Effect of Defoliation Prior to a Frost on Postharvest Respiriation Rate, Extractable Sucrose, and Invert Sugar Concentration of Sugarbeet

L.G. Campbell¹, K. Klotz-Fugate¹, and L.J. Smith²

¹USDA-ARS Northern Crop Science Laboratory, Fargo, ND 58102-2765; and ²University of Minnesota, Crookston, MN 56717

Corresponding author: Larry Campbell (larry.campbell@ars.usda.gov)

DOI: 10.5274/jsbr.52.3.2

ABSTRACT

To investigate the effect of defoliation prior to a frost on postharvest storage properties, roots of plants with canopies intact until harvest were compared to roots of plants that had been defoliated prior to a frost on multiple harvest dates following a damaging frost. The average storage respiration rates of roots harvested from plots that had been defoliated prior to a damaging frost were 1.30, 1.52, and 2.67 mg CO₂ kg⁻¹ h⁻¹ greater than the postharvest respiration rates of roots harvested on the same day that had their canopies intact until harvest, 30, 60, and 90 days after harvest (DAH), respectively. The average extractable sucrose concentrations of roots from plots that had been defoliated prior to a frost were 2.39 and 3.49 kg Mg⁻¹ less than the extractable sucrose concentration of roots harvested on the same day that had their canopies intact until harvest, 0 and 90 DAH, respectively. The average increase in the invert sugar concentration of crowns due to defoliation prior to a frost was 6.49 g (100 g S)-190 DAH. The increase in the invert sugar concentration of taproots attributable to defoliation was one tenth the invert sugar increase of comparable crowns

Additional key words: *Beta vulgaris*, harvest, processing quality, storage.

In areas with temperate climates, extending the growing season by delaying sugarbeet (*Beta vulgaris* L.) harvest increases both the yield and risk of frost damage to the roots (Smith, 2001; Milford et al, 2002; Yonts et al., 2009). In spite of efforts to complete harvest before a severe frost, unseasonably cold weather during harvest or low temperatures associated with weather delayed harvests may result in frost injury. The canopy provides protection to the crown and root so that the first freeze often damages only the foliage (Yonts, et al., 2009; Dean and Millard, 2009).

During a hard frost, cell contents of exposed portions of the root freeze, resulting in perforation of cell membranes and cell rupture by the ice crystals formed. Upon thawing, leakage of the cell contents from damaged cells and membranes supports the proliferation of opportunistic microflora present in the root, on the root, and in the surrounding soil (Halden, 1982; Harvey and Dutton, 1993; Cole, 1983). Within limits, the modifications in the cell membranes induced by freezing are reversible, depending on thawing conditions (Barbier, et al, 1982; Giffel, 2000). An increase in invert sugar concentration occurs in frost injured roots. (de Bruijn, 2000; Oldfield et al., 1971). Invert sugars can be formed by endogenous or microbial sucrolytic enzymes. Two-fold increases in invert sugar concentrations have been observed 14 days after frost injury (de Bruijn, 2000). In processing, invert sugars degrade to colored, acidic compounds that hinder the formation of white sugar, require additional soda ash to maintain juice pH, and increase sucrose loss to molasses (Dutton and Huiibregts, 2006). Postharvest respiration rate is presumed to increase after frost injury, since mechanical injury generally elevates root respiration (Campbell and Klotz, 2006). The effect of frost damage prior to harvest on postharvest storage respiration rate is not as well documented as the impact of frost during postharvest storage.

This study investigated the effect of defoliation prior to a frost on postharvest storage properties; roots of plants with canopies intact until harvest were compared to roots of plants that had been defoliated prior to a frost on multiple harvest dates following a damaging frost. The objectives of the study were 1) to document the effects of defoliation prior to a damaging frost, 2) to provide information that would assist in determining when to resume harvest after a frost, and 3) to indicate potential postharvest storage problems that may be associated with roots that have been subjected to freezing temperatures prior to harvest.

MATERIALS AND METHODS

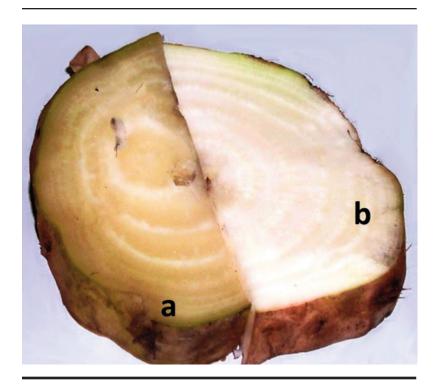
Experimental procedures and analysis

All roots used in the postharvest analyses were obtained from trials at Crookston, MN in 2006, 2007, and 2008, and at Fargo and Prosper, ND in 2006 and in 2007, respectively. All trials were planted during the first two weeks of May. Crookston was planted to Alpine

(Seedex, Inc., Fargo, ND) in 2006 and 2007 and to Hilleshög 3035 (Syngenta, Longmont CO) in 2008. Horizon (Syngenta, Longmont CO) was planted at Fargo in 2006 and Prosper 2007. Seed spacing was 6 cm in rows 9.1 m long and 56 cm apart. Each experimental unit consisted of six rows. All trials were fertilized and managed for optimal yield and quality of sugarbeet.

One plot from each replicate was mechanically defoliated and immediately harvested prior to an anticipated damaging frost. At the same time, half of the remaining plots also were defoliated. The post-frost harvests began when numerous roots in the previously defoliated plots had visual signs of frost damage (Fig. 1). The morning of the first damaging frost and each morning following, one plot per replicate with the canopy intact was defoliated and immediately harvested and one of the plots that had been defoliated at the time the pre-frost roots were obtained also was harvested. The number of harvest dates at a site following a frost ranged from five to ten. Some of

Figure 1. Cross section of (a) a frost-damaged root (damaged tissue is yellow to light tan and water soaked due to rupturing of cells), and (b) healthy root tissue.



the planned daily harvests were not possible due to rain or wet soil. Harvest dates are indicated by the number of days after a damaging frost (DAF). The harvest on the morning of the initial frost is designated '0 DAF"; each pre-frost harvest is noted with a negative number indicating the days prior to the initial post-frost harvest. Plots at all three locations were defoliated with a commercial beet defoliator. Plots at Crookston were harvested with a commercial-type harvester and roots from Fargo and Prosper were harvested by hand. Only roots from the two center rows of each six-row plot were included in the postharvest storage trials.

Harvested roots were transported to Fargo, ND, washed, and placed in perforated plastic bags. The bags were placed on shelves in a room maintained at 5°C and 90-95% relative humidity. Respiration rate (mg CO₂ kg⁻¹ of roots h⁻¹) was measured on different 10root samples 30, 60, and 90 days after harvest (DAH). Extractable sucrose and invert sugar concentrations were determined at harvest (0 DAH) and 90 DAH. The respiration rate of 10-root samples was determined using an infrared carbon dioxide gas analyzer (LICOR LI-6252, Lincoln, NE) and an open system with continuous airflow over the roots (Campbell et al., 2011). Sucrose concentration and purity were used to calculate extractable sucrose concentration. Sucrose was measured polarimetrically (Autopol 880, Rudolph Research Analytical, Flanders, NJ) using aluminum sulfate-clarified brei samples (McGinnis, 1982). Purity was determined using the procedures described by Dexter et al. (1967). Twenty-gram brei samples were oven dried at 80°C until reaching a stable dry weight (>72 h) to calculate dry matter concentration. Extractable sucrose concentrations for the 0 DAH samples were expressed on a fresh weight basis. Concentrations for the 90-DAH samples were adjusted to account for changes in water content during storage and expressed on a fresh weight concentration with a water content equivalent to the corresponding sample 0 DAH. Aluminum sulfate-clarified filtrate was used to measure invert sugar concentrations. Invert sugar (glucose + fructose) concentrations were determined colorimetrically using end point, enzyme-coupled assays (Klotz and Martins, 2007) and expressed as grams per 100 grams of sucrose [g (100 g S)-1]. The invert sugar concentration of crowns and taproots were determined separately. The crown contained all the tissue above the lowest leaf scar.

Data were analyzed as a randomized complete block design with three replicates using the PROC GLM procedure (SAS 9.4; SAS Institute, Inc., Cary, NC). Experimental units were harvest date (days after frost) by time of canopy removal (prior to frost or at harvest) combinations. The least significant difference (LSD) with = 0.10 was used to determine when differences among treatment means were significant. The 0.10 probability level was chosen over the frequently used 0.05 level to reduce the probability of Type II errors (Chew, 1976; Carmer, 1976). It seemed reasonable to assume that the treatment means were more likely than not to be unequal, so Type II errors

rors (declaring two treatments equal when, in fact, they are different) were considered as important as Type I errors (declaring two treatments unequal when, in fact, they are equal). Each environment (location within a year) was analyzed separately because the number of harvest dates and the intervals between harvests were not constant. The "estimate" function of the SAS GLM procedure was used to quantify the difference between roots from plots with the canopy intact until harvest and roots from plots that had been defoliated prior to a frost for all post-frost harvest dates within each environment. The difference between treatment means of roots from plants defoliated before a damaging frost and roots from plants with canopies intact until harvest for all harvest dates following a frost, replicates, and environments (n = 90) were compared using a paired t-test (PROC TTEST; SAS 9.4).

Harvest dates and conditions

In 2006, the initial harvest at Crookston occurred on 11 October, two days before frozen roots were harvested (-2 DAF). High temperatures three days prior to 11 October ranged from the low- to midteens to lows near -3°C (Fig. 2). The first frost-damaged roots were harvested on the morning of 13 October (0 DAF). Minimum air temperature prior to the 13 October harvest was -7°C. Morning lows again dropped to -6°C on the 14th (1 DAF) and then did not drop below -3°C again during the sampling period. Daily low temperatures after 14 October were probably not low enough to cause additional frost damage. Maximum temperatures rose to 16°C and 12°C on the 15th (2 DAF) and 16th of October (3 DAF), respectively. Between the 17th (4 DAF) and 23rd of October (10 DAF), maximum daily temperatures ranged from 1 to 6°C.

The initial harvest at Fargo also occurred on 11 October 2006 (-2 DAF). The first frozen roots were harvested 13 October (0 DAF) following low temperatures of -6°C on October 11 and 12 (Fig. 3). The next harvest date was 16 October, three days after the initial freeze, (3 DAF) following low temperatures of -5 and -2°C on 14 and 15 October, respectively. Daily low temperatures between 16 and 18 October were above freezing with highs between 3 and 14°C. After 19 October, daily high temperatures never exceeded 3°C and daily low temperatures of -4 and -5°C occurred on 21 and 22 October, prior to the last sampling date, 23 October (10 DAF).

In 2007, the Crookston pre-frost samples were harvested on 26 October (-2 DAF), two days before the initial harvest of frost-damaged roots on 28 October (0 DAF). Five days prior to the 26 October harvest, maximum daily temperatures ranged from 11 to 19°C and daily minimums from -3°C to a high of 6°C on 25 October (Fig. 2), followed by a low temperature of -1°C the morning of the 26 October harvest (-2 DAF). A low temperature of -6°C was observed on 27 October and prior to the 28 October harvest (0 DAF). Daily maximum temperatures between 29 October (1 DAF) and 2 November (5 DAF)

Figure 2. Hourly temperatures at a site near Crookston, MN (NDAWN: Eldred, MN: http://www.ndawn.ndsu.nodak.edu) prior to and during sugarbeet harvest 2006 - 2008 [date and days after damaging frost (DAF)]. Shaded areas indicate temperatures five days prior to frost (DAF = -5 to DAF = 0). Green vertical lines denote date of pre-frost harvest and date of defoliation for plots with canopy removed prior to frost; black vertical lines indicate initial post-frost harvest date (DAF = 0). Blue horizontal line = -2.5°C.

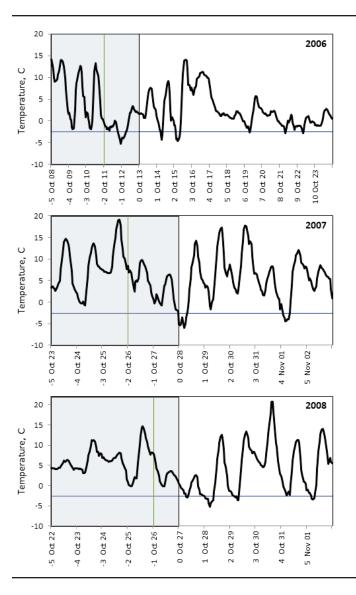
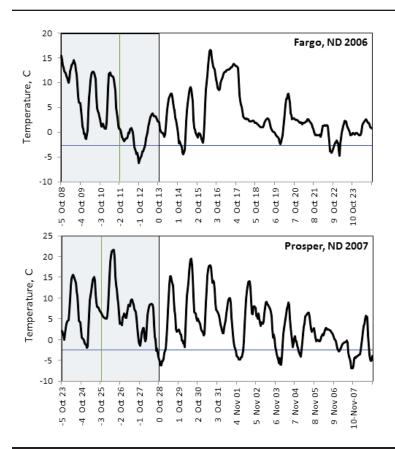


Figure 3. Hourly temperatures at Fargo, ND, 2006 and Prosper, ND, 2007 (NDAWN: http://www.ndawn.ndsu.nodak.edu) prior to and during sugarbeet harvest [date and days after damaging frost (DAF)]. Shaded areas indicate temperatures five days prior to frost (DAF = -5 to DAF=0). Green vertical lines denote date of pre-frost harvest and date of defoliation for plots with canopy removed prior to frost; black vertical lines indicate initial post-frost harvest date (DAF = 0). Blue horizontal line = -2.5°C.



ranged from 8 to 15° C. Daily minimum temperatures for the same dates ranged from 5° C on 30 October (2 DAF) to -5° C on 1 November (4 DAF).

Roots were first harvested at Prosper on 25 October 2007, three days before a damaging frost (-3 DAF). Daily maximum temperatures ten days prior to 25 October ranged from 10 to 17°C with daily minimum temperatures ranging from -1 to 10°C (Fig. 3). Frozen roots

were first harvested on 28 October (0 DAF) after an overnight low of -7°C. Between 29 October (1 DAF) and 31 October (3 DAF), daily maximum temperatures ranged from 10 to $20^{\circ}\mathrm{C}$ with daily lows ranging from 0 to -4°C. A low temperature of -5°C was recorded on 1 November, the day before the 2 November (5 DAF) harvest. Between 2 November and 7 November (10 DAF), daily minimum temperatures ranged from -1 to -8°C with three days -6°C or lower.

Five days prior to the initial 2008 harvest at Crookston, daily minimum temperatures ranged from -3 to 4°C while maximum daily temperatures ranged from 7 to 12°C (Fig. 2). The initial pre-frost harvest occurred on 26 October (-1 DAF) following a 0°C low temperature. Low temperatures of -4, -6 and -5°C preceded the 27 (0 DAF), 28 (1 DAF) and 29 October (2 DAF) harvests, respectively. The overnight temperature remained above freezing for the 30 October (3 DAF) harvest then dropped to -3, -4, and 0°C for the 31 October (4 DAF) and the 1 (5 DAF)and 2 (6 DAF) November harvests, respectively. Daily maximum temperatures between 28 October (1 DAF) and 1 November (5 DAF) ranged from 12 to 22°C.

Hourly temperature and other weather data are available on the North Dakota State University NDAWN website (http://ndawn.ndsu.nodak.edu). The Fargo and Prosper, ND fields were close to NDAWN recording stations (Fig. 3). Initial post-frost harvest dates at Crookston, MN were based upon temperature and observations of frost damage at the Northwest Research and Outreach Center (University of Minnesota) and are very similar to observations from a nearby NDAWN site near Eldred, MN (Fig. 2).

RESULTS

Postharvest respiration rate

Thirty days after harvest in 2006, respiration rates of roots from Crookston ranged from 3.93 mg CO₂ kg⁻¹ h⁻¹ for roots harvested prior to a frost (-2 DAF) to 7.72 mg $\rm CO_2\ kg^{-1}\ h^{-1}$ for roots harvested two days after the initial frost (2 DAF) from plants that had been defoliated four days earlier (Table 1). The respiration rate of roots 30 DAH harvested the morning of the initial frost (0 DAF) from plants with canopies intact until harvest (5.06 mg CO₂ kg⁻¹ h⁻¹) were significantly higher than the respiration rate of roots harvested prior to the frost. Subsequent differences between the respiration rate 30 DAH of roots harvested before a frost and roots from plots with canopies intact were not significant, except for the last harvest date (10 DAF). Respiration rates of roots from plants with intact canopies with the same harvest dates were generally higher 60 DAH than those observed 30 DAH but followed a pattern similar to that for roots stored for 30 d. Ninety days after harvest, the elevated respiration rate of roots harvested 1, 2, and 4 d after the initial frost from plots with canopies intact until harvest, compared to roots harvested before the frost (-2 DAF), was significant. Differences between the respiration rate of

Table 1. Postharvest respiration rate 30, 60, and 90 days after harvest (DAH) and extractable sucrose concentration at harvest (0 DAH) and 90 DAH of roots of plants with canopies intact until harvest and roots of plants that had been defoliated (removed) prior to a frost, on multiple harvest dates following a damaging frost, Crookston, MN, 2006 – 2008. Averages for the prefrost harvest are highlighted in blue. Postfrost harvests that had the canopy removed prior to a damaging frost are highlighted in gray.

V	Days	C			Respira	ation ra	te		Extractable sucrose				
Year	after frost	Canopy	30 D	AH	60 I	DAH	90 D	AH	0 D	AH	90 I	DAH	
				1	$mg\ CO_2\ k$	g-1 h-1				kg N	⁄/g⁻¹		
2006	-2		3.93	g*	4.52	f	3.37	f	154	bc	133	с-е	
	0	Intact	5.06	de	9.29	a	4.71	ef	155	bc	126	d-f	
	0	Removed	6.76	ab	6.65	de	6.31	de	157	a-c	145	ab	
	_ 1	Intact	4.51	e-g	4.83	f	5.33	e	154	bc	133	с-е	
	1	Removed	6.11	bc	7.34	b-d	8.89	bc	150	c	126	d-f	
	2	Intact	4.38	e-g	5.33	ef	5.97	de	157	bc	133	b-e	
	2	Removed	7.22	a	8.92	a	12.15	a	160	ab	118	f	
	4	Intact	4.20	fg	4.55	f	5.76	de	158	ab	135	b-d	
	4	Removed	5.52	cd	7.09	cd	7.15	cd	156	a-c	124	d-f	
	6	Intact	4.34	e-g	5.14	\mathbf{f}	4.58	\mathbf{ef}	156	a-c	131	$_{ m de}$	
	6	Removed	6.34	bc	8.35	a-c	10.24	b	150	c	123	$_{ m ef}$	
	10	Intact	4.76	d-f	5.49	ef	4.86	\mathbf{ef}	163	a	154	a	
	10	Removed	6.72	ab	8.51	ab	9.36	b	151	c	144	a-c	
	Mean		5.37		6.62		6.82		155		133		

2007	-2		3.43	f	2.90	е	3.12	е	169	a	167	ab
	0	Intact	4.08	с-е	3.59	d	3.88	b-e	160	c	132	c
	0	Removed	4.33	b-d	3.87	$^{\mathrm{cd}}$	4.21	b-d	166	ab	139	c
	1	Intact	3.76	d-f	4.37	b	3.83	b-e	166	ab	157	ab
	1	Removed	3.83	c-f	4.32	bc	4.06	b-d	161	bc	154	b
	2	Intact	3.60	ef	4.55	b	4.30	a-c	161	bc	138	c
	2	Removed	4.37	bc	5.03	a	4.61	ab	154	d	135	c
	3	Intact	4.24	cd	4.53	b	4.46	a-c	159	cd	126	c
	3	Removed	5.16	a	4.66	ab	5.08	a	159	cd	135	c
	4	Intact	4.98	a	4.52	b	3.48	de	171	a	164	ab
	4	Removed	5.06	a	4.77	ab	3.88	b-е	162	bc	158	ab
	5	Intact	4.15	с-е	3.79	d	3.71	с-е	171	a	169	a
	5	Removed	4.86	ab	3.68	d	4.02	b-d	168	a	161	ab
	Mean		4.30		4.20		4.05		164		149	
2008	-1		5.57	cd	5.02	de	4.72	cd	177	b-d	169	a-c
	0	Intact	5.84	cd	5.09	de	5.03	cd	192	a	167	a-d
	0	Removed	5.34	cd	5.67	de	6.72	c	191	a	166	а-е
	1	Intact	5.62	cd	5.71	de	5.03	cd	178	bc	172	a
	1	Removed	7.24	a	8.30	c	9.59	b	174	b-e	157	de
	2	Intact	5.14	d	4.74	e	5.73	cd	167	e	160	b-e
	2	Removed	5.80	cd	9.94	ab	13.71	a	180	b	162	а-е
	3	Intact	6.94	ab	5.74	de	5.46	cd	175	b-e	171	ab
	3	Removed	4.96	d	8.01	c	10.57	b	169	с-е	155	e
	4	Intact	5.40	cd	5.31	de	4.40	d	168	de	167	a-d
	4	Removed	7.63	a	8.48	bc	10.88	b	169	с-е	161	a-d
	5	Intact	6.05	c	6.37	d	4.93	cd	167	e	159	с-е
	5	Removed	7.14	a	10.03	a	13.14	a	170	с-е	158	с-е
	6	Intact	6.06	bc	5.54	de	5.28	dc	172	b-e	168	a-d
	6	Removed	7.60	a	9.19	a-c	9.80	b	175	b-e	164	а-е
	Mean		6.16		6.88		7.67		175		164	

^{*}Within each year, differences among means within a column followed by the same letter are not significant, based upon $LSD_{0.10}$.

roots harvested prior to the frost (-2 DAF) and the respiration rate of roots harvested from plants defoliated prior to the frost were significant for all six harvest dates at 30, 60, and 90 days after harvest. The differences between 16 of the 18 within harvest date comparisons of respiration rates of roots from plants defoliated prior to a frost with roots from plants with canopies intact up until harvested were significant (Table 1). For Crookston in 2006, the average respiration rate over all six harvest dates of roots of plants defoliated prior to a damaging frost was 1.90, 2.04, and 3.82 mg $\rm CO_2~kg^{-1}~h^{-1}$ greater than the respiration rate of roots of plants with the canopy intact until harvest, 30, 60, and 90 DAH, respectively (Table 2).

Relative differences between the respiration rate of roots harvested before a frost (-2 DAF) and roots harvested after the frost from plots with the canopies intact until harvest at Fargo in 2006 (Table 3) were similar to those observed at Crookston in 2006 (Table 1). With the exception of roots harvested the morning following the damaging frost (0 DAH), differences between the respiration rates of roots harvested before a frost and those harvested after a frost from plots with intact canopies were not significant 30 and 60 DAH. Thirty days after harvest the respiration rate of roots harvested 3, 5, 6, and 10 days after the initial frost from plots that had been defoliated prior to the frost were higher than roots harvested before a frost. Sixty days after harvest of the defoliated plots, only the respiration rate of roots harvested the morning following the frost (0 DAF) and those harvested 10 days later (10 DAF) were significantly higher than roots harvested prior to a frost; 90 DAH roots harvested 5, 6, and 10 DAF from defoliated plots had higher respiration rates than roots harvested before the frost. Seven of the 15 within harvest date comparisons of respiration rates of roots from plants defoliated prior to a frost with those from plants with canopies intact up until harvest were significant (Table 3). For Fargo in 2006, the average respiration rate over all five harvest dates of roots of plants defoliated prior to a damaging frost was 1.05, 0.52, and 1.31 mg CO₂ kg⁻¹ h⁻¹ greater than the respiration rate of roots of plants with the canopy intact until harvest, 30, 60, and 90 DAH, respectively (Table 2).

Thirty days after the 2007 harvest, the respiration rate of roots from Crookston ranged from 3.43 mg CO₂ kg⁻¹ h⁻¹ for roots harvested before a frost (-2 DAF) to 5.16 mg CO₂ kg⁻¹ h⁻¹ for roots harvested 3 d (3 DAF) after a frost from plots defoliated before the frost (Table 1). All differences between roots harvested prior to a frost and all treatments except for roots harvested 1 and 2 DAF from plots with canopies intact until harvest and 1 DAF from plots that had been defoliated prior to the initial frost were significant 30 DAH. The respiration rate of roots from both canopy treatments and all post-frost harvest dates were greater than the respiration rate of roots harvested before the frost, 60 DAH. Ninety days after harvest, differences between the respiration rate of roots harvested before a frost and roots harvested 0, 1, 4 and 5 DAF from plots with the canopies

Table 2. Average differences between respiration rate 30, 60, and 90 days after harvest (DAH) and extractable sucrose concentration at harvest (0 DAH) and 90 DAH of roots from plants with their canopies intact until harvest and roots from plants that had been defoliated prior to a frost for all post-frost harvest dates, Crookston, MN, 2006 -2008, Fargo, ND, 2006, and Prosper, ND, 2007.

Days				Confiden	ce Interval _(0.90)
after harvest	Location / year	$\mathbf{Difference}^{\dagger}$	\mathbf{P}^{\ddagger}	Lower limit	Upper limit
		Respin	ration ra	te, mg CO ₂	kg ⁻¹ h ⁻¹
30	Crookston, 2006	-1.90	< 0.01	-2.24	-1.56
	Prosper, 2007	-1.80	< 0.01	-2.31	-1.28
	Crookston, 2008	-1.23	< 0.01	-1.57	-0.90
	Fargo, 2006	-1.05	< 0.01	-1.45	-0.65
	Crookston 2007	-0.46	< 0.01	-0.71	-0.22
	All environments	-1.30	< 0.01	-1.51	-1.08
60	Crookston, 2008	-3.02	< 0.01	-3.60	-2.34
	Crookston, 2006	-2.04	< 0.01	-2.62	-1.46
	Prosper, 2007	-1.46	< 0.01	-1.93	-1.00
	Fargo, 2006	-0.52	0.10	-1.05	0.01
	Crookston, 2007	-0.16	0.15	-0.35	0.02
	All environments	-1.52	< 0.01	-1.85	-1.19
90	Crookston, 2008	-5.51	< 0.01	-6.28	-4.73
	Crookston, 2006	-3.82	< 0.01	-4.53	-3.10
	Prosper, 2007	-1.64	< 0.01	-2.22	-1.05
	Fargo, 2006	-1.31	< 0.01	-1.96	-0.66
	Crookston, 2007	-0.37	0.06	-0.69	-0.04
	All environments	-2.67	< 0.01	-3.15	-2.19
		Ext	ractable	sucrose, kg	Mg ⁻¹
0	Fargo, 2006	7.66	0.01	3.46	11.87
	Crookston, 2006	3.10	0.08	0.15	6.07
	Crookston, 2007	2.94	0.05	0.51	5.37
	Prosper, 2007	0.94	0.63	-2.44	4.33
	Crookston, 2008	-1.23	0.54	-4.69	2.21
	All environments	2.39	0.04	0.48	4.30
90	Crookston, 2008	5.95	0.03	1.58	10.33
	Crookston, 2006	5.27	0.08	0.32	10.24
	Fargo, 2006	3.40	0.41	-3.55	10.35
	Prosper, 2007	1.56	0.59	-3.33	6.44
	Crookston, 2007	0.86	0.80	-4.87	6.60
	All environments	3.49	0.03	0.87	6.12

[†]Difference between roots that had canopies intact until harvest minus roots harvested on the same day that had been defoliated prior to a frost for all harvest dates following a damaging frost.

^{*}Significance level of difference; if P>0.10 then 90% Confidence Interval includes 0, indicating difference between the canopy treatments was not significant when averaged over all harvest dates following a frost.

intact until harvest, were not significant. Only 4 of the 18 within harvest date comparisons of respiration rates of roots 30, 60, and 90 DAH from plants defoliated prior to a frost with those from plants with canopies intact up until harvest were significant for roots from Crookston in 2007. The average respiration rate 30 and 90 DAH over all five harvest dates of roots of plants defoliated prior to a damaging frost was 0.46 and 0.37 mg $\rm CO_2~kg^{-1}~h^{-1}$ greater than the respiration rate of roots of plants with the canopy intact, respectively; the average difference 60 DAH was not significant (Table 2).

With one exception, differences between the respiration rates of roots harvested before a frost (-2 DAF) at Prosper in 2007 and roots harvested fewer than 10 d after a frost from plots with canopies intact until harvest were not significant 30, 60, and 90 DAH (Table 3). The one exception was the 60-DAH respiration rate of roots harvested 1 DAF. The respiration rates 30 and 60 DAH for all harvest dates of roots from plots defoliated prior to a frost were greater than the respiration rate of roots harvested prior to the frost (-2 DAF). Ninety days after harvest, differences between the respiration rate of roots harvested before a frost and roots harvested 0, 2, and 3 DAF from plots that had been defoliated prior to the initial frost were not significant. The respiration rate 30, 60, and 90 DAH of roots harvested 10 DAF, regardless of time of defoliation, were greater than the respiration rates of roots harvested prior to the initial frost (-2) DAF). The elevated respiration rates 10 d after the initial damaging frost probably were a response to minimum daily temperatures between -6 and -8°C for three of the five days preceding the 10-DAF harvest. The respiration rate of roots harvested 10 DAF from plots that had been defoliated prior to the initial frost was greater than the respiration rate of roots harvested 10 DAF from plots defoliated at harvest 30, 60, and 90 DAH. The differences between 10 of the 18 within harvest date comparisons of respiration rates of roots from plants defoliated prior to a frost with roots from plants with canopies intact up until harvest were significant (Table 3). For Prosper in 2007, the average respiration rate over all six harvest dates of roots of plants defoliated prior to a damaging frost was 1.80, 1.46, and 1.64 mg CO₂ kg⁻¹ h⁻¹ greater than the respiration rate of roots of plants with the canopy intact until harvest, 30, 60, and 90 DAH, respectively (Table 2).

With the exception of the 30-DAH respiration rate of roots harvested 3 DAF, differences between the roots harvested before a frost at Crookston in 2008 and roots harvested after a frost from plots with canopies intact until harvest were not significant 30, 60, and 90 DAH (Table 1). Differences between the respiration rates of roots harvested prior to the frost and roots harvested the morning following the damaging-frost (0 DAF) from plots that had been defoliated prior to the frost also were not significant 30, 60, or 90 DAH. However, on subsequent harvest dates the respiration rates of roots from plots defoliated prior to the frost were greater than the respiration rate of roots

harvested before the frost, with the exception of the 30-DAH respiration rate of roots harvested 2 and 3 d after the frost. The respiration rate of roots from plots defoliated prior to the frost was greater than the respiration rate of roots from plots with the canopy intact for 16 of 21 within harvest date comparisons (Table 1). The average respiration rate over all seven harvest dates of roots of plants defoliated prior to a damaging frost at Crookston in 2008 was 1.23, 3.02, and 5.51 mg $\rm CO_2~kg^{-1}~h^{-1}$ greater than the respiration rate of roots of plants with the canopy intact until harvest, 30, 60, and 90 DAH, respectively (Table 2).

Extractable sucrose

At harvest (0 DAH), the extractable sucrose concentration of roots from plots harvested prior to a frost ranged from 141 kg Mg⁻¹ for Fargo in 2006 (Table 3) to 177 kg Mg⁻¹ for roots from Crookston in 2008 (Table 1). In general, there were fewer significant differences in extractable sucrose concentration associated with harvest date or the presence or absence of the canopy than were observed for respiration rate. Of the 30 possible comparisons between plots with the canopy removed prior to a frost and those with the canopy intact until harvest, within a harvest date, only eight were significant; for six, the greater extractable sucrose concentration was associated with the canopy being intact until harvest and for two, the extractable sucrose concentration associated with the canopy being removed prior to a frost was greater. The average extractable sucrose concentration 0 DAH over all harvest dates of roots of plants defoliated prior to a damaging frost was 7.66, 3.10, and 2.94 kg Mg⁻¹ less than the extractable sucrose concentration of roots of plants with the canopy intact until harvest at Fargo and Crookston in 2006, and Crookston in 2007, respectively; average differences for Prosper in 2007 and Crookston in 2008 were not significant (Table 2).

The average decrease in extractable sucrose concentration during the 90 d in storage (90 DAH) ranged from 11 kg Mg⁻¹ for both Crookston in 2008 and Prosper in 2007 to 22 kg Mg⁻¹ for Crookston in 2006. Only seven of the 30 possible comparisons between the extractable sucrose concentration of plots with the canopy removed prior to a frost and those with the canopy intact until harvest, within a harvest date (DAF), were significant 90 DAH (Tables 1 and 3). In only two cases, (Fargo, 2006, 0 and 10 DAF) was this difference significant both at harvest (0 DAH) and after 90 d (90 DAH) in storage. The average extractable sucrose concentration 90 DAH over all harvest dates of roots of plants defoliated prior to a damaging frost was 5.27 and 5.95 kg Mg-1 less than the extractable sucrose concentration of roots of plants with the canopy intact until harvest at Crookston in 2006 and 2008, respectively; average differences for Crookston in 2007, Fargo in 2006, and Prosper in 2007 (Table 2) were not significant.

Table 3. Postharvest respiration rate 30, 60, and 90 days after harvest (DAH) and extractable sucrose concentration at harvest (0 DAH) and 90 DAH of roots of plants with canopies intact until harvest and roots of plants that had been defoliated (removed) prior to a frost, on multiple harvest dates following a damaging frost, Fargo, ND, 2006 and Prosper, ND, 2007. Averages for the prefrost harvest are highlighted in blue. Postfrost harvests that had the canopy removed prior to a damaging frost are highlighted in gray.

£7	Days	Canopy		Respiration rate						Extractable sucrose			
Year	after frost		30 I	DAH	60 D	АН	90 L	OAH	0 Г	АН	90	DAH	
				1	$ng\ CO_2\ k_b$	g-1 h-1				kg	Mg ⁻¹		
2006	-2		4.38	de*	4.56	cd	3.53	c	141	b-d	134	a	
	0	Intact	5.41	bc	7.34	a	4.26	bc	152	a	131	ab	
	0	Removed	5.22	cd	6.51	ab	4.76	bc	123	fg	110	de	
	3	Intact	4.80	с-е	4.84	cd	4.51	bc	145	ab	123	a-c	
	3	Removed	5.56	bc	4.88	cd	4.78	bc	142	bc	127	a-c	
	5	Intact	4.03	e	4.07	d	4.27	bc	132	d-f	104	e	
	5	Removed	5.39	c	5.54	bc	5.66	b	137	b-e	122	a-c	
	6	Intact	4.38	de	4.34	d	4.05	c	122	g	113	с-е	
	6	Removed	6.47	a	4.63	cd	5.55	b	131	e-g	116	b-€	
	10	Intact	5.05	cd	4.43	cd	4.36	bc	154	a	123	a-c	
	10	Removed	6.29	ab	6.08	b	7.26	a	134	с-е	102	е	
	Mean		5.18		5.20		4.82		138		119		

De
Defoliation
Prior
to Fr
F

2007	-3		2.05	orle	0.67		2.02	٦	150	a b	147	a la
2007	_		3.95	gh	2.67	g	3.03	d	150	ab		ab
	0	Intact	4.02	f-h	3.01	fg	3.08	d	157	a	132	cd
	0	Removed	6.30	bc	4.55	b-e	4.25	b-d	148	b	124	d
	1	Intact	4.79	d-g	4.13	c-f	3.47	b-d	154	ab	144	a-c
	1	Removed	5.28	c-f	5.25	bc	4.55	bc	153	ab	146	ab
	2	Intact	3.43	h	3.74	d-g	3.39	cd	155	ab	144	a-c
	2	Removed	5.41	b-e	4.85	b-d	4.08	b-d	153	ab	139	bc
	3	Intact	4.30	e-h	3.00	fg	3.09	d	150	ab	136	bc
	3	Removed	5.64	b-d	4.47	b-e	4.35	b-d	158	a	140	bc
	5	Intact	4.88	d-g	3.64	e-g	3.04	d	154	ab	153	a
	5	Removed	6.59	b	4.76	b-e	4.61	bc	157	a	155	a
	10	Intact	6.60	b	5.38	b	4.88	b	152	ab	145	ab
	10	Removed	9.60	a	7.81	a	8.92	a	147	b	140	bc
	Mean		5.45		4.40		4.21		153		142	

^{*}Within each year, differences among means within a column followed by the same letter are not significant, based upon LSD_{0.10}.

Table 4. Invert sugar concentration at harvest (0 DAH) and 90 days after harvest (DAH) of crowns and taproots of roots of plants with canopies intact until harvest and roots of plants that had been defoliated (removed) prior to a frost, on multiple harvest dates following a damaging frost, Fargo, ND, 2006 and Prosper, ND, 2007. Averages for the prefrost harvest are highlighted in blue. Postfrost harvests that had the canopy removed prior to a damaging frost are highlighted in gray.

T 7	Days	C		own	Taproot					
Year	after frost	Canopy	0 D	AH	90 D	AH	0 D	AH	90 D	AH
					Invert	sugai	; g (100g	S)-1		
2006	-2		0.29	c*	4.82	b	0.22	b	2.10	b
	0	Intact	4.65	a	2.08	b	5.08	a	2.11	b
	0	Removed	3.97	ab	6.02	b	5.15	a	3.30	b
	3	Intact	0.58	bc	1.86	b	0.37	b	0.25	b
	3	Removed	0.64	bc	5.58	b	0.53	b	0.23	b
	5	Intact	0.91	bc	2.73	b	0.43	b	0.39	b
	5	Removed	0.92	bc	6.85	b	0.76	b	0.34	b
	6	Intact	2.06	a-c	1.59	b	0.38	b	0.24	b
	6	Removed	0.52	c	5.26	b	0.32	b	0.35	b
	10	Intact	0.76	bc	5.89	b	0.44	b	9.57	a
	10	Removed	0.43	c	21.41	a	0.82	b	9.29	a
	Mean		1.43		3.78		1.32		2.56	

2007	-3		1.73	bc	0.74	е	1.12	a	1.14	bc
	0	Intact	0.83	c	0.77	e	0.62	a	0.87	c
	0	Removed	1.48	bc	2.90	b-d	0.90	a	1.12	bc
	1	Intact	1.66	bc	1.42	de	1.70	a	1.79	ab
	1	Removed	3.24	a	3.01	bc	2.01	a	1.27	bc
	2	Intact	0.92	bc	1.54	с-е	1.91	a	0.86	c
	2	Removed	0.74	c	1.75	b-e	0.93	a	1.15	bc
	3	Intact	1.93	b	1.85	b-e	1.20	a	1.20	bc
	3	Removed	1.54	bc	2.44	b-d	1.49	a	1.28	bc
	5	Intact	1.91	b	1.74	b-e	1.06	a	1.07	bc
	5	Removed	1.46	bc	3.07	b	0.89	a	1.26	bc
	10	Intact	1.17	bc	2.61	b-d	0.66	a	1.22	bc
	10	Removed	1.37	bc	5.60	a	0.70	a	2.28	a
	Mean		1.54		2.26		1.70		1.27	

^{*}Within each year, differences among means within a column followed by the same letter are not significant, based upon $LSD_{0.10}$.

Table 5. Invert sugar concentration at harvest (0 DAH) and 90 days after harvest (DAH) of crowns and taproots of roots of plants with canopies intact until harvest and roots of plants that had been defoliated (removed) prior to a frost, on multiple harvest dates following a damaging frost, Crookston, MN, 2006 - 2008. Averages for the prefrost harvest are highlighted in blue. Postfrost harvests that had the canopy removed prior to a damaging frost are highlighted in gray.

£7	Days	C	Crown				Taproot			
Year	after frost	Canopy	0 D	АН	90 D	AH	0 DA	АН	90 D	DAH
					Invert	sugar	, g (100g	S)-1		
2006	-2		0.43	b*	5.81	c	0.23	b	2.42	a-c
	0	Intact	0.50	ab	4.83	c	0.31	b	1.89	a-c
	0	Removed	0.56	ab	7.02	c	0.31	b	0.92	bc
	1	Intact	0.32	b	4.58	\mathbf{c}	0.19	b	0.46	c
	1	Removed	0.74	ab	7.32	c	0.18	b	0.52	c
	2	Intact	0.53	ab	3.73	c	0.24	b	0.78	bc
	2	Removed	0.77	ab	17.04	b	0.26	b	2.28	ab
	4	Intact	0.46	b	2.40	\mathbf{c}	0.23	b	1.06	bc
	4	Removed	0.69	ab	7.90	c	0.26	b	1.86	a-
	6	Intact	0.51	ab	4.93	c	0.24	b	2.78	ab
	6	Removed	0.55	ab	24.38	a	0.27	b	3.45	a
	10	Intact	0.30	b	3.59	c	0.70	a	1.06	bc
	10	Removed	1.21	a	18.51	ab	0.40	b	3.92	a
	Mean		0.58		8.64		0.29		1.84	

2007	-2		1.02	c	1.06	d	1.03	b	0.80	c	
2001	0	Intact	0.87	c	1.53	cd	0.71	b	1.10	bc	
	0	Removed	1.30	c	1.90	b-d	1.52	b	0.84	c	
	1	Intact	2.95	a	1.56	cd	1.63	b	1.14	bc	July-Dec. 2015
	1	Removed	1.33	bc	3.12	ab	3.10	a	2.66	a	l y-
	2	Intact	0.65	c	1.79	b-d	1.82	ab	1.27	bc	D
	2	Removed	0.91	c	2.21	b-d	1.33	b	1.39	bc	č.
	3	Intact	1.10	c	2.74	bc	0.67	b	1.93	ab	20
	3	Removed	0.81	c	4.20	a	1.05	b	1.66	bc	15
	4	Intact	2.73	a	1.79	b-d	1.10	b	1.38	bc	
	4	Removed	1.31	c	2.16	b-d	0.96	b	1.07	bc	
	5	Intact	2.24	ab	1.56	cd	1.71	b	1.02	bc	
	5	Removed	1.18	c	2.02	b-d	1.66		1.33	bc	
	Mean		1.41		2.13		1.40		1.35		Defoliation Prior to Frost
2008	-1		1.64	с-е	2.58	е	0.60	c	2.59	b	Ď.
	0	Intact	1.00	de	2.18	e	1.36	a-c	1.80	b	P
	0	Removed	3.00	a-c	18.38	a-d	2.47	ab	7.96	a	or
	1	Intact	2.57	a-d	4.43	de	2.63	a	0.94	b	to
	1	Removed	2.04	b-e	20.61	a-c	1.81	a-c	3.01	b	멑
	2	Intact	3.89	a	2.63	e	2.74	a	2.75	b	so.
	2	Removed	3.48	ab	7.76	с-е	1.44	a-c	3.53	b	+
	3	Intact	1.35	de	3.15	de	1.23	a-c	3.91	b	
	3	Removed	0.81	e	10.16	b-e	2.69	a	2.18	b	
	4	Intact	0.95	de	5.23	с-е	1.01	a-c	1.16	b	
	4	Removed	1.06	de	6.96	с-е	1.35	a-c	2.64	b	
	5	Intact	1.26	de	4.62	de	1.38	a-c	2.74	b	
	5	Removed	1.12	de	28.24	a	1.56	a-c	3.97	b	
	6	Intact	1.77	с-е	2.43	e	1.15	a-c	0.79	b	
	6	Removed	0.83	e	24.42	ab	0.77	bc	1.49	b	21
	Mean		1.78		9.58		1.61		2.77		•

^{*}Within each year, differences among means within a column followed by the same letter are not significant, based upon $LSD_{0.10}$.

Table 6. Average differences between invert sugar concentration of crowns and taproots at harvest (0 DAH) and 90 days after harvest (DAH) of roots from plants with their canopies intact until harvest and roots from plants that had been defoliated prior to a frost for all postfrost harvest dates, Crookston, MN, 2006 - 2008, Fargo, ND, 2006, and Prosper, ND, 2007.

Days			Confidence Interval $_{(0)}$								
after harvest	Location / year	Difference [†]	P ‡	Lower limit	Upper limit						
		Invert s	ugar in	crowns, g ((100g S) ⁻¹						
0 DAH	Crookston, 2006	-0.32	0.08	-0.62	-0.02						
	Prosper, 2007	-0.23	0.91	-0.67	0.20						
	Crookston, 2008	0.06	0.86	-0.56	0.69						
	Fargo, 2006	0.50	0.57	-1.02	2.02						
	Crookston, 2007	0.60	0.01	0.22	0.98						
	All environments	0.11	0.57	-0.21	0.43						
90 DAH	Crookston, 2008	-13.12	< 0.01	-19.07	-7.18						
	Crookston, 2006	-9.75	< 0.01	-12.52	-6.97						
	Fargo, 2006	-6.20	< 0.01	-8.58	-3.81						
	Prosper, 2007	-1.47	< 0.01	-2.08	-0.87						
	Crookston, 2007	-0.77	0.03	-1.36	-0.19						
	All environments	-6.49	< 0.01	-8.27	-4.72						
		Invert s	ugar in	taproots, g	(100g S)-1	!					
0 DAH	Crookston, 2007	-0.33	0.31	-0.87	0.21						
	Fargo, 2006	-0.18	0.87	-1.96	1.60						
	Crookston, 2008	-0.08	0.84	-0.75	0.59						
	Prosper, 2007	0.04	0.91	-0.53	0.61						
	Crookston, 2006	0.04	0.54	-0.07	0.14						
	All environments	-0.10	0.59	-0.40	0.20						
90 DAH	Crookston, 2008	-1.53	0.09	-2.99	-0.07						
	Crookston, 2006	-0.91	0.09	-1.80	-0.02						
	Prosper, 2007	-0.22	0.24	-0.54	0.09						
	Fargo, 2006	-0.19	0.87	-2.17	1.78						
	Crookston, 2007	-0.18	0.43	-0.57	0.20						
	All environments	-0.65	0.01	-1.08	-0.22						

[†]Difference between roots that had canopies intact until harvest minus roots harvested on the same day that had been defoliated prior to a frost for all harvest dates following a damaging frost.

^{*}Significance level of difference; if P>0.10 then 90% confidence Interval includes 0, indicating difference between the canopy treatments was not significant when averaged over all harvest dates following a frost.

Invert sugar

The 5-environment mean invert sugar concentration of taproots and crowns of roots harvested before a damaging frost and processed immediately (0 DAH) was 0.64 (CI₉₀: 0.40 - 0.88, n = 15) and 1.02 g (100 g S)-1 (CI₉₀: 0.71 - 1.34), respectively. Corresponding invert sugar concentrations of roots harvested before a frost and stored for 90 d (90 DAH) were 1.81 (CI_{90} : 1.25 – 2.37) and 3.00 g (100 g S)⁻¹ $(CI_{90}: 1.77 - 4.24)$ for taproots and crowns, respectively. The average invert sugar concentration of the crowns of all roots harvested after a frost and processed immediately after harvest (0 DAH) was 1.39 g $(100 \text{ g S})^{-1}$ (CI₉₀: 1.21 – 1.56, n=180); 1.4 times the invert sugar concentration of crowns of roots harvested prior to a frost and processed immediately. After storage for 90 d, the average invert sugar concentration of crowns of all roots harvested after a damaging frost was $6.04 \text{ g} (100 \text{ g S})^{-1} (\text{CI}_{90}: 5.01 - 7.07); 4.3 \text{ times the concentration of}$ crowns of roots harvested after a frost but processed immediately and 2.0 times the concentration of crowns of roots harvested before a frost and stored for 90 d. The average invert sugar concentration of the taproots of all the roots harvested after a frost from all environments and processed at harvest (0 DAH) was 1.21 g (100 g S)-1 (CI₉₀:1.01 - 1.41,); 1.9 times the invert sugar concentration of taproots of roots harvested prior to a frost and processed immediately. After storage for 90 d, the invert sugar concentration of taproots of all roots harvested after a damaging frost was $1.98 \text{ g} (100 \text{ g S})^{-1} (\text{CI}_{90}: 1.66 - 2.29);$ 1.6 times the concentration of taproots of roots harvested after a frost but processed immediately and 1.1 times the concentration of taproots of roots harvested before a frost and stored for 90 d.

Only a few of the differences in invert sugar concentrations of taproots or crowns at harvest (0 DAH) associated with harvest dates or the presence or absence of a canopy were significant (Tables 4 and 5). With one notable exception, trends related to harvest date and or canopy treatment were not apparent. The invert sugar concentration of the taproots of roots harvested the morning after a damaging frost (0 DAF) from Fargo in 2006 and processed immediately (0 DAH) were greater that the concentrations of taproots of roots harvested before a frost and roots harvested on subsequent harvest dates (Table 4). The invert sugar concentration of the corresponding (0) DAH) crowns from plots with the canopy intact until harvest was also greater than all other harvest dates and canopy treatments. The average difference between the invert sugar concentration of crowns from plots with the canopy intact and crowns from plots defoliated prior to a frost 0 DAH was significant for only two environments, Crookston in 2006 and 2007 (Table 6). Average differences in invert sugar concentration of taproots from plots with the canopy intact until harvest and plots that had been defoliated prior to a frost 0 DAH were not significant for any of the five environments sampled (Table 6).

Ninety days after harvest, differences between the invert sugar

concentration of crowns of roots harvested before a frost and those harvested after a frost were significant for 17 of the 60 possible comparisons (Tables 4 and 5). In contrast, only four of the differences between the invert sugar concentration of taproots of roots harvested before a frost and taproots of roots harvest after a frost were significant, 90 DAH.

For 13 of the 30 within harvest date comparisons the invert sugar concentration of crowns of roots from plots that had been defoliated prior to a frost was greater than the invert sugar concentration of crowns of root harvested the same day from plots with the canopy intact until harvest. The contrast between the invert sugar concentration of crowns from plots with the canopy intact until harvest and crowns from plots defoliated prior to a frost 90 DAH was significant in all five environments, ranging from 13.12 g (100 g S)-1 for Crookston in 2008 to 0.77 g (100 g S)-1 for Crookston in 2007 (Table 6). The difference between the invert sugar concentration of taproots from plots with the canopy intact until harvest and taproots from plots defoliated prior to a frost 90 DAH was smaller than that observed for crowns and significant in only two environments, Crookston in 2006 and 2008.

DISCUSSION AND CONCLUSIONS

When all five environments and all post-frost harvest dates were included, the average respiration rates of roots harvested from plots that had been defoliated prior to a damaging frost were 1.30, 1.52, and 2.67 mg $\rm CO_2\,kg^{-1}\,h^{-1}$ greater than the postharvest respiration rates of roots harvested on the same day that had their canopies intact until harvest, 30, 60, and 90 d after harvest, respectively (Table 2). Furthermore, the lower respiration rate of roots from plots with the canopies intact until harvested, compared to roots from plots with the canopies removed prior to a frost, was significant in each of the five environments, 30 and 90 DAH and four of the five environments 60 DAH. The respiration rate of roots from plots that had been defoliated prior to a frost was significantly higher than the respiration rate of roots from plots with the canopies intact until harvest for 21, 18, and 14 of the 30 within harvest date comparisons, 30, 60, and 90 DAH, respectively (Table 1 and 3).

The average respiration rate of all roots harvested before a frost was $4.25~(\mathrm{CI}_{90};~3.89-4.60,~n=15),~3.93~(\mathrm{CI}_{90};~3.46-4.40),$ and $3.55~\mathrm{mg~CO}_2~\mathrm{kg^{-1}~h^{-1}~(CI}_{90};~3.23-3.87),~30,~60,}$ and 90 DAH, respectively. Thirty days after harvest, roots harvested after a frost from plots with the canopy intact until harvest had an average respiration rate of $4.76~\mathrm{mg~CO}_2~\mathrm{kg^{-1}~h^{-1}~(CI}_{90};~4.59-4.93,~n=90),~1.1$ times the respiration rate of roots harvested prior to a frost. Sixty and 90 d after harvest, the average respiration rates of all roots harvested after a frost from plots with the canopy intact until harvest was $4.88~(\mathrm{CI}_{90};~4.64-5.12)$ and $4.36~\mathrm{mg~CO}_2~\mathrm{kg^{-1}~h^{-1}~(CI}_{90};~4.26-4.61),~approxi-$

mately 1.2 times the corresponding respiration rate of roots harvested before a frost and stored for 60 or 90 d. The respiration rate of roots harvested after a frost from plots that had the canopy intact until harvest was greater than the respiration rate of roots harvested before a frost for all but ten of the 90 comparisons in Tables 1 and 3. However, the difference was significant for only 24 of the 90 comparisons. Twelve of the 24 significant differences occurred in comparisons of roots from Crookston in 2007.

Differences in extractable sucrose concentration between harvest dates or the presence or absence of a canopy prior to a damaging frost did not necessarily correspond to differences in respiration rate nor follow any consistent pattern. When averaged over all five environments and harvest dates, the average extractable sucrose concentration of roots harvested from plots that had been defoliated prior to a damaging frost were 2.39 and 3.49 kg Mg⁻¹ less than the extractable sucrose concentration of roots harvested on the same day that had their canopies intact until harvest, 0 and 90 d after harvest, respectively (Table 2). However, the increased extractable sucrose concentration of roots from plots with the canopies intact until harvested, compared to roots from plots with the canopies removed prior to a frost, was significant in only three environments at harvest and two ninety days later. The time between the initial harvest and the final harvest ranged from 7 d for Crookston in 2007 and 2008 to 13 d for Prosper in 2007. During this time between harvests, extractable sucrose concentration may have increased, decreased, or remained relatively constant, depending upon conditions at the site and the presence or absence of a canopy when the frost occurred. Furthermore, changes in moisture conditions between harvest dates may have impacted extractable sucrose concentration based upon fresh weight at harvest.

Significant differences among the invert sugar concentration of crowns or taproots due to the time between a frost and harvest or the presence or absence of a canopy at the time of a frost were generally small and infrequent when roots were processed immediately after harvest (0 DAH). The 0.32 g (100 g S)-1 average increase in invert sugar concentration of crowns of roots harvested from plants that were defoliated prior to a frost at Crookston in 2006 was the only average increase in invert sugar that was attributable to the absence of a canopy at the time of a frost that was significant for either crowns or taproots, 0 DAH (Table 6). The average invert sugar concentration of crowns and taproots across all environments and treatments 0 DAH was 1.35 and 1.26 g (100 g S)-1, respectively. In contrast, the average concentration of crowns and taproots 90 DAH was 5.27 and 1.95 g (100 g S)-1, respectively, indicating that most of the increase in invert sugar accumulation in response to a damaging frost occurs in the crowns. The difference in the invert sugar concentration between crowns from plants that had been defoliated prior to a frost and crowns of plants with the canopy intact until harvest that

had been stored for 90 d was significant in all five environments and the average of all locations and treatments (Table 6). The five-environment average increase in the invert sugar concentration of crowns due to defoliation prior to a frost was 6.49 g (100 g S)-1 while average individual environment increases ranged from 0.77 g (100 g S)-1 at Crookston in 2007 to 13.12 g (100 g S)-1 for Crookston in 2008. Ninety days after harvest, the five-environment average increase in the invert sugar concentration of taproots attributable to defoliation prior to a frost was 0.65 g (100 g S)-1, one tenth the invert sugar increase of comparable crowns (Table 6).

Sugar companies recommend that the time between defoliation and harvest be short even under favorable harvest conditions and warn growers to be especially vigilant about allowing defoliated plants to be subjected to a frost prior to harvest (Dean and Millard, 2009; Poindexter and Wenzel, 2013). While the magnitude of the detrimental effects of allowing defoliated roots to freeze may vary from environment-to-environment (Fig. 4), the results summarized in this report (Tables 2 and 6) point out that removal of the canopy prior to a frost almost always has a negative impact on extractable sucrose and processing quality and increases postharvest respiration rate. Furthermore, the negative impact of the damage to roots exposed to frost prior to harvest tends to increase as the time in storage increases. In a storage pile where healthy and frost-damaged roots are mixed, the temperature increases due to the elevated respiration

Figure 4. Longitudinal sections through frost damaged roots illustrating the variability in response to frost. (a) Root of a defoliated plant three days after the initial damaging frost at Crookston, 2006, (b) frost-damaged roots from Crookston after 90 d in storage, 2006, and (c) frost-damaged root from Fargo after 90 days in storage, 2006.







rates of the damaged roots would increase the respiration and inversion rates, and accelerate microbial activity of both the damaged roots and the surrounding healthy roots. The magnitude of the detrimental effects of the damaged roots on nearby healthy roots would depend on the extent to which heat is dissipated from the pile. The samples upon which the relationships observed in this report are based were stored in a refrigerated room with fans for circulation. These favorable storage conditions would minimize contrasts between healthy and frost-damaged roots to the extent it negates temperature increases associated with elevated respiration rates in storage piles.

The detrimental impact of frost on plants defoliated prior to harvest is widely recognized among agriculturalists and processors in regions in which frost during harvest is a threat. However, knowing when, after a frost, to resume harvesting fields with canopies intact at the time of a frost is often problematic. Post-frost harvest recommendations are often based upon a widely held assumption that, at least, some 'healing' occurs if temperatures remain above freezing for 48 hours or more after the damaging frost (Barbier, et al., 1982; Griffel, 2000). Conditions during the 2006 Crookston harvest (Table 1) were assumed to be favorable for healing. This also was suggested in the 30 and 60-d respiration rates of roots with the canopy intact until harvest from Crookston in 2006. Respiration rates appeared to have been initially elevated in response to the frost and then decreased for the later harvest dates but generally remained higher than roots from the before-frost harvest (Griffel, 2000). Similar patterns were suggested in the 30 and 60-d respiration rates of the roots with canopies intact until harvest from Fargo in 2006. Observations from these trials provided very limited insight into the healing process or when frozen roots should be harvested. Agriculturalists will need to continue to rely on experience, the probability of additional freezing temperatures, and the appearance of root sections to determine when to resume harvest after a damaging frost (Griffel, 2000). If the area impacted by a frost event is extremely small, immediately harvesting and processing the roots may be a viable alternative (Milford et al., 2002; Kenter and Hoffman, 2006).

ACKNOWLEDGEMENTS

We thank Nyle Jonason, Joe Thompson, John Eide, Jeff Nelson, Todd Cymbaluk, and Norman Cattanach for technical assistance. Trade, firm, or corporate names are mentioned to disclose information that may be of interest to the reader. Such use does not constitute an endorsement by the Agricultural Research Service or the University of Minnesota of any product to the exclusion of others that may be equally suitable or superior. USDA is an equal opportunity provider and employer.

LITERATURE CITED

- Barbier, H., F. Nalin, and J. Guern. 1982. <u>Freezing injury in sugar</u> beet root cells: sucrose leakage and modifications of tonoplast properties. Plant Sci. Letters 26: 75-81.
- Campbell, L.G., K.K Fugate, and W.S. Niehaus. 2011. <u>Fusarium yellows affects postharvest respiration rate and sucrose concentration in sugarbeet.</u> J. Sugar Beet Res. 48: 17-39.
- Campbell, L.G., and K.L. Klotz. 2006. Storage. p. 387-408. In: A.P Draycott (ed.) Sugar Beet, Blackwell Publishing, Inc, Oxford.
- Carmer, S.G. 1976. Optimal significance levels for application of the Least Significant Difference in crop performance trials. Crop Sci. 16:95-99.
- Chew, V. 1976. Comparing treatment means: a compendium. HortScience 11: 348-357.
- Cole, D.F. 1983. Effect of freezing on sugarbeet storage losses. 1982 Sugarbeet Res. Ext. Rept., Coop. Ext. Serv. North Dakota State Univ., Fargo, ND: 13:164-165.
- Dean, G.A., and C.W, Millard. 2009. Sugarbeet tops insulate roots from daytime heat and nighttime freezing temperatures. J. Sugar Beet Res. 46: 59-60.
- De Bruijn, J.M. 2000. Processing of frost-damaged beets at CSM and the use of dextranase. Zuckerindustrie 125: 898-902.
- Dexter, S.T., M.G. Frakes, and F.W. Snyder. 1967. A rapid and practical method of determining extractable white sugar as may be applied to the evaluation of agronomic practices and grower deliveries in the sugar beet industry. J. Am. Soc. Sugar Beet Technol. 14: 433-454.
- Dutton, J., and T. Huijbregts. 2006. <u>Root quality and processing</u>. p. 409-422. In: A.P Draycott (ed.) Sugar Beet, Blackwell Publishing, Inc, Oxford.
- Giffel, M. 2000. What are the effects of frost on sugarbeets in storage? Sugar Producer: (November) 8-9.
- Halden, H.E. (revised by M. Bolinder). 1982. Microbiology and plant sanitation. p. 723-740. In: R.A. McGinnis (ed.) Beet-Sugar Technology, 3rd ed. Beet Sugar Development Foundation, Denver. CO.

- Harvey, C.W., and J.V. Dutton. 1993. p. 571-617. Root quality and processing. In: D.A. Cooke and R.K. Scott (eds.) The Sugar Crop, Chapman and Hall, London.
- Kenter, C., and C. Hoffman. 2006. Quälitatsveränderungen bei der lagerung frostgeschädigter zuckerrüben in abhängigkeit von temperature und sorte. Zuckerindustrie 131: 1-12. (English abstract).
- Klotz, K.K., and D.N. Martins. 2007. Microplate assay for rapid determination of sucrose, glucose, fructose, and raffinose. J. Sugar Beet Res. 44: 169-170.
- McGinnis, R.A. 1982. Analysis of sucrose content. p. 67-76. In: R.A. McGinnis (ed.) Beet Sugar Technology, 3rd ed. Beet Sugar Development Foundation, Denver, CO.
- Milford, G., M. Armstrong, and M. Patchett. 2002. Frost damage to sugar beet estimating the risk. Brit. Sugar Beet Rev. 70(3): 41-45.
- Oldfield, J.F.T., J.V. Dutton, and H. J. Teague. 1971. The significance of invert and gum formation in deteriorated beet. Internat'l. Sugar J. 73: 3-8, 35-40, 66-68.
- Poindexter. S.S., and T.J. Wenzel. 2013. <u>Comparison of temperature changes in defoliated and non-defoliated sugarbeets.</u> J. Sugar Beet Res. 50: 38.
- Smith, J.A. 2001. Sugarbeet harvest. p. 179-188. In R.G, Wilson, J.A. Smith, and S.D. Miller (ed.) Sugarbeet Production Guide. Univ of Nebraska Coop. Ext. Serv. EC101-156.
- Yonts, C.D., R.M. Harveson, L. Panella, and L.E. Hanson. 2009. Other disorders. p. 85-91. In R.M. Haverson, L.E.Hanson, and G.L. Hein (ed.) Compendium of Beet Diseases and Pests. Am. Phytopathological Soc. St. Paul, MN.