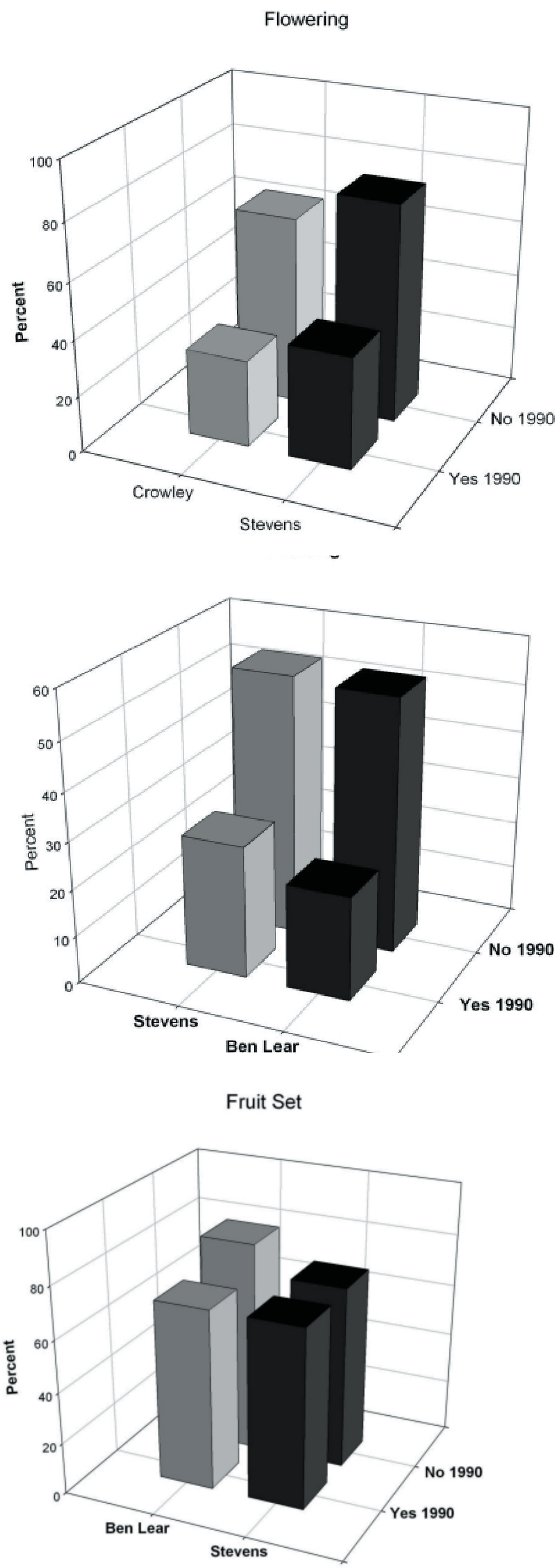

Figure 2. The effect of fruiting one year on flowering, fruiting, and fruit set the subsequent year.

Massachusetts (Fig. 1B). Most of the values for return fruit were between 25 and 50%. This suggests that individual uprights that produce fruit one year are unlikely to produce fruit the following year. In this study OR and MA were least likely to have return fruit set while WI and NJ were the most likely. That may have reflected environmental conditions during 1989 and 1990. Within each state cultivars behaved similarly suggesting that genetics was not significant, at least among cultivars tested in this trial.

A second study was instigated to look more closely at biennial bearing. Only two cultivars were used in this study, Stevens and Ben Lear. In each bed 60 uprights that fruited in 1990 were tagged with vinyl tape and 60 uprights that did not fruit were tagged. After fruit set in the summer of 1991 50 of the 60 tagged uprights were examined for the presence of at least one fruit. The results are shown in Figure 2. Uprights that fruited in 1990 were about half as likely to flower or produce fruit as those that did not for both Stevens and Ben Lear. For Stevens the percent fruit set was the same regardless of the upright condition in 1990 suggesting that other factors control fruit set. For Ben Lear percent fruit set was slightly higher for uprights that did not fruit in 1990 compared to those that did.

One way growers manage upright density and thus indirectly the proportion of fruiting uprights is through sanding and pruning. Pruning is less common in Wisconsin than it is in other areas. In Oregon, Strik and Poole (1991, 1992) studied the severity and timing of pruning with a commercial mechanical pruner. They found that timing of pruning, December (early) or March (late), was not important. Severity of pruning was important. Moderate or heavy pruning resulted in greater fruit anthocyanin (color) but significantly reduced yields, particularly in the second year. Fruit set and the number of fruiting uprights (primary determinants of yield) was also reduced in the second year. After one year of not being pruned, yields increased substantially for all treatments except the control. So, for the best sustained yield OR growers are encouraged to prune lightly in alternate years.

Sanding is a more common Wisconsin practice. Leroy Kummer studied the effect of sanding and pruning on yields in cranberry (Kummer 1994). He found that sanding and pruning reduced yield the year following the practice, but that yields were enhanced in the subsequent two years. The decrease in yield was largely a result of fewer berries, not smaller berries. Unfortunately, the research didn't examine yield components so we could see what caused the changes in yield, both upwards and downwards.

Increasing the proportion of uprights that flower is a challenge. When upright density is too high yield declines. Individual uprights tend to flower every other year. We now know that there is a genetic component to biennial bearing. Some of the newer cultivars have a greater tendency to rebud than existing cultivars. However, these data are from immature plantings. Time will tell if the increased propensity to rebud will continue in mature plantings.

Summary

In this article we learned:

- The two most important components of yield are the proportion of flowering uprights and fruit set.
- Individual uprights tend to bear fruit every other year.
- Sanding and pruning can increase the proportion of fruiting uprights

References:

Eaton, G.W. and T.R. Kyte. 1978. Yield component analysis in the cranberry. J. Amer. Soc. Hort. Sci. 103:578-583.

Kummer, L. 1994. Sanding. Wisc. Cranberry IPM Newsletter 8(10):1-3.

Roper, T.R., et al. 1993. Fruiting of cranberry uprights reduces fruiting the following year. HortScience 28:228.

Strik, B.C. and A. Poole, Alternate-year pruning recommended for cranberry. HortScience 27:1327.

Strik, B.C., et al. 1991. Cultivar and growing region influence return bloom in cranberry uprights. HortScience 26:1366-1367.

POLLINATION AND FRUIT SET

Fruit set is defined as the number of fruit that are produced from a given number of flowers. It is usually defined as a percentage. Fruit set is perhaps the most important yield component and it has been studied over a number of years. One way to understand what is important to determining fruit set is to limit factors that contribute to fruit set and then see which one reduces fruit set the most.

Before discussing research related to this topic it is important to describe the flowering situation of cranberries. Cranberry pollen is a tetrad that is shed from the pore hole in the bottom of the anther. The pollen tetrads are heavy and are not windborne. Flowering uprights typically have five flowers and they open from the bottom to the top. The lower flowers are more likely to produce fruit than flowers in the upper postions.

One of the first requirements for fruit set is pollination. Pollination is the movement of pollen grains from the anther to the stigma. Pollination in cranberries is carried out by insects. Growers typically rent honeybee hives during flowering to ensure there are sufficient insects to pollinate the flowers once they are open. Native insects including bumblebees and various wasps and flies are also effective pollinators.

In New Jersey researchers (Cane and Schiffhauer, 2003) examined the relationship between the number of pollen tetrads (grains) applied to the stigma of flowers with fruit set and fruit size. Emasculated individual flowers were given 2, 4, 8, 16, or 32 pollen tetrads by hand. Experiments were conducted in a greenhouse so insects were excluded. They found that fruit set did not increase when at least 8 pollen tetrads were deposited on the stigma (Fig. 1). Fruit size increased slightly above 8 pollen tetrads (Fig. 2). However, seed number per fruit, a contributor to fruit size, increased with increasing pollen deposition.

In one study (Birrenkott and Stang, 1989) the researchers supplemented insect pollination with hand pollination to ensure that pollination was not the limiting factor. In both years of their study fruit set with insect pollination alone was 30%. When insect pollination was supplemented with hand pollination fruit set increased to 38%. However, yield was not increased significantly even when fruit set was

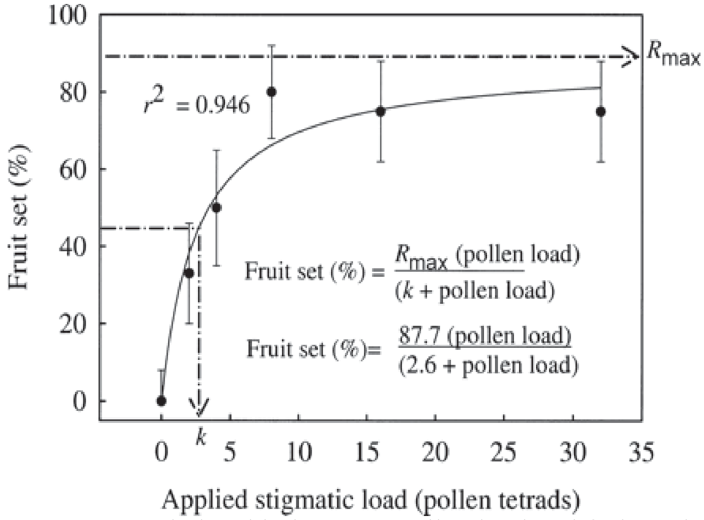

Figure 1. Relationship between pollen load and fruit set in cranberries.

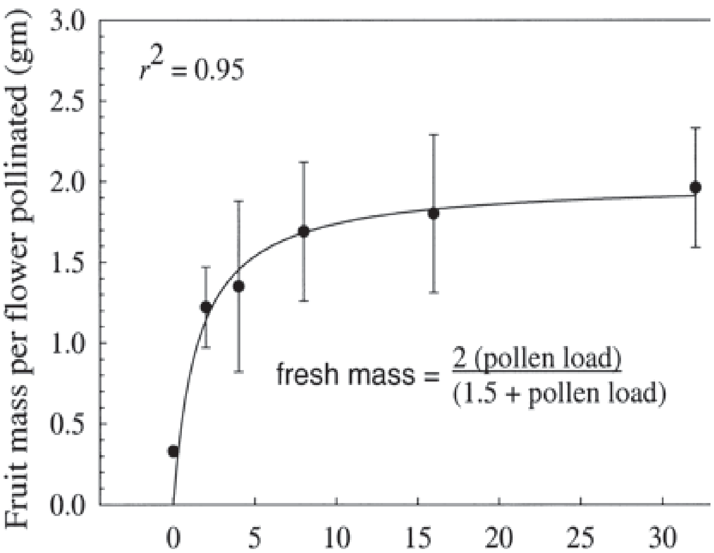

Figure 2. Relationship between pollen load and fruit size in cranberries.

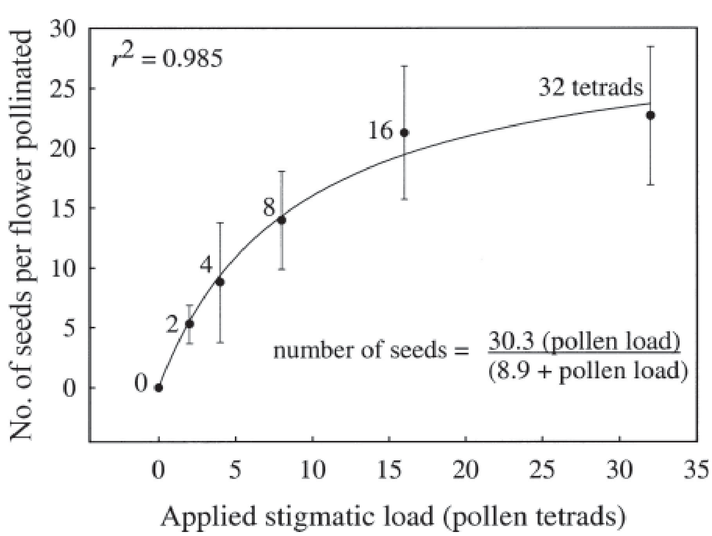

Figure 3. Relationship between pollen load and seed number per fruit in cranberry. Data from Cane and Schiffhauer, 2003.

increased. Thus, pollination can be limiting to fruit set, but not necessarily to yield.

Interestingly, this research also found that setting a higher percentage of flowers in the lower positions also reduced the number of fruit that set in the upper positions. This suggests that there is competition for resources among berries on an individual upright.

These same researchers studied the effect of removing lower flowers/fruit on fruit set on upper flowers. They found that if the lower two flowers were removed at hook stage that 45% of upper position flowers produced fruit. If fruit removal were delayed until full bloom fruit set in the upper position was still about 46%, but if fruit removal were delayed until early fruit development (fruit set) only 36% of upper position flowers set fruit. If no lower position fruit were removed fruit set in the upper positions was about 25%. Thus, flowers and fruit on an individual upright compete with one another for resources. This further supports the conclusion that fruit set in cranberries is at least partially limited by resources such as carbohydrates.

In another study (Baumann & Eaton 1986) researchers looked at fruit set, fruit size, and seed number by position across three cultivars: Ben Lear, Bergman, and McFarlin. The results are shown in Table 1. As we go from the lower to upper flowers on an upright fruit set declines along with seed number and berry size. The reduction in seed number suggests that pollination may be involved, underscoring the importance of having adequate pollination through honeybees and other insects for pollination. This also supports the hypothesis of competition between berries on an upright.

Table 1. The effect of position on the upright on fruit set, seed number and size of Ben Lear, Bergman and McFarlin cranberries in British Columbia. N=100
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Position	Fruit set	Seed Number	Berry wt. (g)
1 (low)	73	12.7	0.83
2	54	9.3	0.58
3	28	4.6	0.28
4	15	2.6	0.15
5 (high)	12	2.1	0.13
LSD	0.07	1.46	0.07

(Data from Baumann and Eaton 1986)

It is possible to increase fruit set to near 100% with the use of plant hormones. Gibberellic acid (GA) is known to increase fruit set through the formation of parthenocarpic (seedless) fruit in other crops in addition to cranberries. Devlin and DeMoranville showed in Massachusetts in 1967 that spraying cranberries with varying concentrations of GA would increase fruit set (Table 2). However, the increase in fruit set also resulted in a decrease in fruit size. Yield was unaffected. Terminal bud set was poor, likely resulting in a reduced crop the following year. Uprights in treated plots were elongated and spindly.

Table 2. Effect of varying concentrations of GA on cranberry fruit set and size.

GA (ppm)	Fruit Set	Berry weight (g)
100	73	0.37
300	87	0.37
500	75	0.43
Control (0)	28	0.71

Data from Devlin and DeMoranville, 1967.

Similar results were found in Wisconsin (Stang, unpublished data). In this study different formulations were used at a constant rate of 100 ppm. The results were very similar.

T**able 3.** The effect of 100 ppm of GA_3 or GA_{4+7} on fruit set, yield, and fruit size of cranberries in Wisconsin.

	Fruit set (%)	**Yield ($g/81cm_2$)**	**Berry Wt. (g)**
GA_3	51 a	17.7 a	0.47 a
GA_{4+7}	51 a	21.2 a	0.53 a
Control	26 b	19.6 a	1.05 b

Stang, unpublished data.

Interestingly, fruit set can be increased by spraying cranberries with Gibberellins, but yield remains unchanged. This further supports the hypothesis that fruit set, and yield, are resource limited.

If fruit set is resource limited we have not yet addressed the question of what resource is limiting. The next article will address this question.

Summary

In this article we have learned:

- That pollination is required for fruit set.
- At least 8 pollen tetrads are required per flower to maximize fruit set.
- That insect pollination alone may not be sufficient for maximum yield.
- That berries compete for resources along a single upright.
- That fruit set, but not yield, can be increased by treating cranberries with the growth regulator Gibberellic Acid.

References:

Baumann, T.E. and G.W. Eaton. 1986. Competition among berries on the cranberry upright. J. Amer. Soc. Hort. Sci. 111:869-872.

Birrenkott, B.A. and E.J. Stang. 1989. Pollination and pollen tube growth in relation to cranberry fruit development. J. Amer. Soc. Hort. Sci. 114:733-737.

Birrenkott, B.A. and E.J. Stang. 1990. Selective flower removal increases cranberry fruit set. HortScience 25:1226-1228.

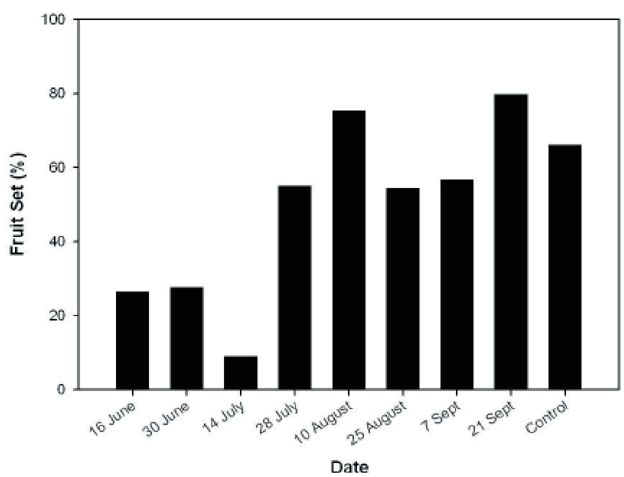
Cane, J.H., and D. Schiffhauer. 2003. Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry. Am. J. Botany 90:1425-1432.

Devlin, R.M. and I.E. DeMoranville. 1967. Influence of gibberellic acid and Gibrel on fruit set and yield in Vaccinium macrocarpon cv. Early Black. Physiol. Plantarum 20:587-592.

RESOURCE LIMITATION

The previous article in this series examined the importance of fruit set and how it might be improved. We concluded that fruit set was likely resource limited, but did not address what the limitation might be. This article will describe what resources might be limiting and when.

One way to determine what resources are limiting and when is to remove the source of the resource to varying degrees and at varying times. Photosynthesis is the source of all carbohydrates used by plants and photosynthesis occurs in green leaves. In one experiment we removed the new growth above the fruit at varying times during the season and the effect on fruit set and berry size was determined at harvest. The results are shown in Figure 1. Percent fruit set and fruit size were reduced the greatest when the new growth was removed on July 14, about when fruit set occurs. This is typically near the end of the flowering period. Fruit size was affected less than fruit set, suggesting that fruit size is conserved. Fruit set was also reduced compared to the control if new growth was removed at either of the June dates. This study showed that fruit set is very sensitive to resource reduction caused by removing leaf area.



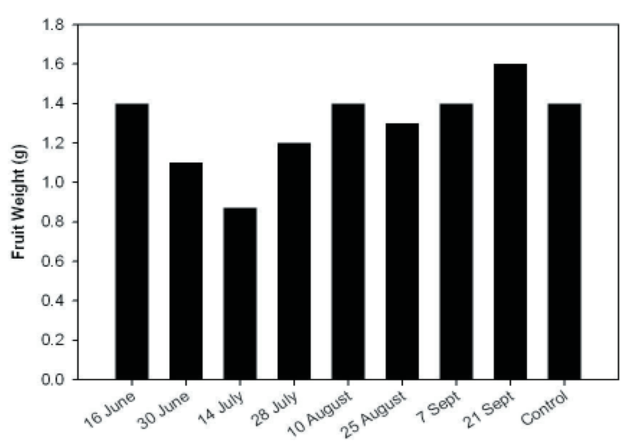


Figure 1. Effect of removing current season growth in 'Crowley' cranberries at different dates during the season on fruit set and berry size. N=10.

Current season growth is not the only potential source of carbohydrates for cranberry growth and development. In a subsequent experiment we removed either the new growth above the fruit, or the one-year-old leaves below the fruit, or both, or neither. From the previous experiment we know that the critical time to remove growth is at fruit set, so it wasn't necessary to remove tissue at all dates. We chose uprights that had at least two fruit beginning to develop and then imposed one of the treatments described above. The results are shown in Figure 2. When the old leaves below the fruit were removed there was little effect on fruit set or fruit size, but when the new growth above the fruit were removed or both the above and below were removed fruit set was reduced. Fruit size was conserved.

We repeated this experiment about 2 weeks after fruit set and there was very little effect on fruit set or fruit size.

Yet another way to look at limiting resources is to shade portions of a bed for various periods of time. We shaded portions of a bed by stretching shade cloth over a cage. The cages covered ½ square meter of bed surface. We used shade cloth that provided either 93% or 72% shade. We imposed the shade treatments for a month at either pre-bloom, post-bloom, or pre-harvest; corresponding to May 15-June 15, July 15-August 15, and August 15 to September 15, respectively (Figure 3).

Fruit set and yield responded similarly to shading (not surprising since fruit set is a primary determinant of yield). The pre-bloom shading was variable from year to year, but was usually not different from the unshaded control. The post-bloom shading of either intensity reduced fruit set and yield except for the 72% shade in the first year. Pre-harvest shading reduced fruit set and yield in the first two years, but not the third year. Through limiting light the concentration of carbohydrates in the tissue was also reduced (Figure 4). This suggests that shading reduced fruit set and yield by reducing the carbohydrate concentration in the uprights. Obviously, removing leaves, thus reducing the photosynthetic area of the leaves would also serve to reduce the carbohydrate concentration in uprights.

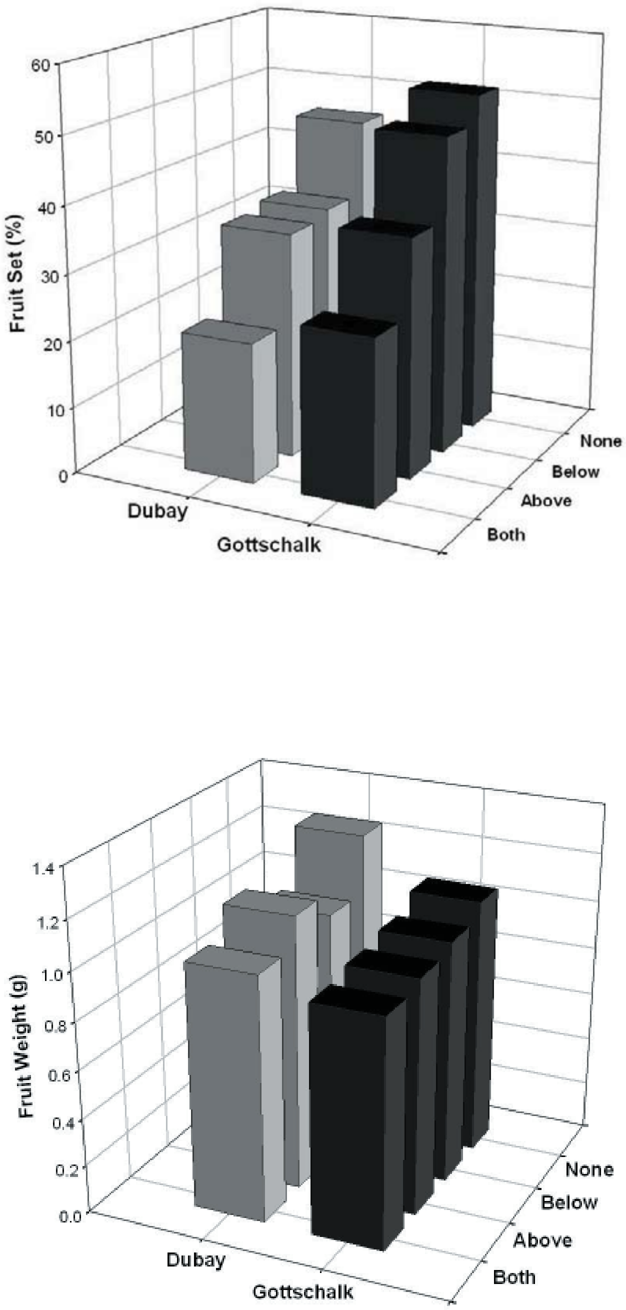


Figure 2. Effect of removing leaves either above, below, both or neither on fruit set and size of Stevens cranberries.

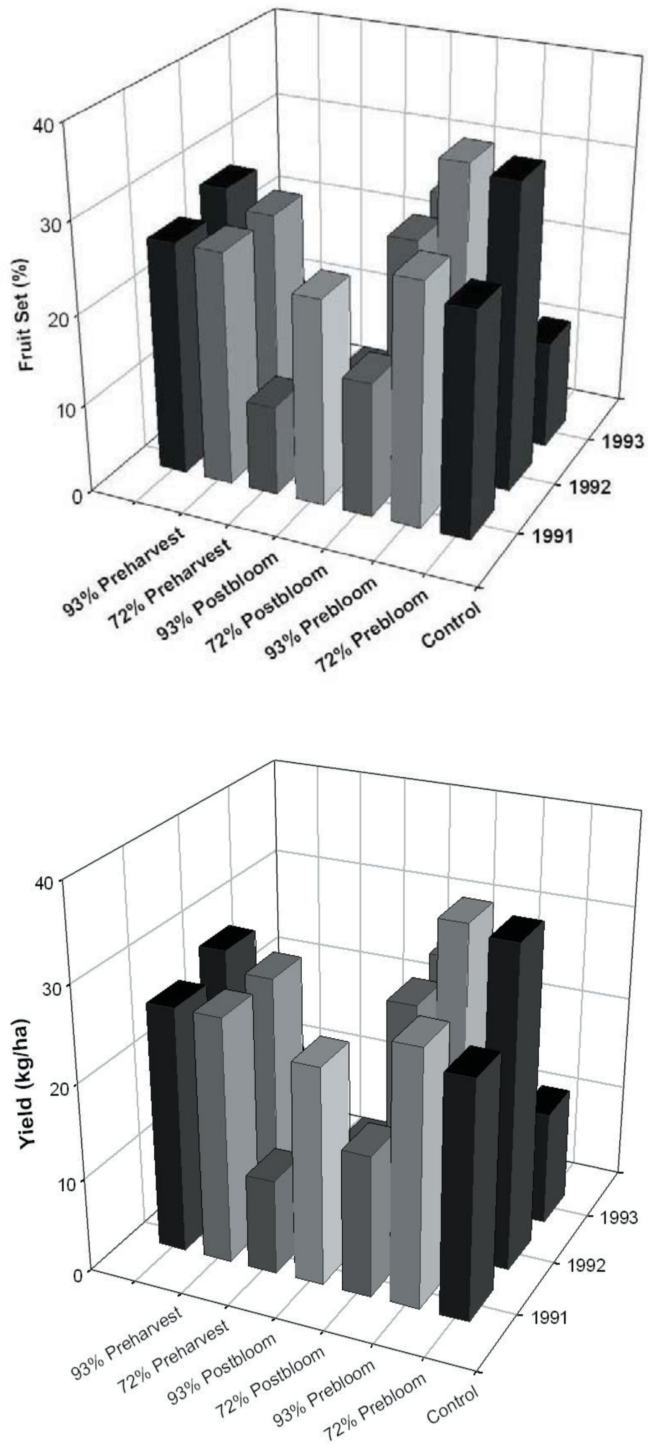


Figure 3. The effect of shading prebloom, post-bloom, or just before harvest on fruit set and yield of Searles cranberries over three years in Wisconsin.

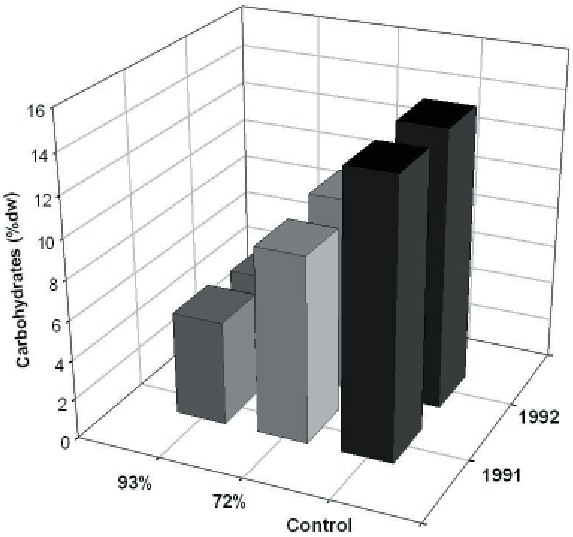


Figure 4. The effect of different levels of prebloom shading on carbohydrate concentrations in Searles cranberries in Wisconsin.

Summary

In this article we learned that:

- Fruit set is the most critical timing for resource limitation.
- The pre-bloom period is more critical than post fruit set.
- New growth above the fruit is more critical in providing resources than old leaves below the fruit.
- Shading postbloom reduces fruit set more than shading either at prebloom or preharvest.
- Shading reduces the carbohydrate concentration in uprights.
- Fruit set and yield can be reduced by reducing resources

References:

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CARBOHYDRATES AND PHOTOSYNTHESIS

In the last article we examined the effects of limiting resources on fruit set and yield of cranberries. We learned that shading cranberries would reduce the amount of carbohydrates (products of photosynthesis) in the vines. Shading reduces light that, in turn, reduces photosynthesis resulting in reduced carbohydrates in the vines.

The primary products of photosynthesis are sugars. Sugars can subsequently be used in various ways in plants. They can be chained together to form starch. They can be latticed together to form cellulose (cell walls, etc.), or they can be used as an energy source for other plant processes (respiration). Once sugars are used to make cellulose plants can no longer use these sugars for other things. They remain linked in cellulose. We use the term 'non-structural carbohydrates' to describe the combination of starch and soluble sugars such as glucose, fructose, and sucrose. These sugars are available for the plant to use to provide energy or more structure.

We examined the seasonal changes in carbohydrates through the course of two years in cranberries. We sampled at two week intervals beginning in early spring and ending in early winter. We cut a piece of the bed out with a golf green cup cutter. We brought them to the lab and divided them into uprights, stems, and below ground tissue. We dried the tissue, ground it, and analyzed for soluble sugars and starch. The results for Searles and Stevens are shown in Figures 1 & 2.

Uprights always had higher concentrations of carbohydrates than stems or below ground stems and roots. Uprights were about 10% sugars and starch before flowering. As flowering began that concentration dropped to about 7% and stayed at about that level during the balance of the growing season, then increased back to near 10% in the fall after harvest. The sugar and starch concentration in the stems and below ground stems remained relatively constant through the season. The pattern was similar for both Searles and Stevens.

When we look at the uprights in more detail we find a similar pattern (Fig. 2). Starch increased early in the season, then declined markedly as flowering began and stayed low throughout the season and declined further just before and after harvest.

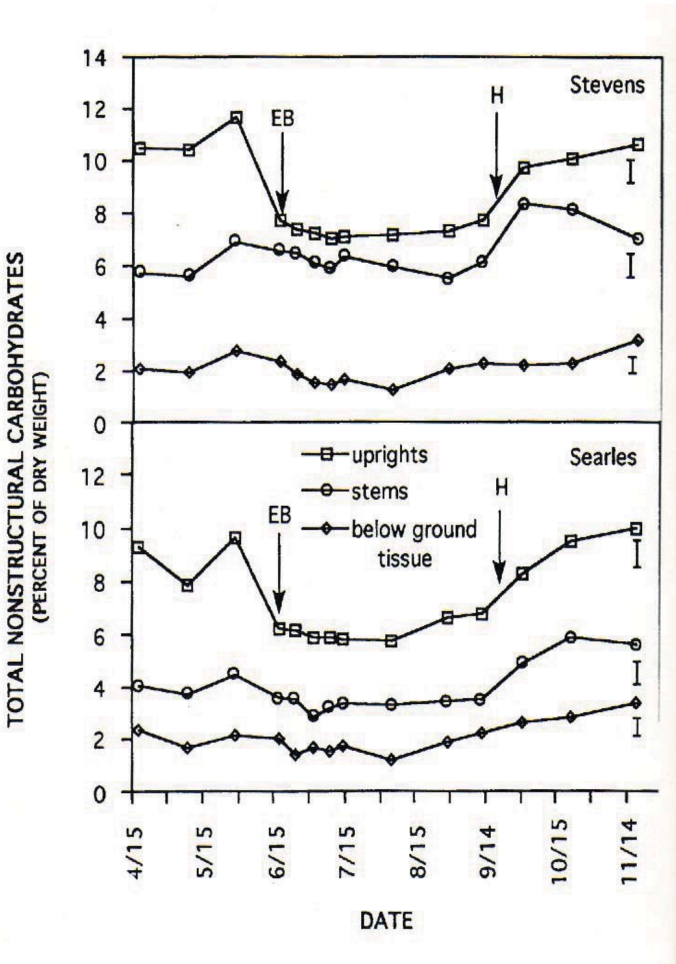

Figure 1. Seasonal changes in total nonstructural carbohydrates in cranberry tissues in 1991.

Fruiting uprights contained less starch than non-fruiting uprights during fruit development. Soluble sugars declined beginning in the early season and remained low until just before harvest. Fruiting uprights had slightly lower concentrations of soluble sugars than non-fruiting uprights. A summation of these two curves is shown in panel A of Figure 2 and the differences in fruiting and non-fruiting uprights are emphasized.

Two important conclusions can be drawn from this research. First, carbohydrates are reduced as fruit begin to develop and the concentration of carbohydrates does not recover until harvest. Second, the reduction in carbohydrates is greater in fruiting than non-fruiting uprights. Fruit appear to be a significant consumer of carbohydrates and attract significant amounts of carbohydrates to support their development. Thus, photosynthesis in the leaves is the source of sugars and fruit and vegetative growth are sinks for sugars.

Because carbohydrates fall to their lowest levels during the flowering and fruit set period, carbohydrate availability may be limiting to fruit set. Previously we

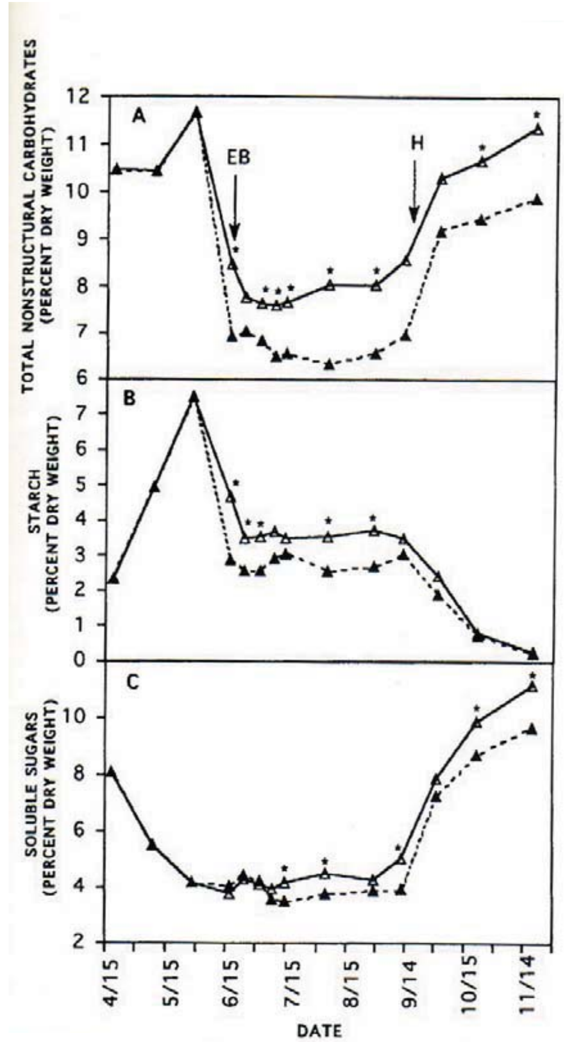

Figure 2. Changes in non-structural carbohydrates in 'Stevens' cranberry vines through a season. A. Total non-structural carbohydrates. B. Starch. C. Soluble Sugars.

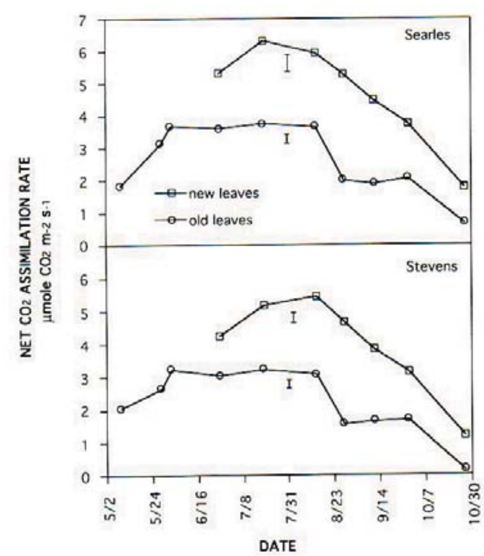

Figure 3. Seasonal changes in net photosynthesis of cranberry uprights during 1991.

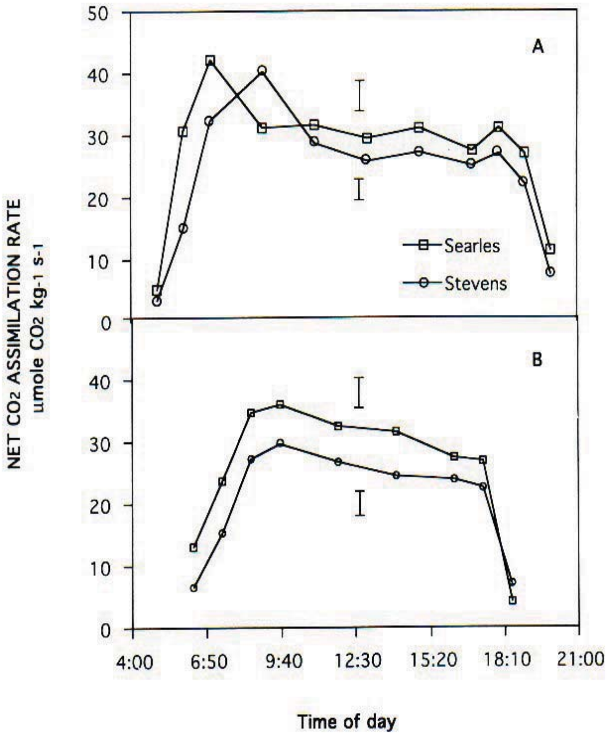

Figure 4. Diurnal changes in photosynthesis of Searles and Stevens Cranberry vines in Wisconsin on two dates in 1991.

showed that fruit along a given upright compete with one another for resources and based upon the shading, leaf removal, and carbohydrate analysis work it seems plausible that the limiting factor is carbohydrate availability.

Fruit are a significant sink for carbohydrates and photosynthesis is the source, but how much carbohydrate do cranberry vines produce through photosynthesis during the course of a season? To estimate that amount we measured photosynthesis every two weeks through a season and we did sunrise to sunset measurements on two days. The bi-weekly measurements were taken on clear sunny days near noon. The results of the bi-weekly measurements are shown in Figure 3. Leaves of current season growth had a rate of photosynthesis that was roughly double that of one-year-old leaves throughout the season. The peak photosynthetic rate occurred in early June, then the rate slowly declined through the remainder of the season. Surprisingly, Searles had a slightly higher rate of photosynthesis than Stevens. In addition, the area of current season leaves on an upright remained steady through the season while the area of on-year-old leaves declined as the leaves dropped. Thus, not only did one-year-old leaves have a lower rate of photosynthesis, they also had declining leaf area. This suggests that current season leaves are the primary source of carbohydrates for fruit growth. Another research project to be described later further supports this conclusion.

The pattern throughout a day is shown in Figure 4. The rate of photosynthesis is low in the early morning while light is low, climbs rapidly during the morning reaching a peak about 10:00 am. The rate then declines slightly, but remains steady through the afternoon. As dusk approaches the rate drops as light once again becomes limiting.

If we sum the carbon fixed through photosynthesis during a season and compare that with the carbon content of mature fruit we can construct a carbon budget. Using the data we had we estimated the carbon fixed by a single upright and the carbon cost of fruit (Table 1).

Table 1. An estimated annual carbon budget for a single cranberry upright

Activity	Carbon
Grams C fixed per upright	0.45
Respiratory cost	0.09
Net C available per upright	0.36
Grams C per mature berry	0.09
Respiratory cost of fruit	0.09
Total C required per fruit	0.18

If these estimations are correct they suggest that the average number of fruit that can be supported by a given upright is two. My experience is that on average about two fruit set per fruiting upright.

In this article we learned:

- Non-structural carbohydrates are at their lowest point during the flowering, fruit set, and fruit development period.
- Uprights show the effect more than woody stems.
- Fruiting uprights have a lower carbohydrate concentration than non-fruiting uprights.
- Current season leaves have a higher rate of photosynthesis than one-year-old leaves.
- On average a fruiting upright can fix sufficient carbon to mature two berries.

References:

Hagidimitriou, M and T.R. Roper. 1994. Seasonal changes in non-structural carbohydrates in cranberry. J. Amer. Soc. Hort. Sci. 119:1029-1033.

Hagidimitriou, M. and T.R. Roper. 1995. Seasonal changes in CO_2 assimilation of cranberry leaves. Scientia Hort. 64:283-292.

CARBOHYDRATE MOVEMENT

In the last article we discussed the probably source of carbohydrates to support cranberry fruit set and development. The rates of photosynthesis of new leaves are roughly double that of one-year-old leaves. In previous article we described indirect evidence that carbohydrates that support fruit growth come primarily from current season leaves. This article will discuss direct evidence showing that fruit growth is supported by current season leaves preferentially to on-year-old leaves.

If one considers the structural makeup of a cranberry vine there are only three potential sources of carbohydrates to support fruit growth: New leaves above the fruit, old leaves below the fruit, and non-fruiting uprights along the same runner.

The best way to track the movement of carbohydrates from the source to where they are utilized is by using radioactive tracers. Using radioactive carbon we were able to track the movement of carbon from the leaves to the fruit. We exposed new leaves above fruit, one-year-old leaves below fruit, or leaves on an adjacent non-fruiting uprights to $^{14}CO_2$ for about 30 minutes then allowed the carbohydrates to move within the vines for three or four days. Samples were then frozen at -80°C and exposed to x-ray film. After the x-ray film was exposed from the radioactivity emitted by the radioactive carbon the radioactivity in the cranberry tissue was quantified by liquid scintillation methods.

We were able to successfully introduce radioactive carbon into cranberry vines using our techniques during both the time of flowering and after fruit set. The results of experiment are shown in Table 1. The amount of radioactivity was high in the leaves where the label was introduced (note above and below). The most important data from this experiment is in the center data column. This shows the amount of radioactivity that moved into the flowers or fruit from leaves above, below, or on an adjacent upright. Clearly the new leaves above developing flowers and fruit move the most carbon into the flowers and fruit. Roughly ten times as much radioactivity was found in fruit when leaves above them were labeled compared to when one-year-old leaves below them were labeled. Surprisingly, almost no carbohydrates moved from adjacent non-fruiting into the flowers and fruit. Roughly ten times as much radioactivity was found in fruit when leaves above them were labeled compared to when one-year-old leaves below them were labeled. Surprisingly, almost no carbohydrates moved from adjacent non-fruiting uprights to a fruiting upright along the same runner. This research clearly and unequivocally shows that the primary source of carbohydrates to support fruit growth are the new leaves above the fruit. This work supports previous research showing that removing new leaves at fruit set reduced fruit set and yield and that removing new leaves was more detrimental than removing one-year-old leaves. Protecting and maintaining the integrity of these leaves is critical to producing a crop. This also supports the contention that a minimum amount of upright length is required each year to maximize cropping potential.

From this research we learn:

- New leaves above the fruit are the primary source of carbohydrates for fruit growth.
- While one-year-old leaves do move some carbohydrates into fruit it is only about 1/10th as much as new leaves.
- Carbohydrates don't move from non-fruiting uprights to fruiting uprights.

Reference:

Roper, T.R. and J.S. Klueh 1996. Movement patterns of carbon from source to sink in cranberry. J. Amer. Soc. Hort. Sci. 121:846-847.

Table 1. Radioactivity counted in leaves and fruit of uprights exposed to $^{14}CO_2$.

14C Labelling		Radioactivity in Tissue (dpm)		
Tissue	**Timing**	Above	Flowers/fruit	Below
Above fruit	Flowering	7,709 a	5,592 a	222 b
Above fruit	Fruiting	4,824 b	10,527 a	118 c
Below fruit	Flowering	27 b	342 b	4,308 a
Below fruit	Fruiting	180 b	957 b	3,827 a
Adjacent upright	Flowering	20	54	32
Adjacent upright	Fruiting	14	126 a	27 b

Within rows, means separation by Duncan's new multiple range test.

TOO FEW FRUIT OR TOO MANY FLOWERS?

In financial investing it is always good advice to diversify portfolios. Diversification could include short term and long term instruments coupled with high-risk and lower risk investments. The exact blend of investments would depend on the time frame of your investment goals and your aversion to risk. Every investment portfolio is slightly different, but in each case, the goal is to protect the principal and create growth to be realized in the future.

Plants also make investments for the future. Different plants invest their resources in different ways. For example, the common mustard weed Arabidopsis can complete its life cycle of germination, growth, and seed production in 30 to 45 days. Compare that to an oak tree that may be 15-20 years old before the first acorn is produced and which will live for hundreds of years. A dandelion will produce viable fruit and seed from every flower while an apple tree will produce a fruit from about 20% of flowers. While plants employ different reproductive strategies they all work to provide for viable progeny.

Ecologists have four hypotheses as to why plants such as cranberry produce more flowers than fruit. 1) to select the best fruit and seed number by aborting inferior fruit, 2) to compensate for uncertainties of pollination, resource availability, or adverse weather such as frost or hail, 3) providing large amounts of pollen to ensure pollination of viable flowers by producing an overabundance of flowers, and 4) having many flowers blooming at the same time would attract more pollinating insects.

To test these hypothesis two Canadian researchers recently conducted some pollination and fruit removal experiments. In one experiment they provided natural insect pollination, hand pollination (with insects excluded), or excluded insects with screened cages. At the end of the season they measured fruit set, fruit mass, and seed number per fruit.

Excluding insects substantially reduced fruit set, fruit size, and seeds per fruit (Figure 1A, B, C). Manual pollination where the supply of pollen to the flowers was more than adequate for fruit set did not increase fruit set or fruit size but resulted in slightly

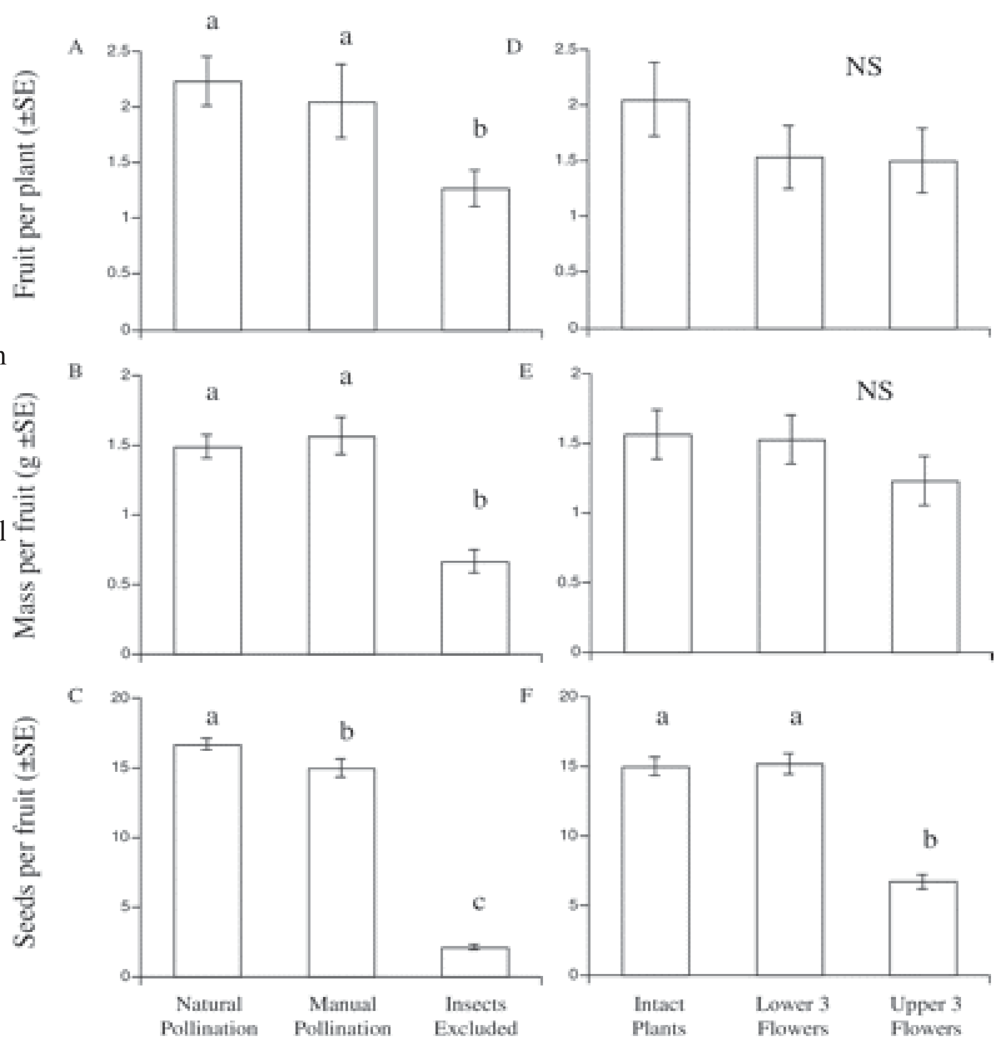

Figure 1. The effect of hand pollination and insect exclusion along with flower removal on fruit set, size and seed number in 'Stevens' cranberries.

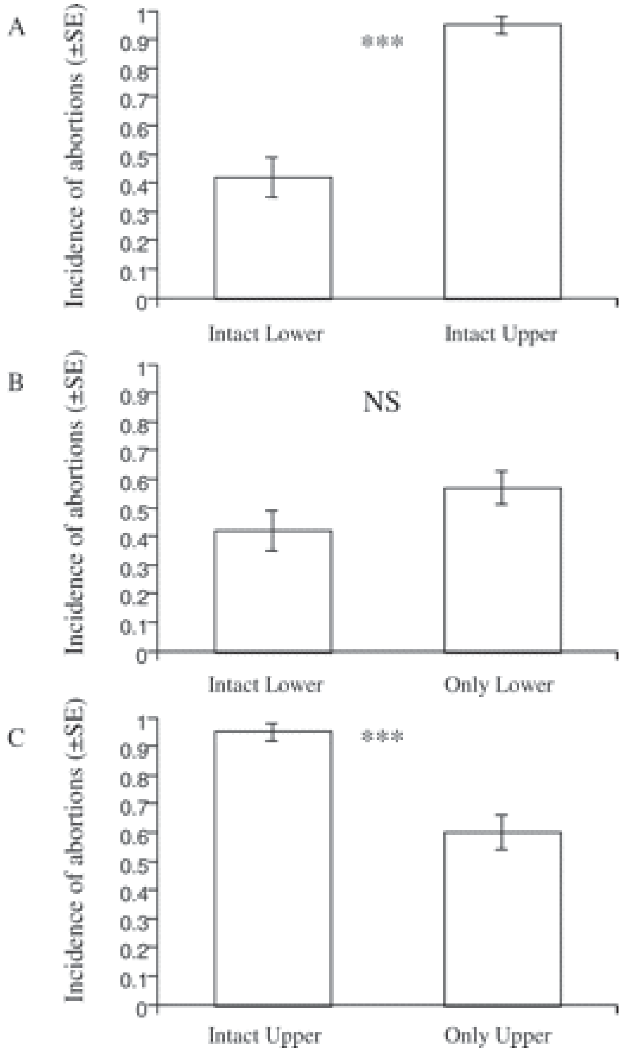

Figure 2. Effect of flower removal on cranberry fruit abortion as a function of flower removal stages, respectively.

fewer seeds per fruit. Removing either the upper or lower three flowers did not significantly fruit set or fruit size, but when only the upper three flowers were left (lower flowers removed) the number of seeds per fruit was reduced (Figure 1D, E, F). In both treatments about two fruit set per upright.

In another experiment these researchers examined by flower position at what time during the fruit development period abortion occurred. They found that 93% of fruit abortion took place after the onset of fruit development with only 7% occurring during flowering. The researchers microscopically examined the styles of the aborted flowers and discovered that fruit abortion may be related to pollination because there were fewer germ tubes in the styles of aborted flowers.

To another series of uprights the researchers either left uprights intact or they removed the lower three flowers or the upper three flowers and recorded the incidence of fruit abortions on those that remained. The results are shown in Figure 2. When no flowers are removed the incidence of fruit abortion is higher in the upper positions than in the lower positions (Fig. 2A). When the upper flowers are removed the incidence of fruit abortion is not different from the situation with intact uprights (Fig 2B). When the lower flowers were removed the incidence of fruit abortions is much lower than for intact uprights (Fig 2C).

This is similar to the work of Birrenkott and Stang who removed the lower two flowers at hook,

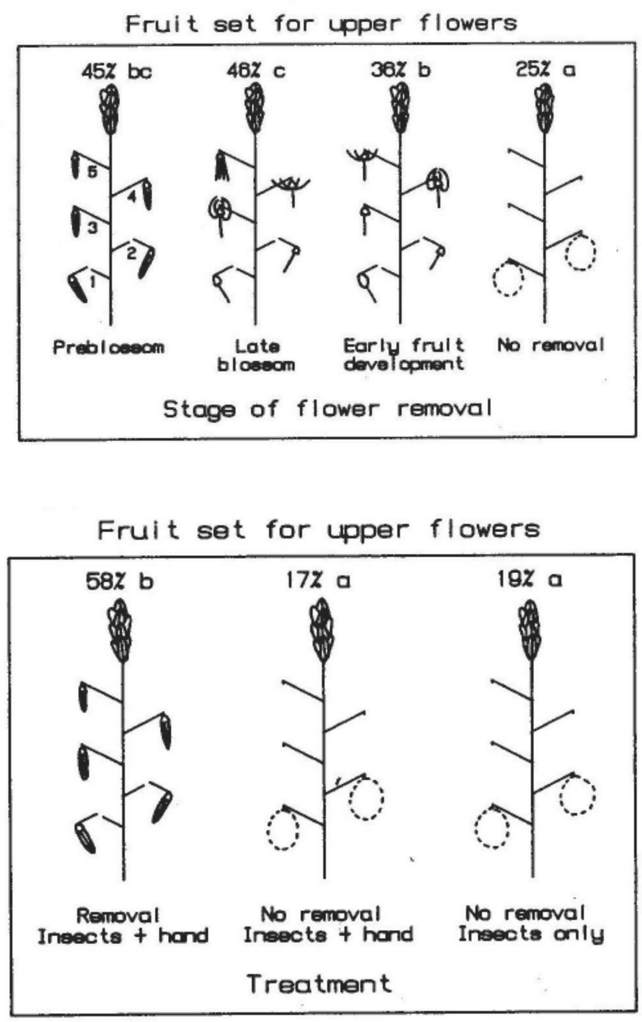

Figure 3. The effect of removing lower position flowers at different times on the fruit set of flowers in upper positions.

flowering, or fruit set stages of fruit development and measured fruit set in the remaining flowers. They found that removing the lower flowers or fruitlets resulted in 45%, 46%, or 36% fruit set when removed at hook, flowering, or fruit set.

This compares to 25% fruit set in upper flower positions when the lower flowers were not removed (Fig 3). When hooks were removed and augmented with hand pollination 58% of upper flowers set fruit compared to 17 or 19% fruit set when hooks were not removed (Fig 4).

Figure 4. The effect of removing lower position hooks on fruit set of upper flowers.

Brown and McNeil conclude from their work: "Thus the proximate cause for the low fruit set in distal (*upper*) cranberry flowers under natural conditions appears to be resource competition between developing fruits, whereas the ultimate or evolutionary causes for the overproduction of flowers in cranberry may (1) allow selection for optimal fruit and seed size and/or quality through selective abortion, (2) result in additional fruit set in years of high resource availability, (3) serve as pollen sources to sire fruit on other plants, and (4) provide an assurance policy for fruit lost to unpredictable events." In short, the low fruit set in cranberry may not be too few fruit, but too many flowers!

In this article we learned:

- Insects are important pollinators for cranberry and excluding insects will reduce fruit set and size.
- Developing fruit compete for limited resources.
- Removing lower fruit results in higher fruit set of upper flowers.

References:

Birrenkott, B.A, and E.J. Stang. 1990. Selective flower removal increases cranberry fruit set. HortScience 25:1226-1228.

Brown, A.O. and J.H. McNeil. 2006. Fruit production in cranberry (Ericaceae: Vaccinium macrocarpon): A bet hedging strategy to optimize reproductive effort. Amer. J. Bot. 93:910-916.

NITROGEN FERTILIZATION AND YIELD COMPONENTS

The goal of most cranberry growers is to produce as many berries as possible with the least input or cost or maximizing return on investment. Achieving this goal requires management that transforms cranberry yield components and sunlight into cranberries. Yield components are the potential yield and in combination with sunlight, water, nutrients, temperature (environment), make carbohydrates or the harvest. Approximately half the yield potential can be turned into cranberries.

Cranberry yield components are: 1) total number of uprights, 2) flowering upright number, 3) flower number, 4) berry number, and 5) individual berry weight. Let's examine how you can manipulate yield components that control cranberry yield.

Nitrogen fertilizer is applied to achieve and maintain tissue sufficiency. When vines have a sufficient N concentration, nitrogen will not limit yields. Understanding the changes nitrogen makes to yield components should help growers manage nitrogen application. A few years ago we completed research that helped us understand the relationship between N fertilization and yield. We identified a cranberry bed in south coastal Oregon that was seriously deficient in nitrogen. For three years, plots in this bed were given either 0, 20, 40 or 60 lb/a applied N. Cranberry yield components were measured after three years of fertilizer application. Yield components, yield component ratios, and yield are given in Table 1.

Table 1 shows that in a nitrogen deficient cranberry bed, application of N increases total upright number, flowering upright number, flower number, and yield or total berry weight. It also increased tissue N concentration (data not shown).

Based on prior research, the two important ratios calculated from these components are

Table 1. The relationship between nitrogen fertilization and yield components of cranberry from an N deficient bed in coastal Oregon.

	Yield Component	N Rate (lb/a)			
Line		**0**	**20**	**40**	**80**
1	Total upright number/sq. ft.	274	334	378	443
2	Flowering upright number /sq. ft.	74	110	126	143
3	Flower number/sq. ft.	282	369	400	555
4	Berry number/sq. ft	76	128	191	264
5	Berry weight, grams/sq. ft.	113	202	315	485
6	Floral induction or proportion of fruiting uprights	27	31	33	32
7	Flowers/flowering upright	3.8	3.6	3.2	3.9
8	Fruit set, Fruit/flowers (%)	28	35	48	48
9	Berry size, grams	1.5	1.6	1.6	1.8
10	Yield increase from increased berry size, bbl/a	0	5	0	52
11	Yield increase from increased berry number, bbl/a	0	80	100	131

floral induction (proportion of flowering uprights per total uprights) and fruit set (Fruit number per flower number). Addition of N to a deficient cranberry bed did not change the proportion of flowering uprights. About one-third the total uprights flower, regardless of the N rate. Fruit set increased from 28 to 48 % or from about one-quarter to one-half when sufficient N is supplied (Table 1, line 8).

Such a large increase in the number of fruit produced from the flowers present (fruit set) indicates a change in the cranberry plant. The likely change is additional leaves to transform carbon from the atmosphere into plant energy for growth and storage (carbohydrates). Average upright length increased from 2 inches to 2 ¾ inches as N rate increased from 0 to 60 lb/a. This upright length is consistent with other recommendations for cranberry fertilization

When 60 lb N/a was applied, 3.9 flowers/flowering upright were counted. At this N rate, the fruit set was 48% or fruit was formed on half the 3.9 flowers (Table 1, line 7). Each flowering upright produced two berries/flowering upright, the theoretical maximum fruit set based on the amount of carbon each upright can transform into carbohydrates and the amount of carbon in a mature fruit.

Let's examine the source of yield or limitation to yield. If each flowering upright will produce two berries and the proportion of flowering uprights to total uprights is constant, then the total upright number is critical. High yielding Stevens beds typically have 400 to 500 uprights per square foot.

As N application increased and as the vines became N sufficient, fruit set increased (Table 1, line 8). If we extrapolate the increase in yield from our small samples to an acre, we see an increase of 80 bbl/a as N increases from 0 to 20 lb/a and an increase of 100 bbl/a resulting from having MORE berries as N increases from 20 to 40 lb/a N fertilizer (Line 11). This is caused by an increase in fruit set and by a slight increase in flowering/fruiting uprights.

Similarly, as N fertilizer increased there was a small increase in berry size (Line 9). If we extrapolate to yield per acre, the increase in yield resulting from **LARGER** berries was 52 bbl/a (line 11).

Some growers focus on increasing berry size. After fruit set, they want to "pump up" berries with fertilizer. The research results represented in Table 1 strongly suggest that there is more yield to be gained from increasing berry numbers (either through fruit set or floral induction) than from fruit size. Remember, carbohydrates, not fertilizer nutrients make berries. Berry size is a less important yield component. It rarely increases or decreases yield. Table 1 shows a slight increase in berry size from nitrogen application. The increase in berry size did not increase yield when the N rate was increased from 0 to 20or from 20 to 40 lb/a. Berry size only slightly increased yield, 50 bbl/a, when the N increased from 40 to 60 lb/a. The increase in yield from berry size was about 1/3 the yield increase from an increase in berry number.

In this article we learned that:

- When N fertilizer is applied to overcome a deficiency vine growth and yield increase.
- Adequate N results in more fruit and larger fruit.
- Yield increases are greater from increasing berry number than from increasing berry size.

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Teryl Roper, UW-Madison

CLIMATE AND CRANBERRY YIELD

In previous articles we discussed various factors that can affect yield in cranberry. These were all considered on a very localized basis. Experiments were conducted on a few uprights to a few square feet of bed surface. While this information is valuable because it increases our understanding of how cranberry vines respond to manipulation or to local conditions, it does not give us the global sense of what affects cranberry yields. Skilled managers can affect local conditions, but none of us can affect the overall climate and there is little that can be done to mitigate climatic conditions. But if we at least have some understanding of climatic effects we can reduce our worry quotient.

Research involving climate is more experiential than experimental. Typically yield data covering a number of years is compared to climatic data and correlations are drawn between the two. Researchers in Massachusetts in the 1940s did this sort of work and drew conclusions from the data they had. As statistical techniques have improved more detailed work could be done. Finally, comparisons can be made among growing regions with vastly different climates. In this article we'll explore the effects of weather on yield.

H.J. Franklin in Massachusetts correlated the hours of sunshine received in various months to the size of the crop the current and following year. He showed that above average sunshine during May, August, September, and November was correlated with above average crops during the following year.

Franklin also examined the relationship of temperature and yield. Temperature had little effect on Massachusetts cranberry yields. They did find a weak correlation between a cold March and above-average yields, presumably because cool temperatures in March kept the vines dormant thus avoiding early spring frosts. Excessive heat in May, June, and August was associated with poor yields as this lead to 'blast' of the vines.

Morzuch created a regression model using 79 years of yield and climate data to predict yield based on technological advances and climate. He found that 91% of the variability in yield was explained by technological advances and only 2% was related to climate.

Degaetano and Shulman working with New Jersey data did find statistical correlations between climatic data and cranberry yield. In their research, "Temperature and sunshine appear to have the greatest effect on cranberry growth and production.

Precipitation, snow cover, estimates of potential evapotranspiration, and available soil moisture are apparently of little importance. Increased berry production is associated with warm temperatures during mid-May to late June and mid-October to mid-November of the year prior to harvest. Cold temperatures during early February to late March and sunny conditions from early May to mid-June also favor above-normal yields. Excessive heat from mid-June to early August and between the accumulation of 392 and 504°C GDD correspond to below normal production."

During May and June of the year prior to harvest temperatures >65°F and minimum temperatures >50°F were associated with above-normal yields. Between mid-October to mid-November maximum temperatures >65°F and minimums >50°F also corresponded to above normal yields. Lower yields were correlated to years when maximum daily temperatures did not reach 65°F or the low temperatures were below 25°F during this same autumn period.

The relationship between warm temperatures at specific times during the season and yield is not surprising. Consider the phenology of the crop during these times. In the spring uprights are growing. Warm sunny weather would promote vigorous growth that would be more likely to result in a fruit bud. Warm temperatures in the mid-fall would provide optimum conditions for continued bud development. Well developed buds going into the winter would be more likely to produce strong flowers that would set fruit the following year. By the same token, during the harvest year hot weather during bloom and fruit set would interfere with pollen germination and growth of the germ tube through the style and into the ovary.

Similar results were found by a national group of physiologists who were looking at the rate of fruit growth in three cultivars across five growing regions. We were trying to explain why the rate of growth of a given cultivar was so variable across different growing regions. For example, for Stevens Wisconsin and Massachusetts had the highest growth rate while Washington and Oregon had the slowest. Yet at harvest fruit size is similar across states. How could this be? The difference is that the Pacific Northwest has a much longer growing season with more moderate cool temperatures overall. When we tried to explain why this would be we discovered that solar radiation (light) accounted for little of the variability if fruit growth. Growing degree days and number of days were also poor predictors. Instead, the number of moderate temperature days (between 61 and 86°F) was the key and accounted for 80% of the variation in fruit growth rate. The most rapid growth occurred when temperatures were in this range. High temperatures were limiting in New Jersey while cool temperatures were limiting in Oregon and Washington.

Why is temperature so important? Likely because most of what occurs in biological systems varies with temperature. We know that the optimum temperature for photosynthesis in cranberries is in the mid-70s. Temperatures above or below that result in less photosynthesis leading to reduced growth. Respiration is also temperature dependent. Respiration uses the products of photosynthesis and as temperature increases 10°C the rate of respiration doubles. Moderate temperatures maximize photosynthesis while maintaining moderate respiration.

Temperature also affects nutrient uptake. In a study of the rate of uptake of applied nitrogen fertilizer we found a much higher rate of uptake in Wisconsin and New Jersey compared to Massachusetts and Oregon. A follow up study in aeroponics demonstrated that N uptake by cranberries is strongly temperature dependent and that growers should wait until soil temperatures are at least 55°F before applying N fertilizer.

In this article we learned that:

- Climate affects yield of cranberries.
- Warm temperatures in the spring and mid-fall the year before harvest contribute to high yields.
- Hot temperatures during bloom and fruit set contribute to low yields
- Moderate temperatures (between 61 and 86°F) were associated with high fruit growth rates
- Nitrogen uptake is temperature dependent.

References:

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WHAT REALLY LIMITS YIELD? (2)

This year I have attempted to describe in grower-friendly language some of the pertinent research related to cranberry physiology. I know that sometimes I failed to explain the research sufficiently well leaving some to scratch their heads and wonder what planet I dropped off from. I have come to realize over time that the grower community is not fully aware of much of the research that has been done (much with grower support) during the past 20 years or so. While we don't understand every potential factor that can affect yield, we do have a working understanding of what affects yield that we can use to draw conclusions about what management practices will or will not make a difference on yield. I hope to summarize the prior nine articles here and then draw some general conclusions. My intention is that you'll also hear more about this at the Wisconsin Cranberry School this winter.

We began with a discussion of external factors that could obviously affect yield. These included light, temperature, crowding, shade, carbon dioxide concentration, and mineral nutrition. We described how each of these can limit or promote yield and under what conditions. Then we described internal factors that can affect yield. We introduced the concept of yield component analysis that tries to identify how yield is limited and discovered that the number of flowering uprights per unit land area and fruit set were the primary limiting factors. We described biennial bearing in cranberries where individual uprights typically will flower and produce fruit every other year.

One of the most important topics was pollination and fruit set. Since fruit set (number of fruit per number of flowers) was so important it was important to understand what limits fruit set. Improving pollination could increase fruit set, but not yield. Lower flowers are more likely to set fruit than upper flowers, but that fruit set in upper flowers could be improved by removing lower flowers. Growth regulators could be used to increase fruit set, but not yield. Thus, increasing fruit set alone could not greatly improve yield.

Then we asked the question, "when are resources most limiting to fruit set and which resources are most important?" We investigated these questions by removing leaves at various times and in various configurations. We learned that resource limitation is most critical at the time of fruit set and that the new growth above the fruit is the primary source of carbohydrates that supports fruit growth. As a follow up to this work we showed data about annual patterns of carbohydrate availability in cranberry vines. We showed that carbohydrates were lowest at fruit set and during the fruit development period. We also showed that the rate of photosynthesis of current season leaves is double that of one-year-old leaves. Using radioactive carbon we also showed that most of the carbohydrates used in fruit growth comes from the new leaves above the fruit and very little comes from one-year-old leaves.

From here we shifted gears to reproductive ecology and learned that as a bet hedging device that cranberry vines routinely produce more flowers than fruit. Having more flowers than fruit and having flowers open over a prolonged period of time spreads risk over time and ensures a greater likelihood of having annual cropping. We also learned that fruit along an individual upright compete with one another for resources—and that the lower flowers win.

We looked at the effect of climate on yield. Climate is something that is completely beyond our control, yet it has a great influence on yield over about an 18 month period. We also learned that uptake of nutrients is related to air and soil temperatures. Along these same lines we learned that increasing fertilizer N in an N deficient bed increased vegetative growth and yield, but that the primary effect of increasing N was through increasing fruit number, not fruit size.

What is the 'take home message' from this series of articles? Fertilizer is not the only determinant of yield. In fact, it is not a very important contributor to yield. Other factors such as weather and genetics are far more important contributors to yield than fertilizer is.

With an understanding of the physiology of yield growers will be better able to make management decisions, including fertility. They'll be less prone to sales pitches that lack sufficient research base to support them.

Our goal with tissue testing and writing nutrient management plans is to apply sufficient fertilizer so that fertility is never the limiting factor for plant growth and yield. To say it another way, we want to obtain and then maintain tissue sufficiency. Adding fertilizer beyond that is wasteful and will not lead to higher yields.