PHOTOSYNTHESIS AND CARBOHYDRATE PARTITIONING IN CRANBERRY

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Yield per area in cranberry has been shown to depend largely on two facts, 1) the number of fruiting uprights per area and 2) the percent fruit set within those fruiting uprights. In order to increase productivity substantially at least one of these factors needs to increase. We have attempted to research these factors at the University of Wisconsin-Madison, focusing on fruit set.

Fruit set is typically limited by one of two factors, pollination and fertilization or resources, primarily carbohydrates. Dr. Stang and his graduate student, Brian Birrenkott, examined pollination. They found that if flowers were hand pollinated in the field they could increase fruit set from 30% to 38%. This was a significant increase. Therefore, pollination is one factor limiting fruit set of cranberry. They also found, however, that if flowers in lower positions on uprights were removed that the fruit set of flowers in upper positions was enhanced. If lower flowers were removed before there was substantial fruit growth, fruit set in upper flowers could be improved from 25% to 45% fruit set (20% increase). This research suggests that fruit set is resource limited.

Resources are required to set fruit. These resources include carbohydrates, proteins and mineral elements. Carbohydrates are typically needed in the greatest supply as they provide energy to support cell functions as well as building materials for cell walls, membranes, organelles and proteins. Mineral elements may be limiting more in terms of limiting photosynthesis and other cell processes rather than being limiting in and of themselves. Minerals exclusive of carbon, hydrogen, and oxygen comprise only about 3 to 5 percent of the dry weight of most plants, and most plants are about 75% water. Our hypothesis is that fruit set in cranberry is limited by availability of carbohydrates.

During a growing season, carbohydrates for fruit set and development (or for vegetative growth) can come either from current photosynthesis or from stored reserves that were produced during previous seasons. One way to understand the carbon economy of a plant is to follow the changes in nonstructural carbohydrates through a season. Nonstructural carbohydrates rise and fall in response to dilution and demand by growing plant organs. Nonstructural carbohydrates include sucrose, glucose, fructose, and starch. These sugars are readily transported or can be easily converted to transportable sugars. This is in contrast to structural elements such as cellulose, lignin and pectin.

We followed the changes in nonstructural carbohydrates during two seasons for Stevens and Searles cranberries. The results are shown in Figures 1 and 2. Nonstructural carbohydrates are high early in the season but begin to decrease just before flowering begins and then drop precipitously, reaching their low point at the time of fruit set. After fruit set, carbohydrate concentration begins to increase until it reaches a high point after harvest. Uprights that bear fruit contain less carbohydrate beginning at bloom and continuing for the remainder of the season. The carbohydrate content of nonfruiting uprights also decreases following the same pattern, but showing a smaller decline. It is interesting to note that carbohydrate content of roots and stems is lower than uprights and that it fluctuates less than uprights. This suggests that storage carbohydrates are less important than current season photosynthesis. It is unclear why the carbohydrate content of nonfruiting uprights declines. It could represent the demand for carbohydrate by vegetative growth or it could decline simply from dilution as the plant dry weight increases, or it could represent exports to adjoining fruiting uprights. However, no data exists to support any alternative.

When these data are combined with data on the rate of carbon assimilation (net photosynthesis) we get a clearer picture of the carbohydrate status of the vines. We measured net photosynthesis during two seasons for Stevens and Searles cranberry. The results are shown in Figures 3 and 4. We found that the rate of photosynthesis was always about twice as high in new leaves than old leaves. Old leaves begin to fix carbon earlier in the season than new leaves and thus may be very important to fruit set. This may be the source of the slight increase in nonstructural carbohydrates early in the season (Fig 1 & 2). By the time the fruit are set and developing it is clear that current photosynthesis of new leaves is an important source of carbohydrates. The rate of net photosynthesis stays relatively constant in the mid part of the season, but begins to decline by late August. This coincides with cooler temperatures and loss of chlorophyll (vine reddening).

The data so far don’t show what happens if carbon resources are altered. We performed three types of experiments and have an additional experiment underway to see what happens if the carbohydrate status of the plant is altered. We altered the carbon status of cranberry uprights by shading and removing leaves.

Dr. Stang and one of his graduate students removed the new growth of fruiting cranberry uprights (above the fruit) at two week intervals beginning in m&June and continuing through September. Removing new growth in June or early July, during the flowering and fruit set period, decreased fruit set, fruit number per upright and the weight per berry (Figure 5). When the new growth was removed in late July, August or September there was no effect on fruit set or fruit number per upright. These data suggest first, that early season photosynthesis is very important for fruit set; second, that current season photosynthesis of new leaves provides a major portion of photosynthate for fruit set; and third, reserves or photosynthate from other sources are less important.

The sources of photosynthate for fruit growth can be spatially partitioned as coming from new leaves above fruit, one-year-old leaves below the fruit, adjacent nonfruiting uprights on the same runner or reserves in perennial portions of the vine. We removed leaves in different portions of the vines in an effort to isolate individual sources of photosynthate for fruit set. Four treatments were imposed: 1) no leaves were removed; 2) leaves above the fruit were removed; 3) leaves below the fruit were removed, or; 4) leaves both above and below the fruit were removed. We attempted to isolate fruit and new leaves by girdling stems below the fruit, but the treatment killed the uprights. When only leaves below fruit were removed fruit set was not decreased (Table 1). When leaves above the fruit were removed fruit set was significantly reduced. When both groups of leaves were removed there was an additional reduction of fruit set but not always significantly so. These data suggest that carbohydrates for fruit growth come from leaves above the fruit and that one-year-old leaves below fruit are secondary sources of carbohydrates.

The importance of an ample supply of carbohydrates for fruit set or development can also be partitioned in time. We divided the season into four periods (prebloom, bloom, postbloom, preharvest) and shaded portions of a bed with shade cloth of two intensities (93% or 72%) during each time period. When beds were severely shaded (93%) before bloom (prebloom, roughly May 15 to June 15) fruit set was reduced in 1991 but not in 1992 (Tables 2 and 3). This was accompanied by a reduction in the number of flowers per flowering upright in 1991. Severe shade after flowering (postbloom, roughly July 15 to August 15) significantly reduced fruit set in 1991 and 1992. Light postbloom shading in 1992 also reduced fruit set. Late shading (preharvest, roughly August 15 to September 15) was not significantly different from the unshaded control.

The fresh weight of individual berries was not reduced by light shading. Heavy shading during the pre and postbloom periods reduced berry size in 1991 but only during the postbloom period in 1992. Postbloom shading at either intensity reduced yields in both 1991 and 1992. Preharvest shading at either intensity was not different than the control both years. Heavy shading during the prebloom period also reduced total yield both years, but not significantly in 1992.

At the end of each shading treatment carbohydrate concentrations were measured in the treated areas and controls. Nonstructural carbohydrates in shaded tissues were typically 50 to 60% that of the controls (Table 4). The degree of shading did not cause differences in carbohydrate concentrations.

The data from this shading study suggest that carbohydrates for fruit set and development come from current photosynthesis and not from storage. The period immediately following bloom was the most susceptible to interruption of carbohydrate supply, followed by the prebloom period. The preharvest period was not effective in reducing berry number, berry size, or yield. The fact that total nonstructural carbohydrate content of uprights was reduced roughly by half supports the hypothesis that carbohydrates limit fruit set and yield.

When these data are taken in aggregate they support our hypothesis that fruit set in cranberry is resource limited. Nonstructural carbohydrates decline beginning at bloom and reach their minimum at the time of fruit set. Removing new leaves limited fruit set early in the season at the time of fruit set. Severely shading uprights prebloom reduced fruit set in 1991 and severe shading postbloom reduced fruit set both years. This was accompanied by a 40 to 50% reduction in nonstructural carbohydrates in shaded uprights.

The primary source of carbohydrates for fruit set appears to be the new growth above the fruit. New leaves have a rate of photosynthesis roughly twice that of one-year-old leaves. Removing new leaves at the time of fruit set reduced fruit set more than removing one-year-old leaves.

Growers should be concerned about providing optimal conditions for photosynthesis around the time of flowering along with providing for pollination of as many flowers as possible. Applying fertilizers at this time does little, if any, good for this year. If the limiting factor is indeed carbohydrates, then we need to look for ways to improve the carbon status of cranberry vines.

Figure 1. Seasonal changes in total nonstructural carbohydrates (TNC) in different tissues of ‘Stevens’ (A) and ‘Searles’ (B) cranberry vines during 1990. TNC between uprights, stems, and roots was significantly different at the 5% level at each measurement. Tissue differences were determined by analysis of variance. EB : early bloom, H : Harvest. n=6.

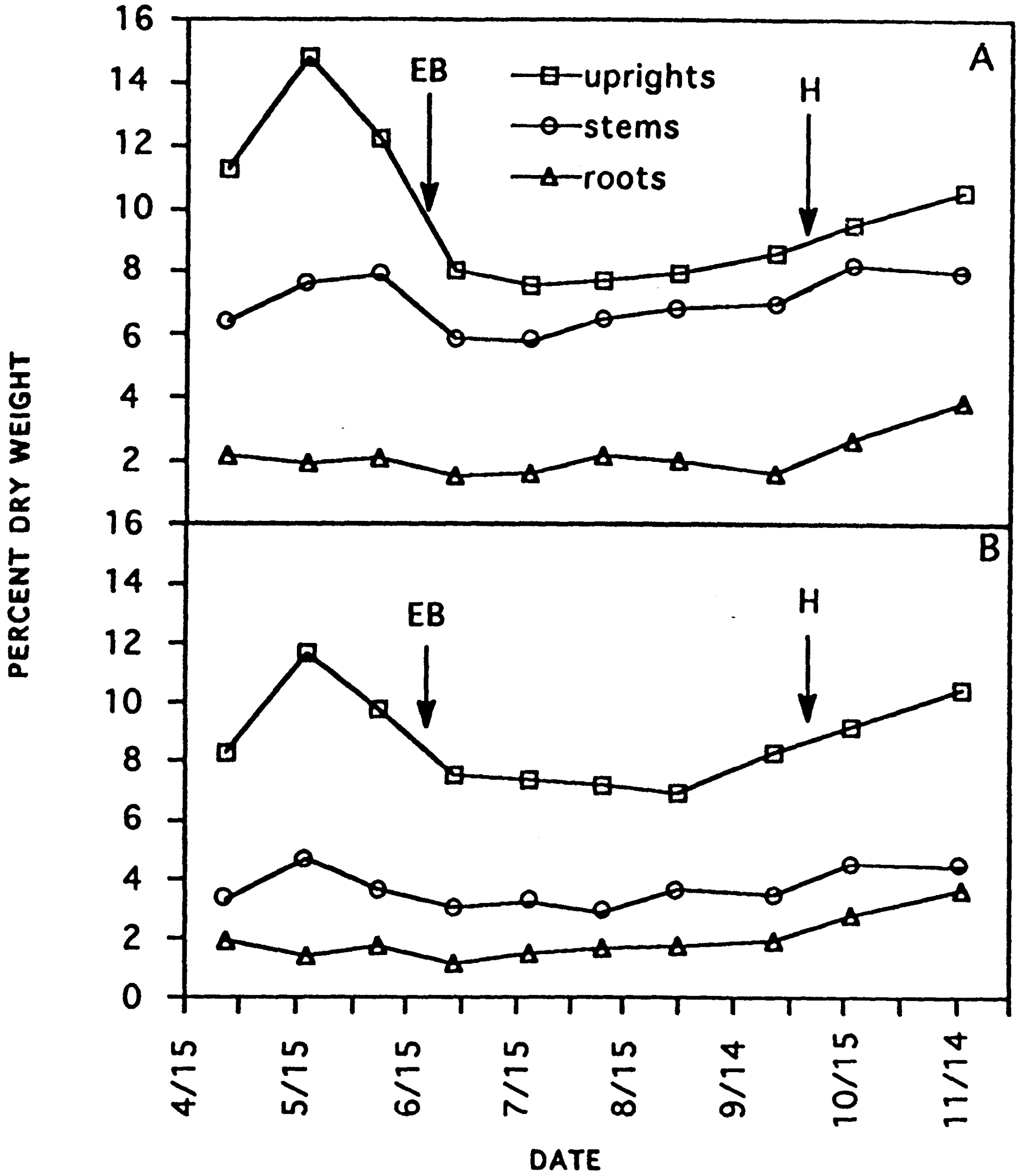

Figure 2. Seasonal changes in total nonstructural carbohydrates (TNC) in different tissues of 'Stevens' (A) and 'Searles' (B) cranberry vines during 1991. TNC between uprights, stems, and roots was significantly different at the 5% level at each measurement. Tissue differences were determined by analysis of variance. EB : early bloom, H : Harvest. n=6.

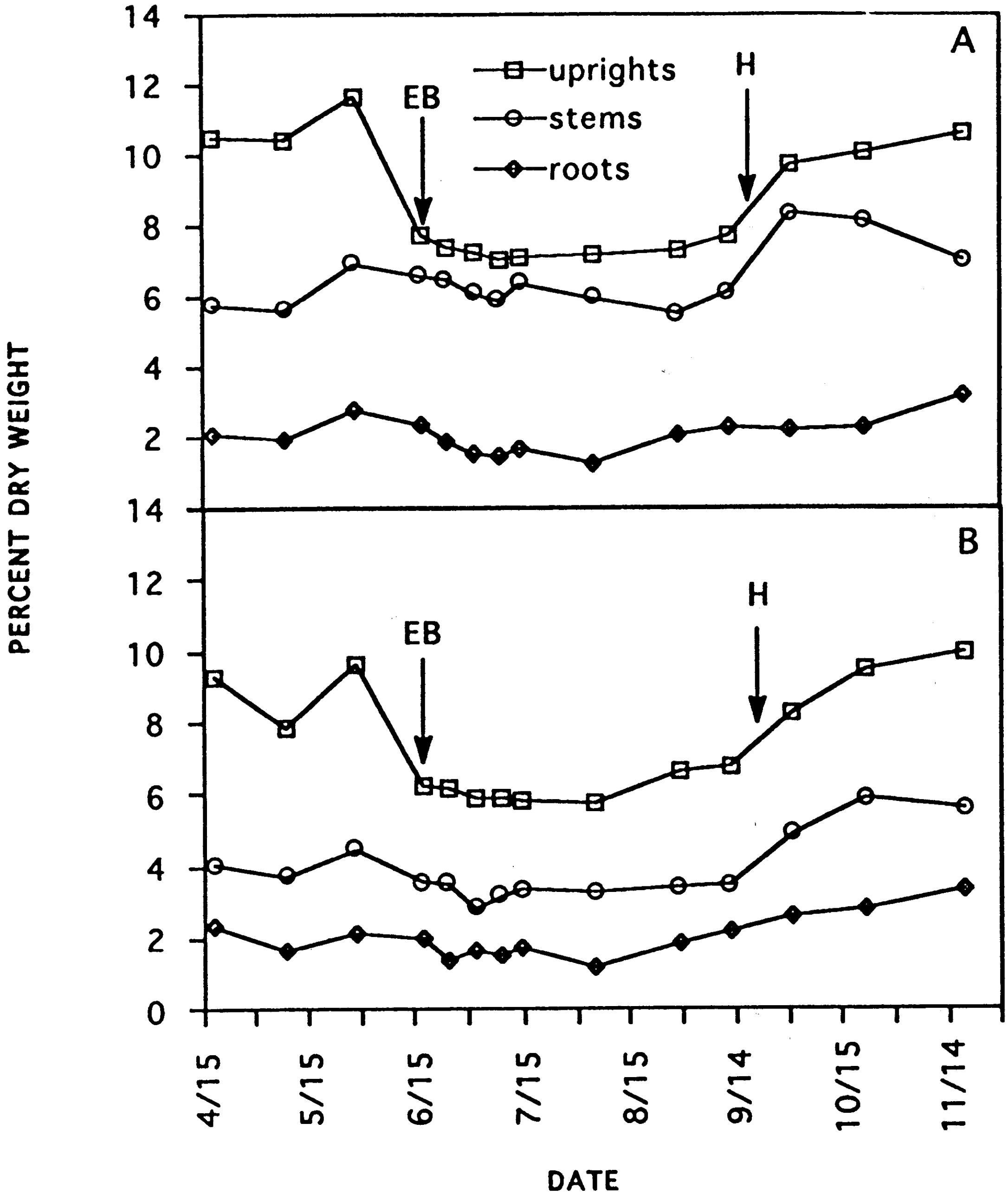

Figure 3. Seasonal changes in the rate of net carbon assimilation of new (acropetal to fruit) and old leaves (basipetal to fruit) of ‘Stevens’ and ‘Searles’ cranberry measured in the field under ambient conditions in 1992. n=8.

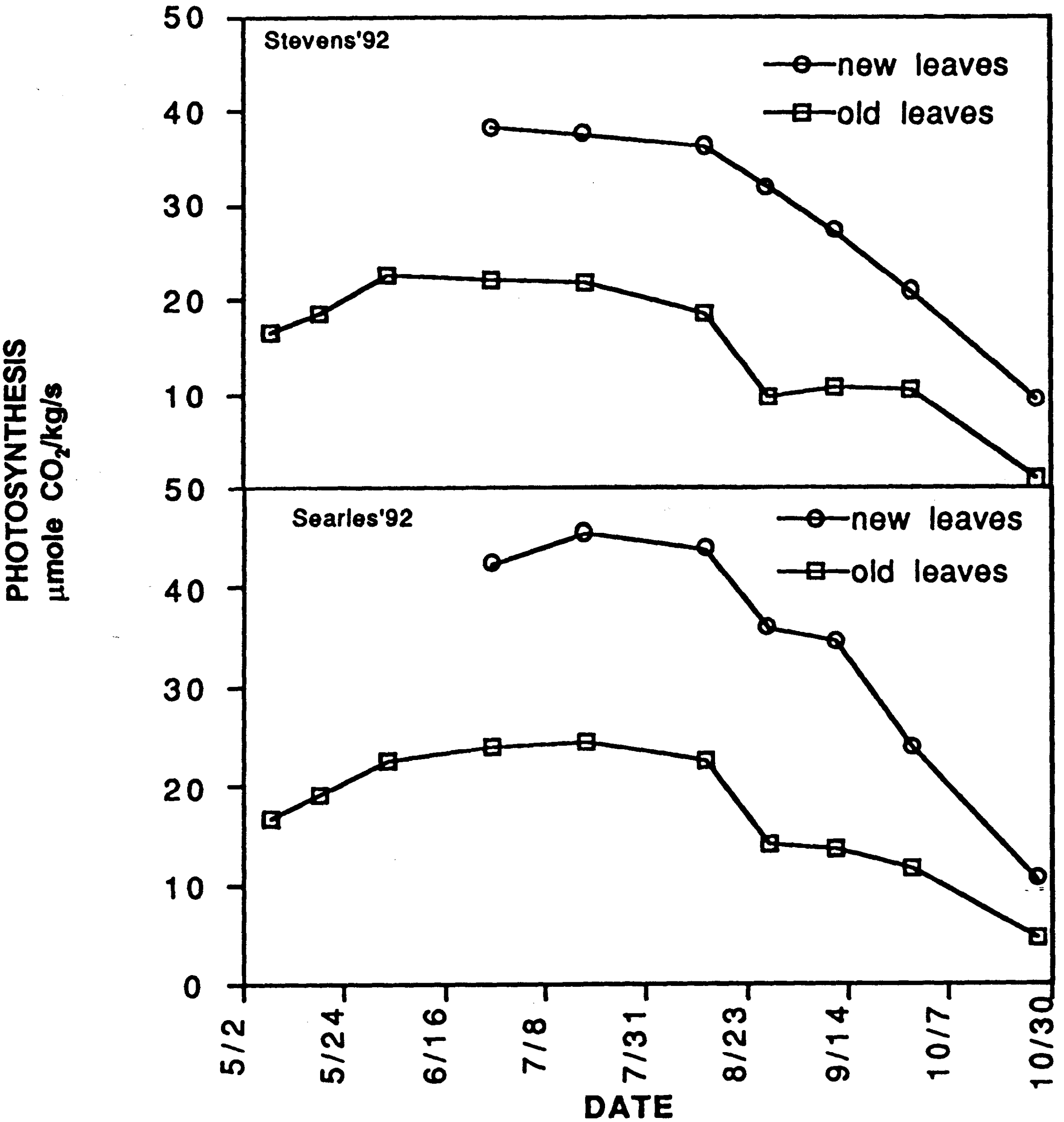

Figure 4. Seasonal changes in the rate of net carbon assimilation of new (acropetal to fruit) and old leaves (basipetal to fruit) of 'Stevens' and 'Searles' cranberry measured in the field under ambient conditions in 1991. n=8.

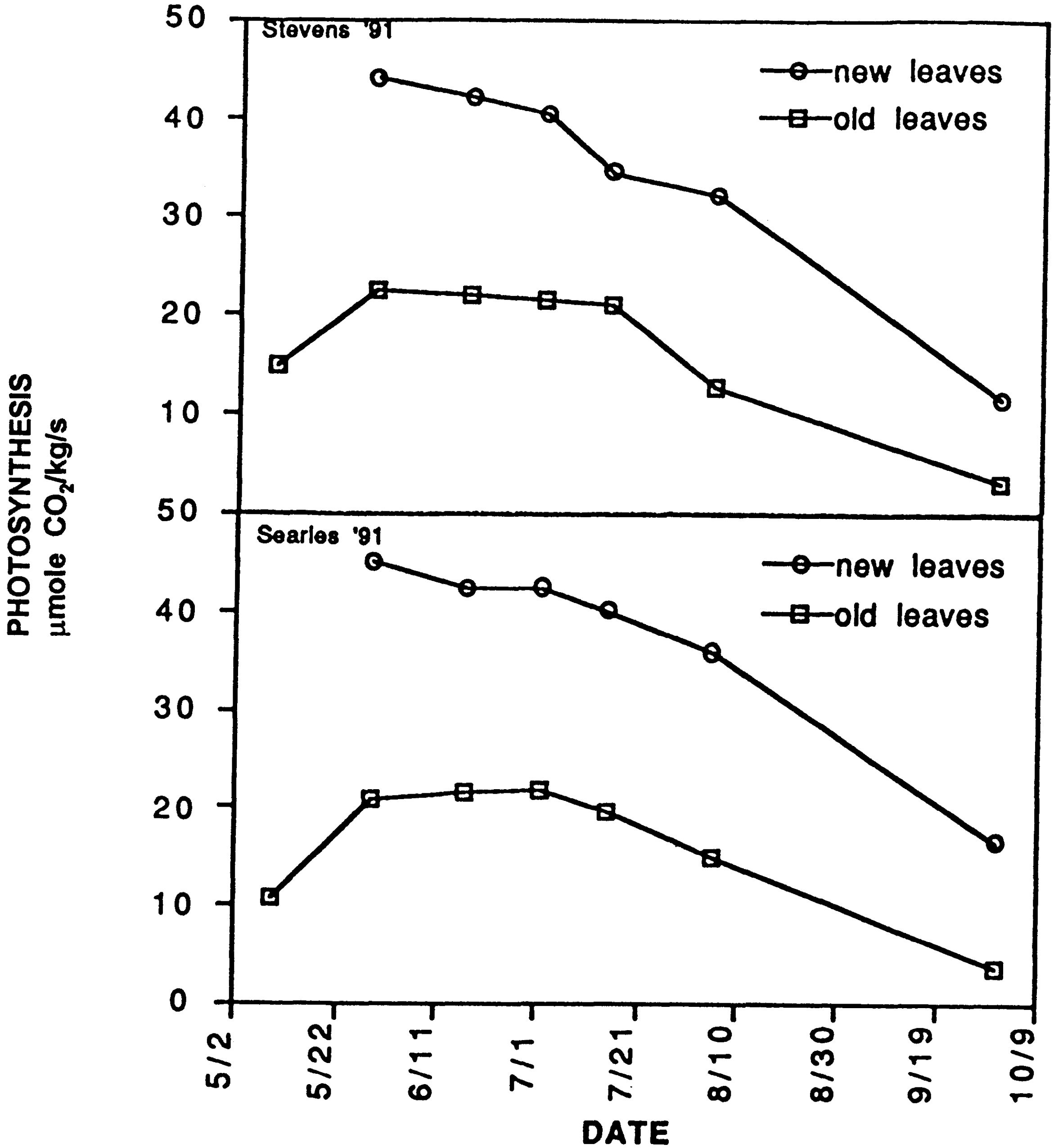

Figure 5. The effect of removing new growth above the fruit on fruit set, fruit number per upright, and fresh berry weight of Crowley cranberry, 1982.

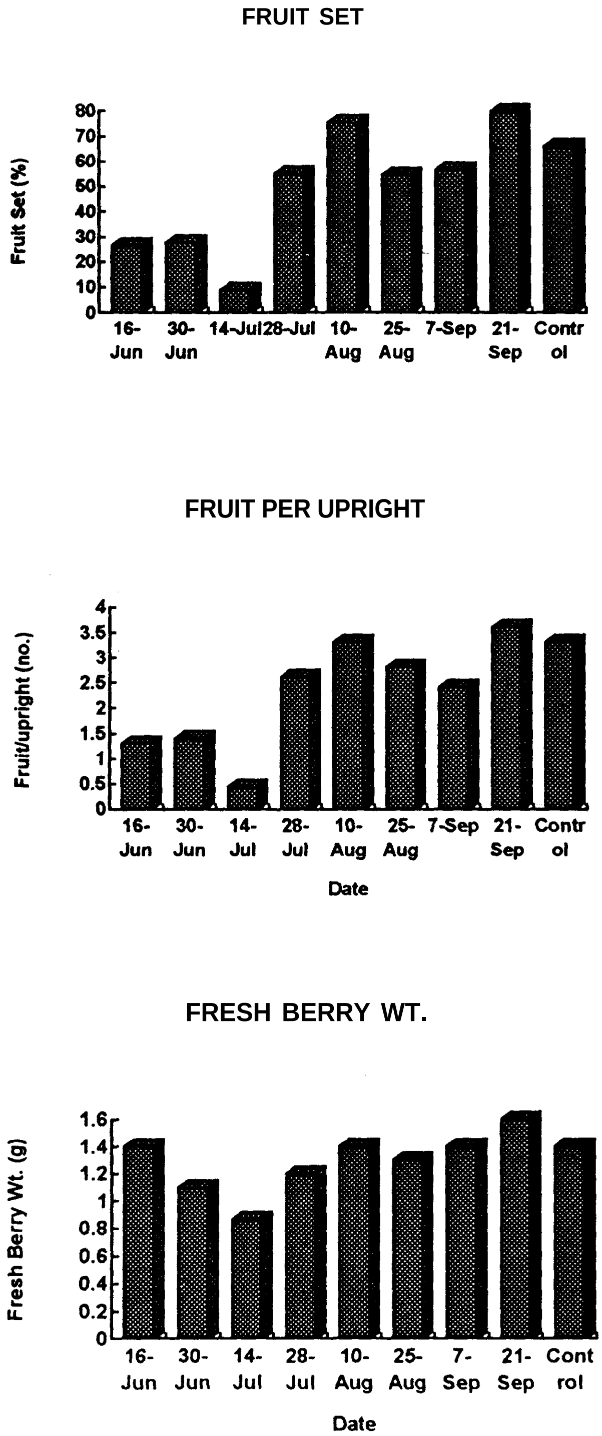

Table 1. Effect of removing different tissues at the time of fruit set on fruit set and yield of 'Searles' cranberry growing at DuBay Cranberry Co. or Gottschalk Cranberry Co. n= 10.

Treatment **DuBay**	Fruit number	Fruit set (%)	Total Fruit Weight (g)	Mean Fruit Weight (g)
		1992		
Control	2.1 a	52 a	2.35 a	1.07
Bottom leaves removed	1.9 a	48 a	1.99 ab	1.01
Upper leaves removed	1.4b	36b	1.51 bc	.98
Both removed	0.9 b	25 c	1.19 c	.95
Significance	** z	**	**	ns x
		1991		
Control	1.8 a	46 a	2.41 a	1.34
Bottom leaves removed	1.6a	41 a	2.09 a	1.32
Upper leaves removed	1.1 b	34 b	1.38 b	1.22
Both removed	0.8 c	20 c	1.26 b	1.23
Significance	**	**	**	ns

Treatment **Gottschalk**	Fruit number	Fruit set (%)	Total Fruit Weight (g)	Mean Fruit Weight (g)
		1992		
Control	1.8 a	46 a	2.21 a	1.27 a
Bottom leaves removed	1.2 b	35b	1.42 b	1.04 b
Upper leaves removed	1.2 b	34 b	1.69 b	1.14 ab
Both removed	0.8 c	21 c	1.26 b	1.02 b
Significance	**	**	**	* y
		1991		
Control	1.9 a	55 a	2.55 a	1.39 a
Bottom leaves removed	1.4 b	39 b	1.91 b	1.10 b
Upper leaves removed	1.1 c	28 c	1.73 b	1.43 a
Both removed	0.8 d	20 c	1.54 b	1.34 a
Significance	**	**	**	**

z. **. Significantly different at p=0.01.
y. *. Significantly different at p=0.05.
x. ns. Not significantly different.

Table 3. Effect of shading cranberry vines during different periods of crop development on fruiting and yield, 1991.

Treatment	Flowers/Upright (#)	Fruit Set (%)	Berry fresh wt. (g)	Total fruit wt. (g)
Control	3.1 abc	25 a	1.14 a	13.2 a
72% shade prebloom	2.9 cd	22 a	0.97 ab	9.5 ab
72% shade postbloom	3.1 abc	22 ab	0.93 abc	8.0 b
72% shade preharvest	3.5 ab	26 a	1.03 ab	12.2 a
93% shade prebloom	2.4 d	15 bc	0.72 c	2.2 c
93% shade postbloom	3.7 a	11 c	0.85 bc	3.0 c
93% shade preharvest	3.2 abc	26 a	0.93 abc	10.6 ab
Significance	** z	* y	*	**

z. ** Significantly different at p=0.01.
y. * Significantly different at p=0.05.

Table 4. Effect of shading cranberry vines during different periods of crop development on fruiting and yield, 1992.

Treatment	Flowers/Upright (#)	Fruit Set (%)	Berry fresh wt. (g)	Total Fruit wt. (g)
Control	2.9	33 a	0.88 a	6.7 b
72% shade prebloom	3.1	34 a	0.84 a	10.9 a
72% shade postbloom	3.0	8 b	0.76 a	2.6 c
72% shade preharvest	2.8	28 a	0.78 a	7.0 ab
93% shade prebloom	2.8	27 a	0.76 a	4.5 bc
93% shade postbloom	2.9	4 b	0.42 b	0.6 c
93% shade preharvest	2.6	30 a	0.82 a	7.7 ab
Significance	ns y	** z	**	**

z. ** Significantly different at p=0.01
y. ns. Not significantly different.

Table 5. The effect of shading cranberry vines at different times during the season on the concentration of total nonstructural carbohydrates in uprights.

Treatment	Total nonstructural carbohydrates, 1991	Total nonstructural carbohydrates, 1992
	Prebloom Shading	
Control	8.86 a	9.07 a
73% shade	4.30 b	4.14 b
92% shade	4.43 b	4.28 b
Significance	** z	**
	Postbloom Shading	
Control	7.21 a	7.19 a
73% shade	4.00 b	3.30 b
92% shade	3.21 b	2.45 b
Significance	**	**

z. ** Significantly different at p=0.01