Seasonal nonstructural carbohydrate patterns in dewberry (*Rubus* spp.) roots

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Abstract

Applying control measures when carbohydrate levels are low can decrease the likelihood of plant survival, but little is known about the carbohydrate cycles of dewberry (*Rubus* spp.), a problematic weed group on cranberry (*Vaccinium macrocarpon* Aiton) farms. Weedy *Rubus* plants were collected from areas adjacent to production beds on commercial cranberry farms in Massachusetts, two locations per year for 2 yr. For each site and year, four entire plants were collected at five phenological stages: budbreak, full leaf expansion, flowering, fruit maturity, and after onset of dormancy. Root sections were analyzed for total nonstructural carbohydrates (TNC; starch, sucrose, fructose, and glucose). Overall trends for all sites and years showed TNC were lowest at full leaf expansion or flowering; when sampled at dormancy, TNC concentrations were greater than or equal to those measured at budbreak. Starch, a carbohydrate form associated with long-term storage, had low levels at budbreak, leaf expansion, and/or flowering with a significant increase at fruit maturity and the onset of dormancy, ending at levels higher than those found at budbreak. The concentration of soluble sugars, carbohydrate forms readily usable by plants, was highest at budbreak compared with the other four phenological samplings. Overall, our findings supported the hypothesis that TNC levels within the roots of weedy *Rubus* plants can be predicted based on different phenological growth stages in Massachusetts. However, recommendations for timing management practices cannot be based on TNC cycles alone; other factors such as temporal proximity to dormancy may also impact *Rubus* plants recovery, and further research is warranted. Late-season damage should allow less time for plants to replenish carbohydrate reserves (before the onset of dormancy), thereby likely enhancing the effectiveness of weed management tactics over time. Future studies should consider tracking the relationship between environmental conditions, phenological stages, and carbohydrate trends.

Introduction

Perennial plants in temperate climates follow predictable carbohydrate cycles. Reserves decrease as plants use stored energy for new leaf and shoot growth in the spring and continue to decrease or remain low while plants flower, after which there is typically a net gain in carbohydrates, and reserve levels increase until the plant becomes dormant in the fall (Kozlowski 1992). These reserves support respiration and metabolism through dormancy until the spring, when photosynthesis can again create new carbohydrates.

The specific patterns of these carbohydrate cycles are species dependent. Considerable work has been done on carbohydrate movement and storage in cultivated plants. Tree species studied include fruit trees, such as apple (*Malus sylvestris* L.) (Kandiah 1979) and sweet orange (*Citrus sinesis* L.) (Monerri et al. 2011), as well as hardwood trees such as sugar maple (*Acer saccharum* Marshall) (Wargo 1971), yellow birch (*Betula alleghaniensis* Britton) (Gaucher et al. 2005), and northern red and white oak (*Quercus rubra* L. and *Quercus alba* L., respectively) (Wargo 1976). Seasonal changes in total nonstructural carbohydrates (TNC), such as soluble sugars and starch, have also been studied in other woody perennial fruit crops such as cranberry (*Vaccinium macrocarpon* Aiton) (Hagidimitriou and Roper 1994; Roper and Klueh 1996), wild blueberry (*Vaccinium angustifolium* Aiton) (Jatinder et al. 2012), and red raspberry (*Rubus idaeus* L.) (Fernandez and Pritts 1994; Palonen 1999).

Understanding these carbohydrate cycles in noncultivated plants is needed from a weed science perspective to better understand weed biology and improve weed management (Bhowmik 1997). Although seasonal TNC changes have been studied in some weed species such as Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decr.), common milkweed (*Asclepias syriaca* L.), and purple loosestrife (*Lythrum salicaria* L.) (Bhowmik 1994; Katovich et al. 1998; Price et al. 2001), little is known about the TNC cycles in weedy dewberry (*Rubus* spp.). It is found as a weed on cranberry farms in Massachusetts (Sandler et al. 2015), in pastures used for animal grazing, and in some annual crops with reduced or absent tillage (Glenn et al. 1997; Sather and Bradley 2012).

Table 1. Mean monthly air (daytime and nighttime) and soil temperatures and total monthly rainfall in East Wareham, MA, for the growing seasons of 2011 and 2012.

	Mean temperature						Rainfall[a]	
	Air minimum[a]	Air maximum[a]	Soil[b]	Air minimum[a]	Air maximum[a]	Soil[b]		
	2011			2012			2011	2012
Month			———C———				———mm———	
April	4.4	13.9	8.3	4.7	15.4	8.1	180	47
May	10.4	18.8	12.6	11.3	19.8	11.9	86	169
June	14.4	23.3	15.1	13.7	23.5	15.4	114	85
July	18.3	27.8	17.3	18.3	28.3	17.5	113	72
August	17.8	27.2	18.1	18.3	27.8	18.4	123	163
September	15	23.3	17.3	12.6	22.4	16.9	126	190
October	8.3	17.8	15.0	8.6	18	14.3	233	116
November	3.4	14.8	10.1	0.6	9.5	10.3	94	85
				Rainfall totals for *Rubus* spp. sampling periods:			1,069	927

[a]Meteorological data sourced from East Wareham, MA, NOAA Weather Service records.
[b]Soil temperature data from USDA-NRCS, http://nesoil.com/climate.

Gleason and Cronquist (1991) describe *Rubus* as plants that form a perennial base (crown), which supports a series of biennial stems. First-year stem growth (primocanes) is typically unbranched with compound leaves; the stems do not flower. Floricanes (second-year growth) produce simple leaves on short lateral branches that usually terminate with an inflorescence. Although *Rubus* are commercially cultivated for their fruit (e.g., *R. idaeus*, black raspberry [*Rubus occidentalis* L.]), three *Rubus* species have been commonly identified as weeds on Massachusetts cranberry farms (bristly dewberry [*Rubus hispidus* L.], northern dewberry [*Rubus flagellaris* Willd.], and Allegheny blackberry [*Rubus allegheniensis* Porter]) (Sandler et al. 2015). In Massachusetts, *Rubus* flower from June through September and fruit from July to October (Demoranville 1986). *Rubus* are highly variable, readily hybridize with one another, and are difficult to identify (Jensen and Hall 1979; Rydberg 1915; Sandler 2001; Steele and Hodgdon 1963). In noncultivated (weedy) situations especially, different species may grow intermingled with one another, further obscuring identification.

Due to their recumbent growth habit (Gleason and Cronquist 1991), exponential growth patterns (HAS, personal observations), and vigorous stems that can root at the tip and woody roots (Demoranville 1986), weedy *Rubus* are challenging to control, can cause serious crop losses in cranberry, and are lacking satisfactory controls for most growers (Else et al. 1995; Sandler 2010). Current management options (Sandler and Ghantous 2018) involve labor-intensive wiping with glyphosate alone or in mixture with 2,4-D products; spot treatments with concentrated solutions of mesotrione can stunt *Rubus* plants. Any herbicide applications must be repeated on an annual basis for multiple years to sufficiently deplete carbohydrate reserves and curtail growth. If an infestation is well established and plant density is high, costly renovation (i.e., removal of all existing plant material combined with replanting new cranberry vines) may be the only option that provides suitable long-term management (Gordon 2009).

Chemical, biotic, or physical damage to aboveground plant structures during active growth phases causes plants to expend TNC on new growth, reducing overall size and vigor. This depletion renders them more vulnerable to mortality (Kays and Canham 1991; Loescher et al. 1990). Herbicide application to the herbaceous perennial weed Canada thistle [*Cirsium arvense* (L.) Scop.] in the spring or fall reduced root carbohydrates similarly at 35 d after treatment, but fall applications gave better control at 8 mo after treatment, because roots could not recover reserves due to the onset of winter (Wilson et al. 2006). Fall herbivore damage reduced nonstructural carbohydrates and inhibited aboveground biomass the subsequent spring in the woody invasive shrub *Tamarix* spp. (Hudgeons et al. 2007). Hand defoliation or clopyralid application temporarily reduced TNC in stems and roots of honey mesquite (*Prosopis glandulosa* Torr.) (Cralle and Bovey 1996). Work in tree species demonstrated that individual species have different seasonal "windows" of time when cutting treatments will result in lower levels of autumn root reserves (Kays and Canham 1991).

Although TNC were not measured directly, Alvarado-Raya et al. (2007) reported root dry weight for *R. idaeus* decreased when floricanes were girdled pre- or postbloom. Because timing of injury can impact carbohydrate production and mobilization of cultivated *Rubus* species, it follows that there might be a window of time in which weedy *Rubus* plants will be more impacted by control measures. The specifics of seasonal carbohydrate cycles for weedy *Rubus* are unknown, and knowledge of fluctuations may improve efficacy of weed control efforts by enabling managers to implement controls during the windows of time when resources for regrowth will be lowest. Our objective was to follow the seasonal changes in levels of TNC within the roots of weedy *Rubus* plants at different phenological growth stages to determine whether changes occur in predictable patterns.

Methods and Materials

Rubus plants were collected from small (300-m²) areas adjacent to production beds on commercial cranberry farms in East Wareham, MA. Soils were classified as Freetown coarse sand (dysic, mesic Typic Haplosaprists), pH 4.9 with <1% organic matter (USDA-NRCS 2020). Plants were growing in full sun in mostly single species stands, with some occasional grasses intermixed. Due to the sprawling growth habit of weedy *Rubus*, crowns were typically a minimum of 1 m apart. Two sites were sampled each year for a period of 2 yr, a common period for data collection in seasonal carbohydrate studies (Horak and Wax 1991; Katovich et al. 1998; Nkurunziza and Streibig 2011). Site 1 (41.76°N, 70.67°W) and Site 2 (41.82°N, 70.62°W) were sampled in 2011. Because Site 1 did not have enough *Rubus* plants for a second year of sampling, 2012 samples came from Site 2 and Site 3 (41.83°N, 70.63°W). Average monthly minimum (nighttime) and maximum (daytime) air temperatures and rainfall data were collected during the research period from a weather station located at the UMass Cranberry Station facility, East Wareham, MA (41.76°N, 70.67°W); soil temperature data were obtained from the USDA-NRCS Northeast Soil Temperature Network website (Table 1).

Table 2. Sampling dates and associated phenological stage of weedy *Rubus* plants when roots were collected from Massachusetts cranberry sites for high-performance liquid chromatography analysis to study seasonal fluctuations of root total nonstructural carbohydrates.

Rubus phenological stage	Sampling dates	
	2011	2012
Budbreak	April 20	April 2
Full leaf expansion	May 24	May 11
Flowering	June 13	June 5
Fruit maturity	August 1	August 1
Dormancy	November 14	October 24

Root samples were collected at five distinct phenological stages from plants with crowns, primocanes, and floricanes evident: initial budbreak, full leaf expansion, flowering, fruit maturity, and after the onset of dormancy as indicated by leaf color change and senescence (Table 2). The use of phenology to select sampling time has been used in other weed studies that measured carbohydrate reserves (Bhowmik 1994; Tworkoski 1992). Dates of phenological sampling varied slightly by year, likely due to normal annual variability in environmental conditions.

At each collection date for each location, four entire individual plants of similar size were collected to prevent resampling plants (Katovich et al. 1998; Richburg 2005). Plants were excavated using shovels and rakes to remove entire plants with intact roots from the soil. Roots were typically found in the top 30 cm of soil. Each plant was considered a replicate (Cyr et al. 1990; Katovich et al. 1998). Upon removal from the ground, plants were placed into a container with their roots in water, then transported to the lab, where they were immediately processed. A root section approximately 10-cm long was clipped from each plant. Carbohydrate concentrations can be dependent on root diameters, so roots of approximately 1-cm diameter were selected (Wargo 1976). Samples were washed to remove soil, cut into small pieces using a razor blade, placed into paper bags, and dried at 60 C for 1 wk until a constant weight was maintained. These samples were then ground in a Wiley mill (Thomas Scientific, Swedesboro, NJ) to pass through a 2-mm screen. Carbohydrates were extracted with ethanol from 100 mg of the ground root samples, and high-performance liquid chromatography (HPLC) analysis was used to determine concentrations of sucrose, glucose, fructose, and starch that collectively represent TNC (Botelho and Vanden Heuvel 2005).

Statistical Analysis

The study was a completely randomized block design with four replications; phenological stage, site, and their interaction were the main (fixed) factors. Each year was analyzed independently due to unmeasured environmental variations such as rainfall, temperature, and soil temperature between years that are known to impact plant carbohydrates (Kozlowski 1992). Data met the assumptions of ANOVA, and no transformations were made. Data were analyzed using SAS (v. 9.2, SAS Institute, Cary, NC). ANOVA was performed on TNC (the sum of sucrose, glucose, fructose, and starch), total sugars (the sum of sucrose, glucose, and fructose), and sucrose, glucose, fructose, and starch individually using PROC GLM per 100 mg of root. When appropriate, means were separated using Duncan's multiple range test, P = 0.05.

Results and Discussion

In 2011, the effect of plant phenological stage varied by site for TNC, starch, and sucrose (P ≤0.05). The site by stage interaction was not significant for any carbohydrate category in 2012; thus data were pooled across sites for all categories for 2012. For both years, TNC were depleted between budbreak and full leaf expansion as plants grew new photosynthetic apparatus and then returned to levels greater than or equal to those measured at budbreak by dormancy (Figure 1). For 2011, Site 1 TNC rebounded to a level similar to that of budbreak at flowering, fruit maturity, and dormancy. For Site 2 in 2011, the TNC level rose significantly between fruit maturity and dormancy, ending at a higher level than measured at budbreak. For 2012, TNC concentrations rose between flowering and the onset of dormancy, when the level was similar to that measured at budbreak.

The site by stage interaction was not significant for soluble sugars, fructose, or glucose; thus 2011 data for these categories were pooled across sites. Changes in concentration of soluble sugars at the five phenological stages was similar at all sites and both years (Figure 2). Levels were greatest at budbreak, with significant decline between budbreak and leaf expansion, then levels were similar for samples from all other stages. Conversely, starch was lower at budbreak for all sites and years, and greatest at dormancy (Figure 3). The decline of soluble sugars between budbreak and leaf expansion suggests that plants were primarily using sugars to support growth until leaves were fully expanded to produce new carbohydrates through photosynthesis. Starches are a form of long-term storage reserve, and starches increased significantly between the time of fruit maturity and onset of dormancy. This indicates that plants accumulated starches to support energy needs through the winter. Plants are likely hydrolyzing starches into sugars to use for energy during winter periods of low temperatures (Kozlowski 1992), resulting in starch levels being lower at the start of the growing season than at the end.

For 2011, fructose followed the same trend as soluble sugars as a whole (Table 3; Figure 2). Levels were greatest at budbreak, with a significant decline between budbreak and leaf expansion, then remaining at similar levels for the rest of the growing season. Glucose showed a decrease between budbreak and leaf expansion. Glucose levels were similar at leaf expansion, flowering, and dormancy and similar at fruit maturity and budbreak. The effect of phenological stage on sucrose concentration varied by site (Table 3). At Site 1, sucrose followed the same trend as glucose (sites pooled). At Site 2, sucrose levels were similar at budbreak, leaf expansion, and dormancy and also similar at leaf expansion, flowering, and fruit maturity. In 2012, sucrose declined between budbreak and leaf expansion. Levels were similar at leaf expansion, flowering, and dormancy and also similar at flowering and fruit maturity. Fructose and glucose did not vary significantly throughout 2012 (data not shown).

Unlike starches that are built for storage, sugars are readily used for metabolism, stress responses, and growth demands. Sugars are likely more sensitive to environmental differences between the sites and years, which likely affected the immediate energy demands of the plants. A study on sugars in dandelion (*Taraxacum officinale* F.H. Wigg.) roots attributed sugar fluctuations to differences in rainfall and soil temperature (Wilson et al. 2001), which were not measured in this study. Sucrose is the major form in which energy is transported in higher plants such as *Rubus*, and it is further broken down to the more reactive forms of glucose and fructose before use (Burley 1961; Ward et al. 1998). The sucrose
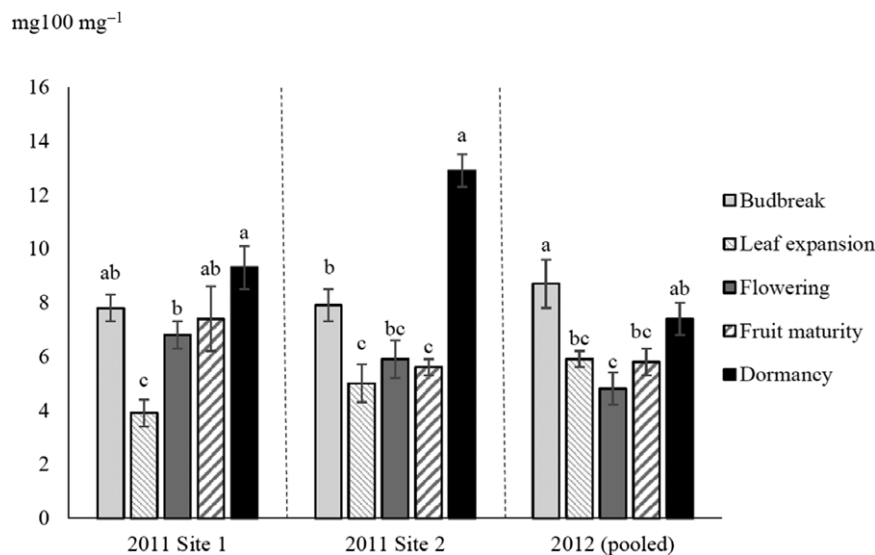
mg100 mg^{-1}

Figure 1. Mean concentration of total nonstructural carbohydrates (TNC) for weedy *Rubus* root samples collected in 2011 and 2012 in East Wareham, MA, by phenological stage. Reported as milligrams per 100 mg of root biomass (mean ± SE, $n = 4$ for 2011 Site 1 and Site 2; $n = 8$ for 2012). Means with similar letters within each site or year are not significantly different according to Duncan's Multiple Range Test (P ≤ 0.05).
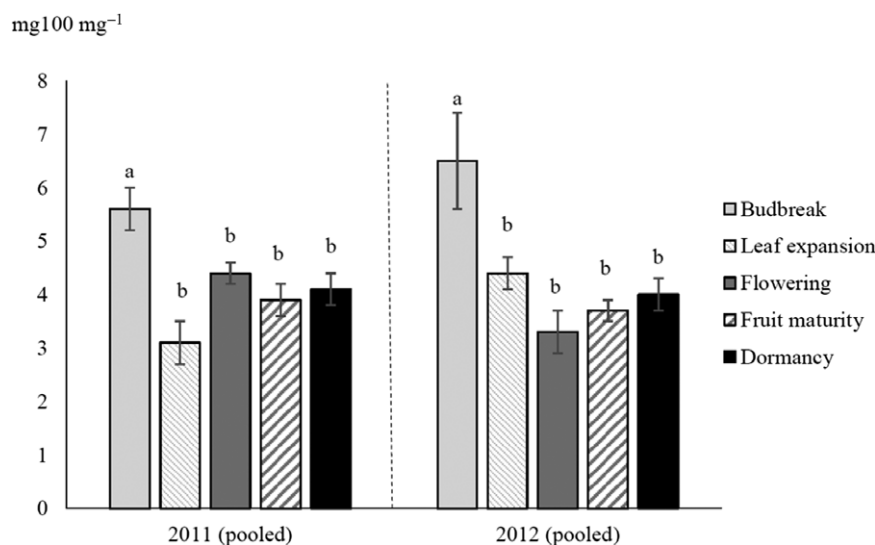
mg100 mg^{-1}

Figure 2. Mean concentration of soluble sugars for weedy *Rubus* root samples collected in 2011 and 2012 in East Wareham, MA, by phenological stage. Reported as milligrams per 100 mg of root biomass (mean ± SE, $n = 8$). Means with similar letters within each year are not significantly different according to Duncan's Multiple Range Test (P ≤ 0.05).

levels in *Rubus* roots tended to be more dynamic that those of the other sugars and may indicate changes in source–sink relationships more than levels of fructose and glucose, which likely reflect metabolic demands of the roots.

Our final sampling date in 2012 was earlier than in 2011 (Table 2). Average soil temperature for November 2012 was also slightly higher than in 2011 (10.3 and 10.1 C, respectively), and 2012 had less rainfall than 2011 during the April to November period when *Rubus* were actively growing (927 mm and 1,069 mm, respectively) (Table 1). Previous research indicates that environmental conditions (e.g., soil temperature) can affect root carbohydrate accumulation more than phenological stage (Tworkoski 1992; Wilson et al. 2006). Kaurin et al. (1981) demonstrated a positive correlation between frost hardiness and the amount of soluble carbohydrates in rhizomes and buds of cloudberry (*Rubus chamaemorus* L.), a *Rubus* species with potential to

transition from the wild to commercial cultivation. Warmer temperature trends in winter may provide an unanticipated opportunity for weedy *Rubus* management, as Kaurin et al. (1982) reported that hardiness of *R. chamaemorus* was directly related to freezing temperatures. Future studies should consider tracking the relationship between environmental conditions, phenological stages, and carbohydrate trends.

Findings suggest that predictable patterns do occur for levels of TNC within the roots of *Rubus* plants at different phenological growth stages. However, recommendations for timing *Rubus* control cannot be based on TNC cycles alone; temporal proximity to dormancy may also be important. Previous work on controlling weedy *Rubus* with flame cultivation showed that a single treatment in mid-June was less effective at reducing shoot biomass 1 yr after treatment compared with a single July or August treatment. Weedy *Rubus* plants treated in July or August resulted in smaller plants in

Table 3. Mean concentration of sugar levels by phenological stage for weedy *Rubus* root samples collected in East Wareham, MA (mean ± SE). Data shown for categories with statistically significant differences between means. For 2011 fructose and glucose, $n = 8$, and for 2011 sucrose, $n = 4$ (for Site 1 and Site 2). For 2012 sucrose, $n = 8$.[a]

	Fructose	Glucose	Sucrose		
		2011			
			Site 1	Site 2	2012
			mg 100 mg^{-1} root biomass		
Budbreak	2.2 ± 0.2 a	1.3 ± 0.2 a	1.9 ± 0.1 a	2.3 ± 0.2 ab	4.3 ± 0.6 a
Leaf expansion	1.0 ± 0.1 b	0.6 ± 0.1 c	1.0 ± 0.1 c	1.9 ± 0.4 bc	2.6 ± 0.2 b
Flowering	1.1 ± 0.1 b	0.8 ± 0.1 bc	1.3 ± 0.1 bc	1.5 ± 0.1 c	1.9 ± 0.3 bc
Fruit maturity	1.3 ± 0.1 b	1.0 ± 0.1 ab	1.7 ± 0.2 ab	1.4 ± 0.1 c	1.3 ± 0.1 c
Dormancy	1.2 ± 0.1 b	0.7 ± 0.1 bc	1.4 ± 0.2 bc	2.9 ± 0.2 ab	2.4 ± 0.3 b

[a]Means followed similar letters within a category are not significantly different according to Duncan's Multiple Range Test ($P \leq 0.05$).
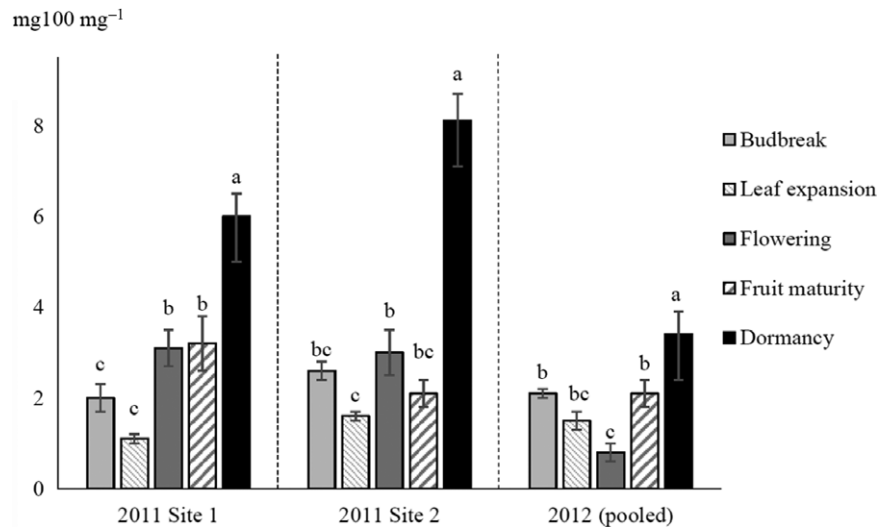

Figure 3. Mean concentration of starch for weedy *Rubus* root samples collected in 2011 and 2012 in East Wareham, MA, by phenological stage. Reported as milligrams per 100 mg of root biomass (mean ± SE, $n = 4$ for 2011 Site 1 and Site 2; $n = 8$ for 2012). Means with similar letters within each site or year are not significantly different according to Duncan's Multiple Range Test ($P \leq 0.05$).

the following year, whereas plants treated in June had more time between injury and dormancy to recover and replenish TNC (Ghantous and Sandler 2016). In addition, factors such as temperature, soil moisture, and fertilizer timing may also impact recommended timing for weedy *Rubus* management. Fernandez and Pritts (1994) reported photosynthetic rates of *R. idaeus* primocane and floricane leaves declined as temperature increased, and Ahn et al. (2011) reported carbohydrates were lowest for Korean raspberry (*Rubus coreanus* Miquel) in wet conditions (−5 kPa). Boulanger-Pelletier and Lapointe (2017) demonstrated that fertilizers improve initial survival and rooting of *R. chamaemorus*. Thus, control strategies for weedy *Rubus* in cranberry may be improved when targeted in temporal separation from fertilizer applications, but this warrants further investigation. Although the current study showed that *Rubus* root TNC did not differ significantly between mid-June (flowering) and mid-August (fruit maturity), late-season damage will likely allow plants less time to replenish reserves and recover from damage before dormancy.

Based on these results, our recommendation would be to employ control methods that damage aboveground *Rubus* plant parts (mowing, flame cultivation, etc.) during growth stages when TNC are low (at or after full leaf expansion but before dormancy), timed such that plants will not have time to fully replenish depleted root reserves before the onset of dormancy. Improvement of management could include integration of certain herbicide treatments (Wilson et al. 2006) with physical removal or treatment with heat.

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