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Fall Nitrogen Fertilization Does Not Affect Total Non-Structural Carbohydrates In 'HyRed' Cranberry Uprights

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Abstract

Woody perennial plants accumulate reserves prior to their dormancy period for winter survival and to support the resumption of growth the following spring. Thus, increasing nutrient availability during fall could increase plant reserves and enhance productivity in woody perennial crops. The objective of this study was to evaluate the impact of fall nitrogen fertilizer on total non-structural carbohydrate reserves in cranberry uprights during the dormant period. A complete randomized block design was established in three 10-year-old 'HyRed' cranberry production beds at a farm in central Wisconsin. The fall fertilization treatments were applied after harvest and consisted of 0% (0 Kg/ha), 10% (6.7 Kg/ha), 20% (13.4 Kg/ha), and 40% (26.8 Kg/ha) of the current and next season's total nitrogen (N) application (67 kg/ha). Over the following growing season, each plot received 67 kg/ha of N application during the summer in addition to the fall fertilization application. Fall N fertilization did not affect the concentration of total nonstructural carbohydrates (TNSC) or N concentration in cranberry uprights during winter or the subsequent spring.

Temperate woody perennial plants strategically accumulate nitrogen (N) and carbohydrates (CHO) prior to their dormant period because both components are essential for winter survival and growth resumption in the spring (Millard 1996; Cheng and Fuchigami 2002; Dong et al. 2004). In cranberry (*Vaccinium macrocarpon* Ait.), N accumulation is positively correlated with vegetative and reproductive growth, and thus, N fertilization is required for consistent yields (Birrenkott et al., 1991; Roper & Klueh, 1994; Vanden Heuvel & Davenport, 2006). Nitrogen can be assimilated by the plant at the expense of CHO for the synthesis of proteins and amino acids (Cheng and Fuchigami 2002; Millard and Grelet 2010). Carbohydrates are derived from photosynthesis and their utilization is important for fruit production and supporting vegetative growth. In cranberry, increasing the amount of N fertilizer during the summer promotes vegetative growth and thus, increases CHO reserves towards the dormant period, possibly derived from more chlorophyll (Vanden Heuvel and Davenport 2006). Higher CHO reserves allow these evergreen vines to survive the winter and support growth and fruit set during spring, and reports of limited CHO reserves in cranberry uprights during the dormant period can negatively affect fruit set (Birrenkott et al. 1991; Roper and Klueh 1994; Hagidimitriou and Roper 1994) and yield (Vanden Heuvel and Davenport 2006; DeVetter et al. 2016).

Fall N fertilization could be an alternative management practice to increase plant reserves by allocating N to reserve organs during a period in which roots are actively growing

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but vegetative growth has ceased (Cheng and Fuchigami 2002; Atucha et al. 2021; Wang et al. 2023). Several studies have demonstrated the positive effect of fall N fertilization on vegetative growth in different fruit crops (Oland 1963; O'Kennedy et al. 1975) including cranberry (Rojas-Barros et al. 2023), as well as fruit set (Sanchez, et al. 1990; Khemira et al. 1998) the subsequent season. However, it is not known how fall N fertilization affects CHO dynamics in cranberry uprights during the dormant period. The objective of this study is to evaluate the effect of different rates of fall N fertilization on CHO concentration in cranberry uprights approaching the dormant season.

Materials and Methods

Site description

The study was conducted at a commercial cranberry farm in Babcock, WI, USA (lat. 44°18'19.2"; long. N 90°01'34.5" W). Soils in the study area are categorized as Markey mucky peat with low drainage, a slope of 0 to 2%, high organic matter, and low pH (Natural Resources Conservation Service, U.S. Department of Agriculture 2022). Soil analysis from production beds at this site documented 4% organic matter, a soil pH of 4.9, and optimal nutrient levels for cranberry production (data not shown). Standard commercial and cultural practices for cranberry production (Sandler and DeMoranville 2009) were implemented by the grower, including sanding the beds every three years for sanitation and rooting of runner growth.

Experimental treatments

The study was established as a randomized complete block design (RCBD), in which the blocking factor consisted of one 10-year-old 'HyRed' production bed (355 m x 45 m area independent production unit) and the experimental unit was an 88 m x 23 m plot. In each of the three beds used in the experiment, four fall nitrogen fertilization treatments using ammonium sulfate (21-0-0) with two samples per bed were randomly assigned to each plot giving a total of six replicates across the three beds. In Fall 2017, treatments were applied at 0%, 10%, 20%, and 40% after harvest of the next season's projected N application (67 kg of N per hectare). During the following summer, each treated plot received 67 kg of N per ha in addition to the fall fertilization, giving a total of 67 kg per ha for the 0% fall treatment, 74 kg per ha for the 10% fall treatment, 80 kg per ha for the 20% fall treatment, and 94 kg per ha for the 40% fall treatment. Fall fertilizer treatments were applied in a single application on September 22, 2017 (four days after harvest), October 30, 2018 (45 days after harvest), and November 5, 2019 (50 days after harvest). During the summers of 2018 and 2019, the 67 kg of N per ha applied to each plot was split into five applications starting the first week of July through the first week of August according to the grower's fertilization plan.

Plant material and sample preparation

Cranberry uprights (i.e., vertical stems containing a terminal bud) were randomly collected from each experimental plot from fall to spring for carbohydrate analysis. Due to the presence of ice covering the vines for winter protection, no collections were made from January until March. During Year 1 of the study, collection dates were September 10, 2018: before the fertilizer treatments were applied to set up a baseline in carbohydrate concentration; December 1, 2017; May 2, 2018; and May 16, 2018. For Year 2 of the study, collection dates were September 10, 2018; December 5, 2018; April 19, 2019; and May 9, 2019. Approximately 50 fruiting and 50 vegetative uprights were collected per plot at each collection date. Fruiting uprights were defined as those that bore fruit during the summer of that collection year (indicated by the presence of pedicels during fall collection) and vegetative uprights were defined as those that did not bear fruit during the growing season (indicated by the absence of pedicels during fall collection). During each collection date, uprights were sorted by type (i.e.,

vegetative or fruiting), oven-dried for seven days at 80 °C, and then ground with a Cyclone Sample Mill with a 1 mm sieve (UDY Corp., Fort Collins, CO). Ground plant material was stored in glass vials at room temperature for later carbohydrates, starch, and N concentration analyses.

Upright N concentration analysis

For the upright N concentration analysis, 100 mg of ground material stored in glass vials from three different collection dates (December 1, 2017; May 2, 2018; and May 16, 2018) in Year 1 was used for N analysis. The samples were digested with nitric acid in hydrogen peroxide solution and analyzed via ICP-OES at the Soil and Forage Analysis Laboratory at the University of Wisconsin-Madison and expressed in percentage of dry weight.

Soluble carbohydrate and starch analyses

High-performance liquid chromatography (HPLC) was used to measure total TNSC, glucose, fructose, sucrose, and starch. Samples were extracted using the method described by (Botelho and Heuvel 2005) and (DeVetter et al. 2016) with some modifications. Free carbohydrates were extracted by adding 2 ml of extraction solution (0.06 g sorbitol per 100 mL of 80% ethanol v/v) to a previously labeled tube containing 100 mg of ground sample and then incubating in a 54 ºC water bath for 1 h. Once samples were cooled to room temperature, tubes were centrifuged (Eppendorf 5920 R, Eppendorf, Hamburg, Germany) for 10 minutes at 4000 rpm and 20 ºC. The supernatant was filtered through an MF-Millipore™ (MilliporeSigma, Burlington, MA) membrane filter (0.45 µm pore size) and put into a centrifuge tube. This extraction process was repeated twice more for a total of three centrifuge tubes per sample. The pellet was retained for later starch extraction. Tubes were then dried overnight in a vacu-fuge (Eppendorf 5301, Eppendorf, Hamburg, Germany) and reconstituted by adding 0.5 ml of HPLC-grade water before continuing with the extraction. The first two tubes were centrifuged again for 10 minutes at 4000 rpm and 20 ºC to avoid filter clogging. All three volumes were combined into a syringe and filtered through a MF-Millipore™ membrane (0.45 µm pore size) in addition to a conditioned Sep-Pak C_{18} cartridge pore size 55 - 105 µm (Waters Corp., Milford, MA). The filtrate was collected and filtered again using a Corning® 4 mm membrane diameter and 0.2 µm pore size (Corning, Inc., New York, NY) before HPLC analysis. The samples were stored at -80 °C.

For the starch extraction, the pellet from the CHO extraction was dried at room temperature for seven days, then resuspended using 5 ml of HPLC-grade water, and then autoclaved at 120 °C for 30 minutes to solubilize starch. A solution of a 100 µl buffer (pH = 4.63) with 0.011 g of amyloglucosidase enzyme (Sigma-Aldrich, St. Louis, MO) was added to the resuspended pellet to hydrolyze the starch by incubating in a water bath for 2 h at 56 °C. From this point, the procedure was similar to the CHO extraction but a Sep-Pak Accell Plus QMA cartridge pore size 37 - 55 µm (Waters Corp., Milford, MA) was used instead of a Sep-Pak C_{18} cartridge.

The HPLC analysis was performed with a Shimadzu prominence HPLC system under the control of LabSolutions LC/GC version 5.97 software (Shimadzu, Kyoto, Japan). A Rezex™ RCM-Monosaccharide 8% Ca^{+2} cross-linked ion exclusion column with 8-micron pore size (part number 00H-0130-K0) (Phenomenex, Torrence, CA) was used for the separation of soluble sugars from the CHO and starch samples. Runs were isocratic at 0.6 ml/minute flow rate of MQ water. The CTO-20AC Prominence column oven operated at 80 °C and the RID-10A refractive index detector at 40 °C was used to detect compounds with a different refractive index from the mobile phase. A text file output with only "chromatogram" selected was processed using MATLAB to quantify area under peaks. The carbohydrates were expressed as mg per 100 mg of dry weight (DW).

Statistical analysis

The initial statistical model included three parameters: plot effect or fall N fertilization treatments (n = 4), block effect (n = 3), upright type (n = 2), and collection date per year (three during the first year and four during the second year, n = 7). The first collection date in September 2017 was used as a baseline for carbohydrate concentration and was not considered in the analysis because the samples were taken before the fertilization treatments. The second analysis considered upright type individually and an analysis of variance (ANOVA) was performed considering the interactions of fertilization treatments and collection date, fertilization treatments and upright type, upright type and collection date, and fertilization treatments with collection date and upright type.

Assumptions of normality and constant variance were assessed using the Shapiro–Wilk test and visual assessments of residual vs fitted plots, respectively. The data output was generated using R Studio (R Core Team 2023).

Results

Fall N fertilization effect on TNSC, starch, and soluble CHO concentrations across all upright types.

Over the two years of the study, the effect of fall N fertilization on the accumulation of TNSC (soluble CHO and starch), starch, and soluble carbohydrates (glucose, fructose, and sucrose) approaching the dormant season was assessed in cranberry uprights. During both years, considering the combined data from fruiting and vegetative uprights, the TNSC concentration from September to December increased, but the concentration was not affected by any fall N fertilization treatment (P value = 0.293, Table 1, Fig. 1A). Then, the TNSC concentration decreased from December to early May in 2018, followed afterward by a slight increase in TNSC concentration until in mid-May (Fig. 1A), but, again, the concentration was not affected by any fall N fertilization treatment (P value = 0.293, Table 1). Starch concentration remained unchanged during both years from September to early May, followed by an increase by mid-May (Fig. 1B), and starch was not influenced by fall N fertilization (P value = 0.474, Table 1). The changes in soluble CHO concentration followed the same pattern as TNSC during both years but decreased slightly in mid-May of 2018 (Fig. 1C), and differences were not significant among fall N fertilization treatments (P value = 0.366, Table 1).

Effect of fall N fertilization treatments on TNSC, starch, and soluble CHO by upright type.

In fruiting uprights, the TNSC concentration in Year 1 increased from September to December, followed by a decrease in May 2018, but was not affected by any fall N fertilization treatment (P value= 0.290, Table 2, Fig. 2A). In Year 2, the TSNC concentration followed the same trend from September to December as in Year 1, but instead of decreasing in May, the TNSC concentration increased. Also, in Year 2 the TNSC concentration in May was higher than in Year 1 (P value = 2.20e-16, Table 1, Fig. 2A). During Year 2, TNSC concentration in December was higher when the fruiting uprights received 10% of N in the fall compared to the control (0% of N in the fall) and the 20% of N in the fall treatment (P value = 0.0533 and = 0.0371, respectively, data not shown, Fig. 2A). In Year 1 and 2, starch concentration slightly increased from September to December, remained unchanged until the beginning of May, and further increased in mid-May 2018 (Fig. 2B). Starch concentration was not affected by any fall N fertilization treatments in Year 1 (P value = 0.726, Table 2, Fig. 2B), but in May 2019 of Year 2, the concentration from uprights that received 40% N fall fertilization was lower compared to the control (P value = 0.0276, data not shown, Fig 3B). The soluble CHO concentration followed the same trend as the TNSC during Year 1 and 2 of the study with no difference between treatments (P value = 0.726, Table 2, Fig. 2C), however soluble CHO concentration in the

Table 1. Analysis of variance for total non-structural carbohydrates (TNSC), starch, and soluble carbohydrates (CHO) concentration of 'HyRed' cranberry fruiting and vegetative uprights on seven collection dates and upright type as affected by fall N fertilization treatments.

	Source	Df	F	P value
TNSC	Fall N fertilization	3	1.16	0.293
	Collection date	6	38.11	$< 2.20e^{-16}$
	Upright type	1	2.46	0.105
	Fall fertilization x Collection date	18	0.33	0.995
	Fall fertilization x Upright type	3	1.22	0.305
	Collection date x Upright type	6	3.47	0.004
	Fall fert. x Collection date x Upright type	8	0.79	0.708
	Residuals	112		
Starch	Fall N fertilization	3	0.842	0.474
	Collection date	6	58.597	$< 2e^{-16}$
	Upright type	1	5.977	0.016
	Fall fertilization x Collection date	18	0.893	0.588
	Fall fertilization x Upright type	3	1.767	0.158
	Collection date x Upright type	6	6.365	$8.94e^{-06}$
	Fall fert. x Collection date x Upright type	18	1.046	0.416
	Residuals	112		
Soluble CHO	Fall N fertilization	3	1.067	0.366
	Collection date	6	35.758	$< 2.20e^{-16}$
	Upright type	1	0.696	0.406
	Fall fertilization x Collection date	18	0.332	0.997
	Fall fertilization x Upright type	3	1.706	0.169
	Collection date x Upright type	6	3.702	0.002
	Fall Fert. x Collection date x Upright type	18	0.702	0.803
	Residuals	112		

10% N fall fertilization treatment was higher than the control in December 2018 (P value = 0.0463, data not shown, Fig. 2C).

In vegetative uprights, the TNSC concentration in Year 1 followed a similar pattern compared to fruiting uprights, but the decrease in concentration from December until May was faster (P value = 2.20e-16, Collection date, Table 1, Fig. 2D). In Year 2, the TNSC concentration followed the same trend from September to December compared to Year 1. There was no effect of fall N fertilization on the TNSC concentration in either year (P value=0.330, Table 3, Fig. 2D). The starch concentration in Year 1 and 2 did not change from September to early May until there was a sharp increase in mid-May of 2018 (Fig. 2E). The starch concentration from uprights fertilized with N in the fall was not affected when compared to the control in both years (P value = 0.183, Table 3, Fig. 2E). In Year 2, fall N fertilization slightly increased starch concentration in May 2019 when the plots that received 10% of N in the fall were compared to the the control (P value = 0.061, data not shown, Fig. 2E). The soluble CHO followed the same trend as the TNSC in both years and there was no effect of fall N fertilization treatments on CHO concentration (P value = 0.250, Table 3, Fig. 2F).

Effect of fall N fertilization treatments on nitrogen (N) concentration in fruiting and vegetative uprights.

During Year 1 of the study, samples of cranberry uprights collected in late fall (December 1, 2017) and in the spring after ice off (May 2, 2018, and May 16, 2018) were analyzed for

Table 2. Analysis of variance for total non-structural carbohydrates (TNSC), starch, and soluble carbohydrates (CHO) concentration of 'HyRed' cranberry fruiting uprights on seven collection dates as affected by fall N fertilization treatments.

	Source	Df	F	P value
TNSC	Fall fertilization	3	1.28	0.290
	Collection date	6	19.92	$< 4.08e^{-12}$
	Fall fertilization x Collection date	18	0.49	0.948
	Residuals	56		
Starch	Fall fertilization	3	0.43	0.726
	Collection date	6	52.62	$< 2.00e^{-16}$
	Fall fertilization x Collection date	18	1.22	0.278
	Residuals	56		
Soluble CHO	Fall fertilization	3	1.31	0.280
	Collection date	6	16.53	$< 1.05e^{-10}$
	Fall fertilization x Collection date	18	0.53	0.926
	Residuals	56		

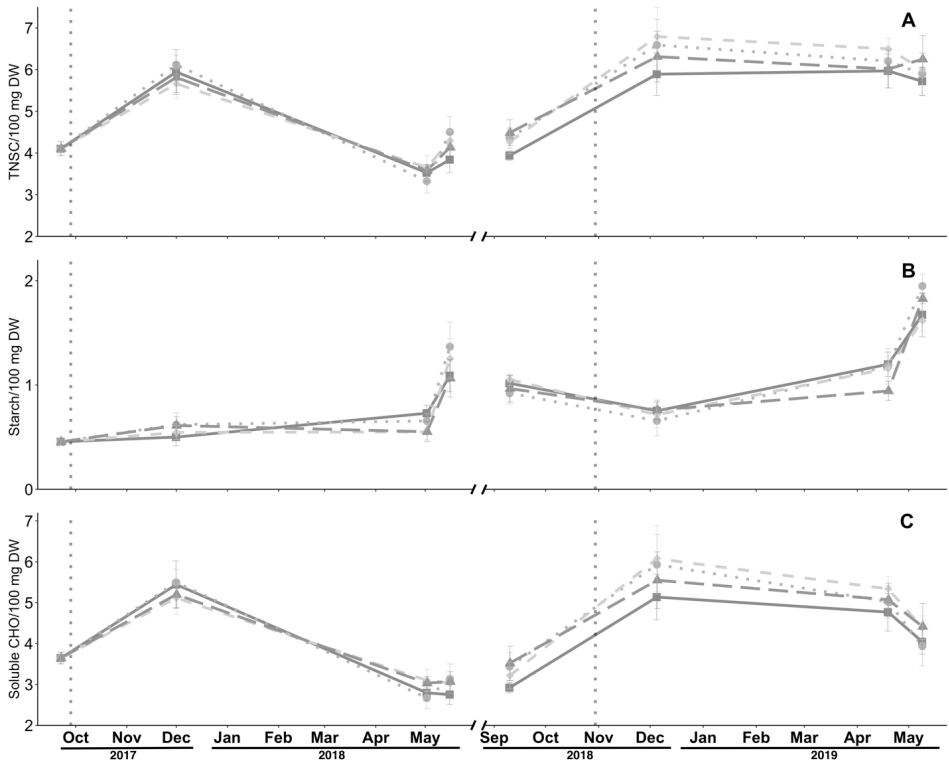

Fig. 1. Effect of fall N fertilization treatments on total non-structural carbohydrates (TNSC), starch, and soluble carbohydrate (CHO) concentrations in 'HyRed' cranberry uprights. Vertical dotted lines correspond to the fall fertilization dates. Treatments were 0% Fall + 100% Summer (solid line ■), 10% Fall + 100% Summer (dotted line •), 20% Fall + 100% Summer (long dashed ◆), and 40% Fall + 100% Summer (short dashed ▲)

Table 3. Analysis of variance for total non-structural carbohydrates (TNSC), starch, and soluble carbohydrates (CHO) concentration of 'HyRed' cranberry vegetative uprights on seven collection dates and upright type as affected by fall N fertilization treatments.

	Source	Df	F	P value
TNSC	Fall fertilization	3	1.16	0.330
	Collection date	6	23.59	$< 1.78e^{-13}$
	Fall fertilization x Collection date	18	0.61	0.869
	Residuals	56		
Starch	Fall fertilization	3	1.67	0.183
	Collection date	6	26.63	$< 1.70e^{-14}$
	Fall fertilization x Collection date	18	0.92	0.557
	Residuals	56		

Table 4. Effect of fall nitrogen fertilization treatments on nitrogen concentration (% of dry weight) of fruiting and vegetative uprights during different collection dates in 'HyRed' cranberry.

Collection date	N Treatment	Nitrogen concentration [ii]	
		Fruiting upright	Vegetative upright
December 2017	0% + 100%	0.74	0.76
	10% + 100%	0.74	0.76
	20% + 100%	0.70	0.72
	40% + 100%	0.70	0.72
	P value	0.62	0.44
May 1st 2018	0% + 100%	0.81	0.83
	10% + 100%	0.78	0.80
	20% + 100%	0.76	0.78
	40% + 100%	0.86	0.88
	P value	0.05	0.27
May 15th 2018	0% + 100%	0.86	0.88
	10% + 100%	0.88	0.90
	20% + 100%	0.82	0.84
	40% + 100%	0.90	0.92
	P value	0.66	0.09

Table 5. Difference in nitrogen concentration (% of dry weight) of fruiting and vegetative uprights during different collection dates in 'HyRed' cranberry.

Collection date	Nitrogen concentration (%)[i]	
	Fruiting upright	Vegetative upright
December 2017	0.718 a[ii]	0.740 a
May 1st 2018	0.796 b	0.826 b
May 15th 2018	0.869 c	0.878 b
P value	< 0.05	

[i] Different fertilization rates for fall Nitrogen fertilization.

[ii] Means presented with the same letter within a table column are not different at $P < 0.05$ using Tukey's HSD.

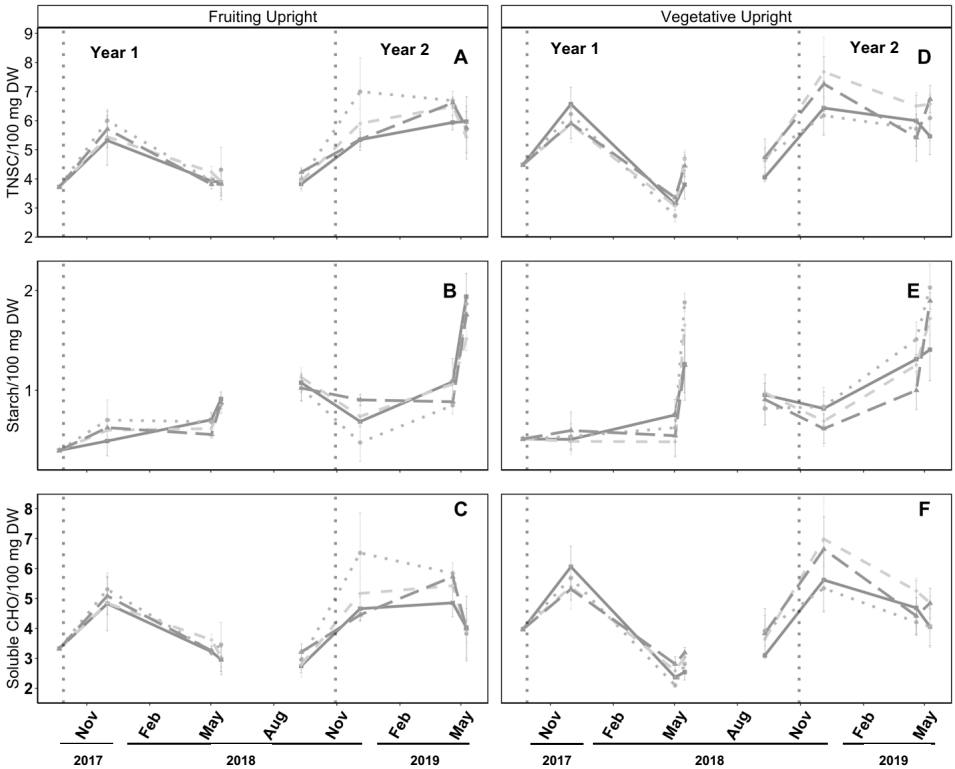

Fig. 2. Effect of fall N fertilization treatments on total non-structural carbohydrates (TNSC), starch, and soluble carbohydrate (CHO) concentrations in fruiting and vegetative 'HyRed' cranberry upright. Treatments were 0% Fall + 100% Summer (solid line ■), 10% Fall + 100% Summer (dotted line •), 20% Fall + 100% Summer (long dashed ◆), and 40% Fall + 100% Summer (short dashed ▲). Vertical dotted lines correspond to the fall fertilization dates.

N concentration (% of dry weight). The fall N fertilization did not affect the N concentration in either fruiting or vegetative uprights (Table 4) but there were differences between collection dates in both type of uprights (Table 5).

Discussion

In this study, we evaluated the effect of different rates of fall nitrogen (N) fertilization on the dynamics of TNSC, starch, and soluble CHO levels in cranberry uprights over multiple years. Fall N fertilization did not consistently affect cranberry uprights' CHO concentrations during the dormant period in either fruiting or vegetative uprights or the N concentration.

Previous studies evaluating the effect of fall N fertilization on CHO content in woody plant tissue have reported different results, depending on whether the application was to the foliage or the soil. Fall foliar N applications in apple (*Malus domestica* Borkh*)* (Cheng and Fuchigami 2002; Dong et al. 2002; Cheng et al. 2004), grapevine (*Vitis labruscana* Bailey) (Xia and Cheng 2004), and almonds trees (*Prunus dulcis* (Mill) D. A. Webb) (Bi et al. 2004) all resulted in a reduction in the TNSC per individual tree, mainly due to the assimilation of the N into the leaves that was later used in the synthesis of amino acids. However,

soil N fertilization in the fall did not affect the TNSC content on any above or below-ground perennial structure in apple trees (Priestley 1972; Priestley and Catlin 1974; Priestley et al. 1976) despite an increase in N uptake after the fertilization. Several studies have reported that N fertilizer applied in the fall to the soil increases the allocation into the roots of deciduous species (Priestley and Catlin 1974; Priestley et al. 1976; Sanchez, et al. 1990; Millard 1996; Khemira et al. 1998; Tagliavini et al. 1999; Dong et al. 2005; Wang et al. 2023), and evergreen species (Akao et al. 1978; Legaz et al. 1995; Martínez et al. 2002). In peach trees (*Prunus persica* var. *nectarina*), where almost 75% of the total plant N was stored in the roots after the fall fertilization (Tagliavini et al. 1999). The allocation of N in the fall towards the roots could be driven by the absence of leaves in deciduous (Priestley et al. 1976; Khemira et al. 1998) and growth cessation in evergreen fruit crop species (Uscola et al. 2015). Therefore, considering that the highest root growth rate in cranberry occurs in the fall after harvest, increasing the plants' ability to take up nutrients during this period (Atucha et al. 2021) may lead to uptake, assimilation, and storage in the roots (Akao et al. 1978; Legaz et al. 1995; Martínez et al. 2002). Therefore, changes in carbohydrates and nitrogen may have occurred at the root level and not at the shoot level (Table 1 and Table 4, respectiveley).

In evergreen woody perennials, the N used to support new growth the following season is mainly remobilized from older leaves (Millard and Grelet 2010) but also from other perennial structures such as roots (Legaz et al. 1995). In the case of mandarin trees, new growth during spring is largely supported by the remobilization of N that was taken up in the fall, with only a smaller proportion came from the spring fertilization (Akao et al. 1978). This might also be the case in our study, as the cranberry uprights' N concentration increased from the dormant period in December 2017 to the stage of bud break in May 2018, probably due to N remobilization from the roots (Table 5). The N remobilization into older leaves in the spring might have also driven the increase in starch concentration, possibly due to higher rates of photosynthesis (Fig. 1). Although there were no differences among fall fertilization treatments on the upright N concentration during early spring, fall N fertilization treatments increased vegetative growth during 2018 growing season (Rojas-Barros et al. 2023). As a result, N from roots may have been gradually remobilized into older cranberry upright leaves during spring, as was reported in apple trees (Dong et al. 2005), almond trees (Weinbaum et al. 1984), and grapevines, in which 68% of the N uptake in the fall was still present as reserves during spring growth resumption (Conradie 1986).

Conclusion

Cranberry upright CHO concentration was not affected by fall N fertilization applications over a two-year study. N applied in the fall was possibly assimilated and stored by the roots, and remobilized into older leaves during spring. However, it is unclear how much of the N stored in the roots was utilized to support new growth. Therefore, considering the complexity of N and CHO dynamics in cranberry, future studies related to fall fertilization in addition to different cultivars should focus on reserve allocation and usage in different storage organs using labeled N and carbon.

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