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The Effect of Partial Defoliation on Vine Carbohydrate Concentration and Flavonoid Production in Cranberries

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Abstract. **The effect of partial defoliation (rate and timing) on vine carbohydrate concentration and the development of phenolic compounds in field-grown 'Stevens' cranberry fruit was investigated in two experiments. In Expt. 1, partial defoliation rates of 0%, 18%, 39%, and 53% of total leaf area were applied before new growth, at fruit set, at midfruit development, and preharvest. In Expt. 2, treatments of 0% and 34% removal of new leaves were applied at postfruit set, and at midfruit development. In both experiments, upright samples were harvested for carbohydrate analysis 10d after defoliation, and fruit were removed for analysis before commercial harvest of the site. While total berry phenolic concentration was unaffected by partial defoliation in both studies, the separate pools of flavonoid compounds were affected differently by treatment. In Expt. 1, total flavonol concentration at harvest was improved by the highest rate of partial defoliation (53% of total leaf area) at both fruit set and midfruit development. Total anthocyanin concentration was improved by partial defoliation rates of 39% and 53% of total leaf area compared to the 18% defoliation treatment, but was not affected by timing of defoliation. Pearson correlation coefficients indicated that total flavonol concentration was positively correlated with vine total nonstructural carbohydrate concentration at preharvest, while total anthocyanin concentration was negatively correlated with vine soluble carbohydrates, starch, and total nonstructural carbohydrate concentration at midfruit development. In Expt. 2, total phenolics, flavonols, and anthocyanins were unaffected by partial defoliation; however there was a negative correlation between total anthocyanin concentration in the fruit and soluble carbohydrate concentration in the vine at midfruit development. In these experiments, partial defoliation early in the growing season improved total flavonols and total anthocyanins. Production of flavonols and anthocyanins appeared to be regulated independently of each other.**

Cranberries (*Vaccinium macrocarpon* Ait.) have gained interest in recent years as a major source of phenolic compounds in the human diet. There is increasing research showing the positive health benefits of cranberries (Neto et al., 2005, and references therein). Phenolic compounds of medicinal interest in cranberry consist primarily of flavonoids, which can be induced by environmental factors such as light and fungal infection (Vvedenskaya et al., 2004). Flavonoids can further be classified into smaller subgroups such as anthocyanins, flavonols, and proanthocyanindins. Flavonols may serve as protection against UV, pathogens, and predators early in fruit development (Vvedenskaya and Vorsa, 2004). Major flavonols in cranberry include myricetin and quercetin (Lees and Francis, 1971). The major anthocyanins that are found in cranberry include: peonidin-3-arabinoside, cyanidin-3-arabinoside, peonidin-3-galactoside and cyanidin-3-galactoside (Lees and Francis, 1971). There are variations in the flavonoid contents among different cultivars of cranberry (Vvedenskaya and Vorsa, 2004; Wang and Stretch, 2001).

Little information exists concerning the development of secondary metabolites in the cranberry fruit. In particular, a full understanding of the mechanism by which carbon backbones are diverted to production of secondary metabolites (such as the phenolic compounds) and the factors affecting this process has not been achieved, although some investigation has been undertaken in other species. For example, Booker and Maier (2001) investigated the effect of resource availability on the production of secondary metabolites in loblolly pine (*Pinus taeda*), and determined that soluble phenolics, catechin, and proanthocyanidins were positively correlated with availability of resources in the environment, particularly CO_2 concentration.

To our knowledge, there has been no study relating carbon requirements and secondary metabolite production in cranberry fruit, although research has been conducted on the effect of berry size (and hence the surface to volume ratio) on anthocyanin content (Sapers et al., 1986; Vorsa and Welker, 1985). The goal of this project was to determine the crucial time in the season at which maximization of the carbon supply by the plant produced these secondary metabolites versus primary materials. It is hypothesized that defoliation and the resulting stress on carbohydrate production in the vine (Vanden Heuvel and Davenport, 2005) may affect phenolic production in the cranberry fruit. Although it has not been quantified, defoliation of uprights likely improves light interception by the fruit.

Due to the interest in cranberry as a source of phytonutrients, as well as the financial incentive received by cranberry growers for improved anthocyanin concentration, investigations into development of phenolic compounds in cranberry are highly warranted. We aimed to use defoliation as a means of decreasing carbon supply available for the production of primary and secondary metabolites in the vine. The objectives of this study were 1) to evaluate the effect of defoliation (i.e., reduced carbon supply and/or increased light interception by the fruit) at different phenological stages on the production of phenolic compounds in the fruit, and 2) to determine the relationship between nonstructural carbohydrate production in the cranberry plant, and content of total phenolics, flavonols, and anthocyanins in the fruit at harvest.

Materials and Methods

Experiment 1

Experimental setup. The experiment was established on 'Stevens' growing at State Bog (University of Massachusetts Amherst Cranberry Station, E. Wareham, Mass., lat. 41°45'N, long. 70°40'W) as a split plot design, with timing of defoliation as the main plots (1 × 1 m) , and defoliation level as the subplots (50 × 50 cm). The experiment was replicated four times. Timing of defoliation treatments were 5 to 7 May, 7 to 8 July, 4 to 5 Aug., and 16 Sept., to correspond with before new growth (D1), fruit set (D2), midfruit development (D3), and preharvest (D4), respectively. At D1, only 1-year-old leaves were present on the uprights. Defoliation treatments were removal of about 0%, 25%, 50%, and 75% of leaves on all uprights in the plot (both old and new leaves if both existed), and were applied by hand. The experimental site was not heavily populated with runners, and runners within plots were not submitted to defoliation treatments. Ten days following defoliation, ten whole fruiting uprights were removed per plot to assay for carbohydrate concentration and leaf area remaining per upright. All the fruits were harvested just before maturity on 1 Oct. 2003 (commercial harvest of the site occurred on 3 Oct. 2003) and were flash frozen with liquid nitrogen and kept frozen at –20 °C until analyzed.

Carbohydrate analysis. Vegetative samples were dried at 80 °C for 5 d, ground to 40 mesh,

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then extracted and analyzed according to the protocol described by Botelho and Vanden Heuvel (2005).

Total phenolics analysis. All fruit samples were lyophilized, pulverized, and analyzed in triplicate using the Folin-Ciocalteu test according to Vinson (2002). Subsamples of 0.100 g of lyophilized berry were weighed into plastic test tubes, and 8 mL (by volume) of 50 MeOH : 50 deionized H_2O solution was added to the tubes and heated at 95 °C while vortexing every half hour for two hours. The samples were allowed to cool, vacuum filtered, and the filtrate brought up to 10 mL with MeOH. To quantify total phenolics, 350 µL of sample prepared as above were placed in a cuvette with 3.5 mL of the prepared Folin reagent (Sigma-Aldrich, St. Louis, Mo.). The mixture was allowed to react for 20 min, after which the absorbance values were read, using a spectrophotometer (UV-160; Shimadzu Scientific Instruments, Columbia, Md.) at a wavelength of 750 nm. The Folin-Ciocalteu solution was reduced to a blue color by the total phenols in the cranberry fruit. Catechin was used as a spectrometric standard. The total phenolics (TP) values were expressed as catechin equivalents (µmoL)/g of dry fruit. These values were determined by preparing a standard curve using catechin standards between 200 to 800 µM. Total phenolics (TP) for each fruit sample was calculated as follows: TP = catechin concentration in $\mu mol \cdot L^{-1} \times 0.010$ L/dry weight of sample (in grams).

Total anthocyanin analysis, total flavonol analysis. The procedure used in the determination of total flavonol (TF) and total anthocyanin (TAcy) concentration was modified from a method previously described by Lee and Francis (1971). Extracts were prepared in triplicate. Ten g berry samples were pulverized with 10 mL of 85 ethanol : 15 1.5 M HCl (by volume) solution. The samples were transferred into a 50 mL beaker, covered and kept overnight in the refrigerator at a temperature of 4 °C. The samples were extracted by vacuum filtration with 10 mL of the extracting solvent and the filtrate was transferred into a graduated cylinder. The filtration process was repeated again to wash off any remaining materials on the filter into the flask. The solution was made up to 50 mL with the extracting solvent and kept in the dark for 2 h. If the pH of the resulting mixture was >1.1, HCl was added to the filtrate to bring down the value to 1.1. Absorbances of solutions were measured at a wavelength of 535 nm for TAcy and 374 nm for TF, using glass cuvettes. Samples were prepared for analysis by diluting 1 mL of the 50 mL filtrate with 10 mL with the extracting solvent. Results are expressed as mg anthocyanins or flavonol equivalents/100 g of fresh fruit. Total flavonols are calculated as quercetin and total anthocyanins as cyanidin, using the method developed by Lees and Francis (1971): TAcy in mg/100g fruit = $(A_{535} \times V \times 100)/ (98.2 \times W)$; TF in mg/100g fruit = $(A_{374} \times V \times 100)/ (76.5 \times W)$, where V = total volume of extract in mL, W= weight of fresh sample (in grams).

Statistical analysis. Analysis of variance of the split plot design was performed according to Bowley (1999) using PROC GLM, and *t* tests were used for mean separation of the main effect of timing of defoliation. Pearson correlation coefficients were determined using SAS (SAS Institute, Cary, N.C.) for the relationships between upright composition and fruit composition. We assumed that a significant correlation of a fruit composition parameter with leaf area indicated improved light interception by the berry.

Experiment 2

A second experiment was established in 2004 immediately adjacent to the 2003 experiment. Four plots of 0.5 × 1.5 m were divided into three treatments: control, 50% defoliation of new growth at post fruit set (27 July; D1), and 50% defoliation of new growth at midfruit development (18 Aug; D2). Ten days following defoliation, samples of 20 uprights were collected from the treated and the control plots for leaf area and carbohydrate analysis. Fruit were harvested just before commercial harvest of the bog which occurred on 5 Oct. 2004. Analysis of carbohydrates, TP, TAcy, and TF were performed as in Experiment 1. Analysis of variance for the randomized complete block was performed according to Bowley (1999) using PROC GLM and Pearson correlation coefficients were determined using SAS.

Results and Discussion

Defoliation treatments successfully reduced leaf area per upright (Table 1), resulting in average leaf areas of 10.0, 8.2, 6.1, and 4.7 cm^2 per upright for the 0%, 25%, 50%, and 75% defoliation treatments, respectively, when samples were collected 10 d after defoliation. Therefore actual leaf area treatments were 0%, 18%, 39%, and 53% partial defoliation, and will hence be referred to as such. Leaf area per upright was also affected by timing of defoliation (Table 1), however the interaction between the defoliation level and timing was not significant. Typically, leaf area per upright will vary over the season due to the dropping of the 1-year-old leaves (Hagidimitriou and Roper, 1995) and upright growth will continue through part of the growing season. In 2003, leaf area of Stevens fruiting uprights on a nearby bed increased from about 7 to 10 cm^2 per upright until early July, and then maintained a leaf area of about 10 cm^2 per upright until early September, after which leaf area decreased to about 7 cm^2 per upright (J. Vanden Heuvel, unpublished data), indicating that leaf area per upright likely increased in the D1 treatment only following partial defoliation. Production of new uprights in the plots likely affected light interception by the berries, but as little carbon moves between uprights (Roper and Klueh, 1996), it is unlikely that upright carbohydrate concentration was affected by new upright growth.

Soluble sugars, starch, and hence TNSC of the uprights were reduced by as much as 15%, 33%, and 23%, respectively, by partial defoliation rates of either 39 and 53% (Table 1; Fig. 1A) but were unaffected by partial defoliation of 18% of leaf area, indicating that the leaves have some capacity to compensate for reduced leaf area, likely through improved net carbon exchange. Interestingly, timing of partial defoliation did not affect upright carbohydrate concentration (Table 1), although timing of defoliation has affected TNSC in greenhouse-grown potted cranberry uprights (Vanden Heuvel and Davenport, 2005).

Rate of partial defoliation significantly affected TAcy and TF of the fruit in Expt. 1 (Table 1, Fig. 1B), but did not affect TP. A partial defoliation rate of 53% significantly increased total anthocyanin concentration by as much as 18% compared to the control and by 35% compared to the lowest rate of partial defoliation (18%). Pearson correlation coefficients indicated that leaf area per upright (collected 10 d postdefoliation) was negatively correlated to TAcy at harvest when uprights were defoliated at midfruit development (Table 2). While light interception by the fruit was not quantified in this study, we visually observed that a greater proportion of fruit were visible in the plots as defoliation level increased, indicating that light interception by the fruit was likely improved by defoliation. We hypothesize that improved light interception by the fruit may at least partially account for the observed increases in TAcy (Boulanger and Singh, 1997; Zhou and Singh, 2002). However, TAcy was also negatively correlated with TNSC and starch concentration at midfruit development, indicating that production of TAcy could be a stress response when primary metabolism becomes limited. In

Table 1. Summary of ANOVA for the effect of defoliation level and timing of defoliation on upright and fruit composition of 'Stevens' cranberry in 2003 (Expt. 1).

Variable	Defoliation level (df = 3) *p* value	Timing of defoliation (df = 3) *p* value	Defoliation × timing (df = 9) *p* value
LA (upright)	<0.0001	<0.0001	0.2178
TNSC (upright)	<0.0001	0.2070	0.5037
SS (upright)	<0.0001	0.0521	0.0087
Starch (upright)	0.0008	0.1680	0.5105
TP (fruit)	0.4249	0.9412	0.5948
TAcy (fruit)	0.0240	0.3278	0.4493
TF (fruit)	0.0436	0.0132	0.7315

[z]LA = leaf area, TNSC = total nonstructural carbohydrates. SS= soluble sugars (surcose + glucose + fructose), TP = total phenolics, TAcy = total anthocyanins, TF = total flavonols. Defoliation treatments were: D1 = partial defoliation applied 5 to 7 May 2003 (before new growth); D2 = partial defoliation applied 7 to 8 July 2003 (fruit set); D3 = partial defoliation applied 4 to 5 Aug. 2003 (midfruit development); D4 = partial defoliation applied 16 Sept. 2003 (preharvest). Upright analysis (leaf area, TNSC, SS, starch) was performed 10 d following defoliation treatment. Fruit analysis (TP, TAcy, TF) was performed before commercial harvest.

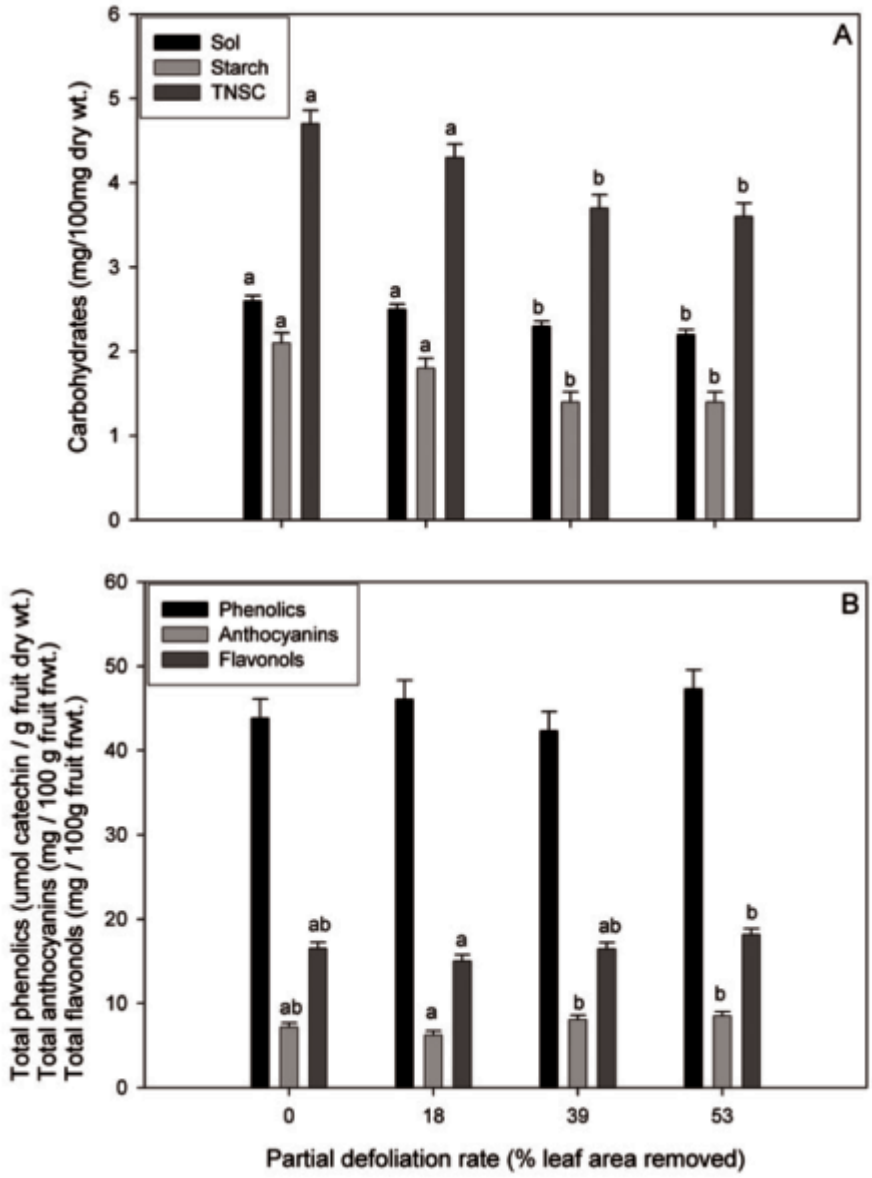

Fig. 1. The effect of rate of partial defoliation on (**A**) nonstructural carbohydrate concentration of fruiting uprights at 10 d after treatment, and (**B**) fruit composition of 'Stevens' cranberry in 2003 (Expt. 1) at harvest. Soluble carbohydrates = sucrose + glucose + fructose. TNSC = total nonstructural carbohydrates = soluble + starch. Means comparisons are by *t* tests between treatments within each class of compounds.

Table 2. Pearson correlation coefficients and *p* values for relationships between upright and fruit composition of 'Stevens' cranberry vines in 2003 (Expt. 1). Correlations of $p \leq 0.10$ are in bold.

Parameter	D1	D2	D3	D4
Upright composition				
LA (upright)-TNSC (upright)	***r* = 0.8157**	*r* = 0.2159	*r* = 0.2928	*r* = 0.2684
	***p* ≤ 0.0001**	*p* ≤ 0.4218	*p* ≤ 0.2895	*p* ≤ 0.3335
LA (upright) – SS (upright)	***r* = 0.8194**	*r* = 0.0696	*r* = 0.1799	***r* = 0.5000**
	***p* ≤ 0.0001**	*p* ≤ 0.7978	*p* ≤ 0.5210	***p* ≤ 0.0577**
LA (upright) – STARCH (upright)	***r* = 0.7261**	*r* = 0.2178	*r* = 0.3089	*r* = 0.0174
	***p* ≤ 0.0014**	*p* ≤ 0.4179	*p* ≤ 0.2625	*p* ≤ 0.9509
Fruit composition				
LA (upright) – TF (fruit)	*r* = –0.1777	***r* = –0.4547**	*r* = –0.2377	*r* = –0.0425
	p ≤ 0.5103	***p* ≤ 0.0768**	*p* ≤ 0.3754	*p* ≤ 0.8805
LA (upright) – TAcy (fruit)	*r* = –0.0899	*r* = –0.2689	***r* = –0.4478**	*r* = –0.1572
	p ≤ 0.7404	*p* ≤ 0.3138	***p* ≤ 0.0820**	*p* ≤ 0.5759
TNSC (upright) –Tacy (fruit)	*r* = 0.1447	*r* = 0.2244	***r* = –0.5657**	*r* = –0.3864
	p ≤ 0.5928	*p* ≤ 0.4034	***p* ≤ 0.0280**	*p* ≤ 0.1548
TNSC (upright)-TF (fruit)	*r* = –0.3044	*r* = 0.0303	*r* = 0.2115	***r* = 0.4469**
	p ≤ 0.2516	*p* ≤ 0.9112	*p* ≤ 0.4493	***p* ≤ 0.0949**
STARCH (upright) – TAcy (fruit)	*r* = 0.1976	*r* = 0.3182	***r* = –0.5597**	*r* = –0.3452
	p ≤ 0.4632	*p* ≤ 0.2297	***p* ≤ 0.0300**	*p* ≤ 0.2076

[z]LA = leaf area, TAcy = total anthocyanins, TF = total flavonols, SS = soluble carbohydrates (sucrose+glucose+fructose), TNSC = total nonstructural carbohydrates. D1 = partial defoliation applied 5 to 7 May 2003 (before new growth); D2 = partial defoliation applied 7 to 8 July 2003 (fruit set); D3 = partial defoliation applied 4 to 5 Aug. 2003 (midfruit development); D4 = partial defoliation applied 16 Sept. 2003 (preharvest). Upright analysis (leaf area, TNSC, soluble sugars, starch) was performed 10 d following defoliation treatment. Fruit analysis (TP, TAcy, TF) was performed before commercial harvest.

an experiment with 'DeChaunac' grapevines, where partial defoliation did not affect light environment of the fruit, TNSC was positively correlated to TAcy, but was still improved by defoliation, as partial defoliation at preharvest actually increased TNSC (Vanden Heuvel et al., 2005). Timing of defoliation did not affect TAcy in this experiment, however correlation coefficients between TAcy and other variables were significant at $P < 0.10$ only at midfruit development in Expt. 1 (Table 2).

Total flavonol concentration of the fruit was increased by 10% in the 53% defoliation treatment compared to the 18% defoliation treatment (Fig. 1B), and was also affected by timing of defoliation with increases in TF of 33% and 27% being noted at fruit set and midfruit development, respectively (Fig. 2). In grapes, flavonol accumulation may start as early as bloom time (Keller and Hrazdina, 1998) although flavonol concentration has been suggested to change during growth of the cranberry fruit (Vvedenskaya and Vorsa, 2004). A positive correlation coefficient was noted between TNSC and TF at preharvest (Table 2). These results are similar to those noted in grape, where TF was positively correlated to leaf, trunk, and root TNSC (Vanden Heuvel et al., 2005). These positive correlations indicate that factors affecting production and allocation of nonstructural carbohydrates (such as improved photosynthesis) may also affect production of TAcy and TF. No significant correlations were noted with TP, indicating that not all phenolic compounds may be affected by plant carbon availability at these phenological stages.

Values of TAcy and TF in the fruit are lower than those previously reported for 'Stevens' (Vvedenskaya and Vorsa, 2004) due to the fruit in this experiment being harvested before maturity.

In Expt. 2, we reduced the treatments to two defoliation timings (postfruit set and preharvest; D1 and D2, respectively), and two defoliation treatments (0% (control) and 50% defoliation of new leaves only), which resulted in total leaf areas of 12.8 and 8.5 cm^2 per upright (or partial defoliation of 34% of total leaf area). The purpose of reducing the defoliation treatments to 50% of new leaves was to reduce the confounding effects of light interception and carbohydrate changes on fruit composition, since new leaves supply most of the carbon to the fruit (Roper and Klueh, 1996).

Timing of defoliation only affected TNSC and starch concentration of the uprights (Table 3; data not shown) in Expt. 2. Partial defoliation treatment reduced soluble carbohydrate concentration from 2.64 to 1.75 mg/100 mg, although this difference was not significant (Table 3). Starch was significantly reduced

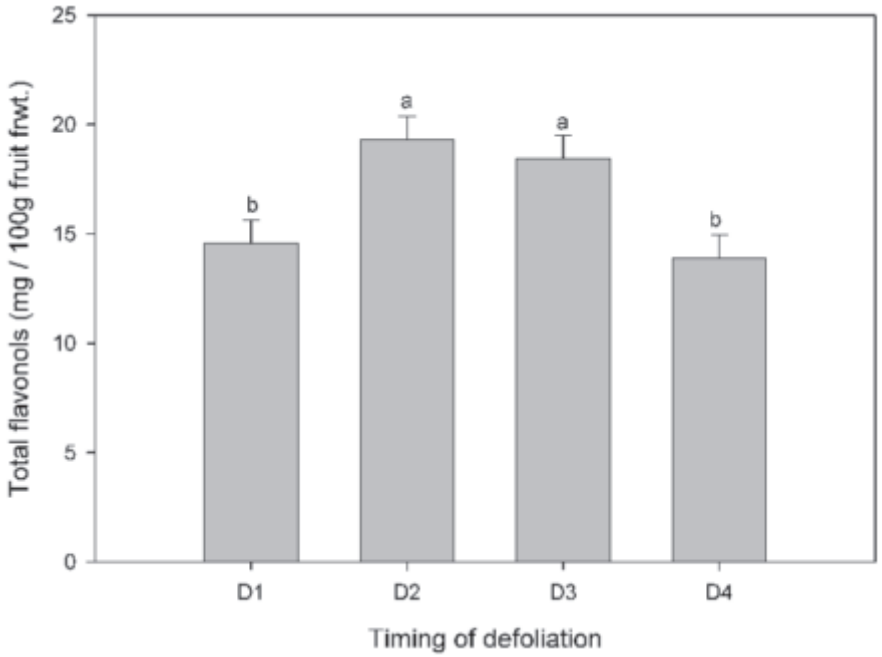

Fig. 2. The effect of timing of defoliation on flavonol composition of 'Stevens' cranberry fruit in 2003 (Expt. 1) at harvest. Vines were partially defoliated at D1 = before new growth (5 to 7 May), D2 = fruit set (7 to 8 July), D3 = midfruit development (4 to 5 Aug.), and D4 = preharvest (16 Sept.). Means separation by *t* tests.

Table 3. Summary of ANOVA for the effect of defoliation level and timing of defoliation on leaf and fruit composition of 'Stevens' cranberry in 2004 (Expt. 2).

Variable	Defoliation level (df = 1) *p* value	Timing of defoliation (df = 1) *p* value	Defoliation × timing (df = 1) *p* value
LA (upright)	0.0001	<0.0001	0.6154
TNSC (upright)	0.0093	0.0153	0.9455
SS (upright)	0.5704	0.2360	0.8067
Starch (upright)	0.0035	0.0125	0.9653
TP (fruit)	0.1770	0.5158	0.5158
TAcy (fruit)	0.1536	0.1081	0.1081
TF (fruit)	0.6596	0.9256	0.9256

[z]LA = leaf area, TNSC = total nonstructural carbohydrates, SS = soluble sugars (sucrose+glucose+fructose), TP = total phenolics, TAcy = total anthocyanins, TF = total flavonols. Defoliation treatments were D1 = partial defoliation applied 27 July 2004 (post fruit set); D2 = partial defoliation applied 18 Aug. 2004 (midfruit development). Upright analysis (leaf area, TNSC, soluble sugars, starch) was performed 10 d following defoliation treatment. Fruit analysis (TP, TAcy, TF) was performed before commercial harvest.

Table 4. Pearson correlation coefficients and *p* values for relationships between leaf and fruit composition of 'Stevens' cranberry in 2004 (Expt. 2). Correlations of $p \leq 0.10$ are in bold.

Parameters	D1	D2
Upright composition		
LA (upright) – TNSC (upright)	$r = 0.0767$	$\mathbf{r = 0.7825}$
	$p \leq 0.8568$	$\mathbf{p \leq 0.0217}$
LA (upright) – starch (upright)	$r = 0.1435$	$\mathbf{r = 0.8048}$
	$p \leq 0.7346$	$p \leq 0.0160$
Fruit composition		
SS (upright) – TA (fruit)	$r = 0.0356$	$\mathbf{r = -0.9496}$
	$p \leq 0.9332$	$\mathbf{p \leq 0.0003}$

LA = leaf area, TAcy = total anthocyanins, SS = soluble carbohydrates (sucrose+glucose+fructose), TNSC = total nonstructural carbohydrates. D1 = partial defoliation applied 27 July 2004 (post fruit set); D2 = partial defoliation applied 18 Aug. 2004 (midfruit development). Upright analysis (leaf area, TNSC, soluble sugars, starch) was performed 10 d following defoliation treatment. Fruit analysis (TP, TAcy, TF) was performed before commercial harvest.

from 2.79 to 1.75 mg/100 mg, and TNSC from 5.43 to 4.30 mg/100 mg. The only significant correlation for fruit composition was a strong, negative one between soluble sugars and TAcy (Table 4), similar to the negative correlation between upright starch and fruit TAcy, and upright TNSC and fruit TAcy that was noted in Expt. 1 (Table 2).

Conclusion

These results indicate that a number of factors may affect production of phenolic compounds through the season. The negative correlation in Expt. 1 between LA per upright and fruit TAcy, and LA per upright and fruit TF, indicates that light interception by the fruit may have a significant impact on production of flavonoids. While this conclusion is not new (Boulanger and Singh, 1997; Zhou and Singh, 2002), and has been practically demonstrated in cranberry though pruning of uprights (Strik and Poole, 1991), the timing of this light effect has not previously been determined. The negative correlation for LA per upright and TF of the fruit when defoliation occurred at fruit set, and of LA per upright and TAcy of the fruit when defoliation occurred at midfruit development indicates that partial defoliation (perhaps through improvement of light interception) early in the growing season may have the greatest effect on TF and TAcy.

These results also indicate that individual groups of flavonoids in the fruit may be able to be modified depending on how and when a treatment is applied. Similar to grapes (Vanden Heuvel et al., 2005), production of TAcy and TF in the fruit appear to be regulated independently of each other in cranberry (Vvedenskaya and Vorsa, 2004), and are likely affected by berry environment as well as whole-plant environment. The positive correlations noted between upright carbohydrate concentration and TF in the fruit (Table 2) and the negative correlation between upright carbohydrate concentration and TAcy in the fruit (Tables 2 and 4) indicate that TAcy and TF may be able to be manipulated through some form of controlled management of upright TNSC (or soluble carbohydrates or starch), perhaps through changes in nutrition (J. Vanden Heuvel, unpublished data) or irrigation regimes. However, manipulation of upright carbohydrate concentration would affect fruit TF and TAcy differently. Ability to regulate development of separate pools of flavonoid compounds may be of interest for commercial production of a variety of cranberry-derived health products.

Vvedenskaya and Vorsa (2004) suggest partitioning in the precursor pool of the biosynthetic pathway of flavonoids is a function of both phenological stage and cultivar; we suggest it is also a function of plant environment, and hence carbon status. Understanding the role of carbon availability in development of flavonoids will allow for future research into targeted production practices to increase their concentration in cranberries and cranberry products.

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