Water Potential Gradients Imply an Apoplastic Separation Between Red Beet Storage Organ Sink Regions and the Central Xylem.

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ABSTRACT

The factors that contribute to the accumulation of sucrose in the storage organs of red beet (*Beta vulgaris* L.) are of interest in that they may reveal how sugar beet achieves high sucrose accumulation. Components of the water potential in the parenchyma tissue in the storage organ, in the petiole, and in the xylem solution were examined. The water potential of the parenchyma tissue of the storage organ was 0.56 MPa more negative than that of the xylem solution passing through the storage organ. Dye introduced to the xylem via the tap root predominantly moved up through the central xylem core of the storage organ and not through the xylem of the outer rings. From correlation analyses, it is concluded that the water potential and sucrose concentration of the storage organ were more closely associated with the diameter of the storage parenchyma cells than were the ring width or the number of cells across the ring. These results are consistent with the presence of an apoplastic separation between the central xylem apoplast and the storage parenchyma tissue, and this may be an important factor in sucrose accumulation in this storage sink.

Key Words: *Beta vulgaris* L., apoplast, parenchyma tissue, sucrose.

Identification of factors that limit the accumulation of sucrose in the storage organ of beet (*Beta vulgaris* L.) is an issue of continuing interest. A study of sucrose accumulation in sugarcane by Welbaum and coworkers (1992) suggests that a separation of the apoplast of the storage tissue from the xylem apoplast contributes to the ability of sugarcane to accumulate sucrose. This separation results in both water potential and sucrose concentration gradients between the storage tissue apoplast and the xylem apoplast. Previous studies examining factors that limit sucrose accumulation in beet have not addressed this point, and instead have examined the possible influence of ring width and the size of the storage parenchyma cells (Meissner and Spanswick, 1994; Milford and Watson, 1971). In this report, estimates of the water potential components of the xylem sap and of storage parenchyma tissue as well as experiments involving dye flow are used to assess if the apoplast of the beet storage organ is continuous or divided.

In beet, as in some other storage sinks (Wolswinkel, 1990; Beruter, 1989; Moore and Cosgrove, 1991), sugars and other osmotica are unloaded from the phloem into the non-living space of the storage tissue which includes the cell wall and intercell wall spaces. This part of the tissue is called the apoplast (Tomos et al., 1992; Canny, 1995), distinguishing it from the living protoplasmic space of the tissue. In the case of beet, the storage organ is a modified hypocotyl (Artschwager, 1926). Beet storage parenchyma cells have been reported to have low levels of plasmodesmatal connections from cell to cell, suggesting that movement of sucrose through this tissue is likely to occur through the apoplast (Zamski, 1986). Results from other studies have suggested that sucrose in the storage tissue apoplast is able to move easily through it (Richter and Ehwald, 1983; Lemoine et al. 1988) and without being cleaved (Giaquinta,1977). Apoplastic accumulation of osmotica should cause the water potential of the storage tissue to become more negative, and thus the water potential maintained in the storage tissue should influence the strength of this storage sink.

To my knowledge, no previous work examines whether the xylem present in the vascular rings of the beet storage organ contributes significantly to the transpirational stream. If the xylem in the outer vascular rings is fully functional then it would be difficult to envision a strong apoplastic separation of the storage tissue apoplast from the xylem apoplast. Conversely, if only the xylem in the central strand of the storage organ is involved in transpiration then it may be possible for the storage tissue apoplast to be distinct from that of the functional xylem apoplast. Previous studies have not examined this issue, but have examined the ringed vascular and parenchyma tissue layers of beets (Artschwager, 1926; Zamski and Azenkot,

1981*a*). Others have focused on the functioning of the phloem, and how the photoassimilates supplied by the leaves are delivered to parts of the storage organ (Belikov and Kostetskii, 1964; Joy, 1964; Stein and Willenbrink, 1976; Zamski and Azenkot, 1981*b*). The possible influence of the xylem on sink strength has not been examined.

MATERIALS AND METHODS

Red beet (*Beta vulgaris* L., hybrid Red Ace, Agway, Syracuse, N.Y.) was grown in a greenhouse to 98 days after planting in Ithaca, N.Y. Plants were harvested from June to August, and grown under conditions similar to those described previously (Meissner and Spanswick, 1994). Upon harvest, the storage organ fresh weight, density, diameter, the width of the second intervascular ring (counting outward) and of 200 of its parenchyma cells at the point of largest diameter of the storage organ examined in cross section were recorded for each of 23 beets. Sucrose was extracted from the parenchyma tissue plugs of three millimeter diameter and up to ten millimeter length by placing them in 70% ethanol. The ethanol was evaporated and the sucrose content was estimated by the anthrone method (Van Handel, 1968). Cellular osmolarity was calculated as described previously by measuring the vacuole to cell diameter ratios of 200 paired measurements using hand sections of storage parenchyma tissue from the second intervascular ring in cross section when placed in 2000 moles m^{-3} sorbitol (Meissner and Spanswick, 1994). The cell diameters and osmolarities of parenchyma cells cut in cross section from the central region of petioles were also recorded. For further details concerning plant growth conditions and sucrose or cellular osmolarity estimation see Meissner and Spanswick (1994).

The water potential of storage parenchyma tissue was estimated using the percent change in fresh weight of either blotted tissue plugs (3 mm in diameter by 10 mm long), or sections of petiole of similar size, after 20 min in a series of concentrations of sorbitol solutions differing in 25 moles m^{-3} steps, and extrapolated to find the water potential via the solution that would give no change in fresh weight (Salisbury and Ross, 1992). The water potential gradient between the different parenchyma tissue rings of the storage organ was tested by placing 24 plugs of tissue from the first, second and third intervascular rings in 600 moles m^{-3} sorbitol for 20 min. This was replicated using tissue plugs from the storage organs of three beets. In this case, for each ring, tissue plugs were taken from a point parallel to the fibrous root axis, and at 45° intervals around the storage organ. The percent change in fresh weight of each plug was calculated and comparisons made between the rings, angular positions, and different storage organs by analysis of variance (Mendenhall, 1975).

Components of water potential for isolated cell, xylem, and apoplastic saps were compared using six beet plants that had been well watered and shielded with clear plastic in dim light for two hours before harvest. The pressure necessary to force the xylem sap out of the exposed end of a detached leaf, for each of three leaves per plant, was estimated using a pressure bomb. Xylem sap was collected by placing a freshly harvested storage organ, sliced at both the tap root below the storage organ and at the base of the petioles, in a pressure bomb with the tap root extending up out of the pressure chamber. Application of 0.15 MPa of pressure forced several hundred microliters of clear solution out of the exposed tap root and the solution was collected into microcapillary tubes for analysis. Cell sap from the storage parenchyma tissue of the second innermost intervascular ring was collected by freezing tissue plugs; then after thawing, the tissue was spun at 1000 x g in a clinical centrifuge to give the cell sap.

Collection of the apoplastic solution from the storage parenchyma tissue was attempted by taking parenchyma tissue plugs, giving a 2 sec dip in 2000 moles m^{-3} sorbitol, blotting dry, and then spinning at 1000 x g in a clinical centrifuge for 20 min (Moore and Cosgrove, 1991). The survival of cells through the centrifugation was confirmed by observation of cyclosis in the parenchyma cells after centrifugation of each tissue plug. Betalaine concentrations in the samples were estimated by the absorbance measured at 537 nm using one hundred-fold dilutions and an extinction coefficient of 6200 L $mole^{-1}$ cm^{-1} (Leigh et al., 1979). The osmolarity of the xylem, cell, and apoplastic saps was determined by use of a freezing point osmometer (Fiske One-Ten Osmometer, Needham Hghts, MA).

For neutral sugar analysis, appropriate dilutions of the sap samples were first passed through BioRad AG50W and AG1 cation and anion membrane filters, dried, and rehydrated to original volume. These samples were then injected into a Waters SugarPak 1 column (Milford, MA) for high performance liquid chromatography (Turgeon et al., 1993). Retention times and peak heights, as indicated using a Waters model 410 differential refractometer, were compared to known sugar standards to allow estimation of the amounts of each sugar present. Total cation analysis of the sap samples was done by atomic emission spectrophotometry.

To examine the pathway of water flow through the plants, detached leaves cut at the base of the petiole, or plants cut at the tap root, were placed in a 0.1% toluidine blue solution for 3, 8, or 24 hours. Two plants, and two detached leaves from each, were examined at each time point. To assess the flow of solution through the xylem in the storage organ, beets were sliced at the tap root, three to five centimeters below the storage organ, or in cross section through the storage organ at its greatest diameter, and the cut surfaces were immersed to 1 cm depth in the dye solution. All

slicing was done under water to avoid cavitation in the xylem. The extent of dye movement was determined by examination of hand sections viewed under a microscope.

In gathering the data for the analysis given in Table 4, 23 storage organs were examined. These storage organs had an average fresh weight of 125.6 g (se = ± 9.3 g), a diameter at their thickest point of 56 mm (se = ± 2 mm), and a density of 1.064 g mL^{-1} (se = ± 0.007 g mL^{-1}). The average width of the second intervascular ring was 7 mm (se = ± 0.4 mm). Division of the width of the second intervascular ring by the average radial parenchyma cell diameter for that storage organ gave an estimate of the number of cells radially across this ring of 73.7 cells (se = ± 3.4). The presence of a significant correlation, either positive or negative, between the items compared in Table 4 was determined by an N-test of the slope compared to zero (Mendenhall, 1975).

RESULTS

The average water potential of the petiole sections, which in cross section have a central region of parenchyma tissue, taken from four beet plants was slightly more positive than that of storage parenchyma tissue plugs from the second intervascular ring (Table 1). The extractable concentration of sucrose in the petiole segments was much lower than that found in the storage parenchyma tissue; 1.9 versus 95.2 mg g^{-1} fresh weight respectively. However, the petiole parenchyma cells had a higher cellular osmolarity than parenchyma cells from the storage tissue; 593.1 versus 479.2 moles m^{-3}. The combination of slightly higher water potential and higher cellular osmolarity gives a higher estimate of turgor in the parenchyma cells of the petiole, 0.51 MPa, compared to that in parenchyma cells of the storage organ, 0.12 MPa.

To test for a gradient of water potential from the inner to outer intervascular rings, the change in terms of percent fresh weight of storage parenchyma plugs placed in 600 moles m^{-3} sorbitol for 20 min was measured. Storage organs from three plants were used. The analysis of variance of the results (Table 2) indicates significant differences among the three storage organs tested, and among the angular positions within the storage organ. However, differences in the percent change in fresh weights of the samples taken from different intervascular rings were not great enough to suggest a significant difference at the 95% confidence level.

Given the negative water potential of the storage parenchyma tissue (Table 1), an attempt was made to isolate parenchyma cell and apoplastic sap, as well as xylem sap from six beet plants so that a comparison of the water potential components could be made. For each of the six plants,

Table 1. Average water potential, isotonic concentration, parenchyma cell size, cell osmolarity, calculated cell turgor pressure, and extractable sugar contents of red beet parenchyma tissue from the second intervascular ring of the storage organ, or from petiole segments. All plants were harvested at 98 days after planting. Mean values are given for petiole segments from four plants, and for storage parenchyma tissue from 23 plants, as well as the standard errors of the means.

Item Measured	Petiole Segments (mean, ±SE, n=4)	Storage Parenchyma Tissue (mean, ±SE, n=23)
Water Potential (MPa)	-0.96 (±0.04)	-1.06 (±0.03)
Isotonic Concentration of Tissue (moles m^{-3})	390.2 (±18.6)	427.8 (±12.1)
Parenchyma Cell Diameter (μm)	121.9 (±3.1)	98.2 (±2.6)
Parenchyma Cell Osmolarity (moles m^{-3})	593.1 (±59.2)	479.2 (±16.9)
Calculated Turgor of Parenchyma Cells† (MPa)	.051 (±0.15)	0.12 (±0.04)
Extractable Sucrose (mg g^{-1} fresh weight)	1.9 (±1.3)	95.2 (±5.6)

†Turgor estimated for each sample by subtraction of the cell osmotic pressure (based upon the cell osmolarity) from the water potential.

three detached leaves were placed one at a time in a pressure bomb. The average pressure necessary to express xylem sap was determined to be 0.37 MPa (se = ± 0.042 MPa). The average osmolarity of the xylem sap, 69.0 moles m^{-3}, was much lower than the sink apoplastic sap, 445.0 moles m^{-3}, which was itself lower than the osmolarity of the cell sap, 671.0 moles m^{-3} (Table 3). Most of the osmolarity of the xylem sap can be accounted for by ions, with neutral sugars comprising only 3.3 moles m^{-3}. The parenchyma cell sap was different from the xylem sap in that it had higher concentrations of both neutral sugars and of total cations. These results suggest that a much more positive water potential was present in the xylem solution than in either the petiole or storage organ parenchyma tissue (Table 1).

Table 2. Analysis of variance in which storage parenchyma tissue of the red beet storage organ, taken in cross section and sampled at 45° increments, is examined. The percent change in the fresh weight of parenchyma tissue plugs placed in 0.6 M sorbitol for 20 min was measured for 24 tissue plugs taken from the first, second, and third intervascular rings from each of three plants.

Items in ANOVA Analysis	Degrees of Freedom	Sums of Squares	Mean Squares	F Values
Intervascular Rings	2	0.383	0.191	0.856
Angular position in Storage Organ	3	18.2	6.08	27.2*
Plants	2	111.2	55.6	248.6*
Error	63	14.1	0.223	-
Total	71	144.0	-	-

* Significant difference at ≥ 95% confidence level.

The results from attempts at isolation of apoplastic solution from the storage parenchyma tissue were ambiguous. All of the concentrations of sugars and most of the ions present in the parenchyma apoplastic sap samples evidently lie between the values measured in the cell and the xylem sap (Table 3). This implies that leakage of contents from the cells may have contaminated the sample. This conclusion is supported by the high concentration of betalaine found in the apoplastic sap. Betalaine is believed to be found only in the vacuole of these storage parenchyma cells, not in the tissue apoplast. If the betalaine is assumed to be a valid indicator of contamination, then the concentrations that would be implied by its presence in the apoplastic sample can be calculated (Table 3). Arguing against contamination are two observations. The putative apoplastic sap shows an osmolarity that is consistent with the negative water potential of the storage tissue. Also, concentrations of some elements deviate from those that would be expected if contamination from the cells were the sole source in this sample. Specifically, the potassium, magnesium, sodium, copper, sulphur, and total cation concentrations are lower than would be expected, while the calcium and boron concentrations are higher than expected.

Table 3. Average contents and standard error of the mean of parenchyma cell and apoplastic sap, and xylem sap from six red beet plants. Cell sap and apoplastic sap were isolated from parenchyma tissue of the second intervascular ring of the storage organ. Betalaine levels were estimated by absorption readings of sap dilutions. The expected apoplastic concentrations were calculated assuming contamination of xylem sap by cell sap similar to that indicated by the betalaine levels.

		Cell Sap		Apoplastic Sap			Xylem Sap	
Items Measured		Mean	SE	Mean	SE	Expected	Mean	SE
Total Osmolarity(moles m^3)		671.0	(62.0)	445.0	(63.5)	406	69.0	(12.1)
Neutral Sugars (moles m^3)	Sucrose	194.4	(19.9)	101.7	(10.9)	110	1.7	(0.7)
	Glucose	15.0	(6.3)	5.9	(1.2)	8.8	0.9	(0.2)
	Fructose	nd†	-	nd	-	-	0.7	(0.1)
	Total	209.4	(20.9)	107.6	(11.0)	119	3.3	(0.7)
Cations (moles m^3)	K	163.1	(11.0)	49.8	(4.8)	100	20.6	(4.0)
	P	16.9	(1.1)	8.0	(0.5)	10	1.9	(0.4)
	Ca	0.32	(0.05)	1.80	(0.09)	0.5	0.75	(0.14)
	Mg	11.9	(1.1)	7.5	(0.7)	10	6.5	(1.4)
	Na	5.5	(0.7)	3.2	(0.3)	5	3.7	(0.4)
	Mn	0.065	(0.005)	0.050	(0.004)	0.05	0.038	(0.007)
	Fe	0.011	(0.002)	0.056	(0.016)	0.08	0.17	(0.05)
	Cu	0.036	(0.007)	0.059	(0.009)	0.4	0.75	(0.32)
	B	0.024	(0.007)	0.11	(0.03)	0.04	0.053	(0.006)
	S	2.8	(0.5)	1.3	(0.2)	2.3	1.7	(0.2)
	Total	200.3	(10.6)	72.5	(5.9)	129	37.3	(6.1)
Betalaine (moles m^3)		6.3	(0.5)	3.6	(0.5)	-	nd	-

† nd: not detected.

Toluidine blue, at 0.1% concentration, was used to trace the transpirational water flow through the plant. Detached leaves were placed in the dye solution and the dye was allowed to draw up into the leaf in the transpiration stream. After three hours, the dye had moved 10 cm up the petiole to the base of the leaf lamina. When the petiole was sliced in cross section and examined under the microscope, the dye was observed in the xylem of the vascular bundles of the petiole. After eight hours the dye was seen in the phloem and cambial regions of the vascular bundles. When petioles were examined at 24 hours the dye was evident in the cell walls inside the vascular bundle, but not in the cell walls of the surrounding parenchyma cells. When the dye was presented to the storage organ via the tap root the majority of the dye was taken up in the central core of xylem; in the middle of the storage organ. This is the xylem directly continuous with the tap root. Very little dye was seen in the xylem of the first inner vascular ring, and no dye was seen in the xylem of any of the rings further out in the storage organ. After three hours, dye was observed in the vascular bundles of the petioles, confirming that the dye moved up through the storage organ to the leaves. The preferential movement of dye up the central xylem core into the petioles, rather than through the xylem in the outer rings of the storage organ, was also seen when the storage organ was sliced in cross section at its thickest point and allowed to take up dye for 24 hours.

Using the results from 23 beet plants, correlation analyses were done to examine if cell size or ring size correlated with lower sucrose accumulation (Table 4). From these data, no significant correlation is indicated for either the width of the second intervascular ring, or for the number of cells calculated radially across this ring, with either the water potential of the storage organ, the osmolarity of the parenchyma cells, or the extractable sucrose concentration of the storage parenchyma tissue. However, the average radial diameter of the parenchyma cells in the second intervascular ring shows a significant correlation with the water potential of the tissue, and with the sucrose concentration in this tissue. The average cell diameter and the width of the ring were not significantly correlated. The estimates of water potential, cellular osmolarity, and sugar concentration for this storage parenchyma tissue were significantly correlated with each other. The estimate of parenchyma cell turgor did not correlate significantly with water potential or sugar concentration. However, a statistically significant correlation was indicated between cell osmolarity and estimated cell turgor.

Table 4. Linear regression analyses using parenchyma tissue of the second intervascular ring of storage organs from 23 red beet plants.

Items Correlated	Slope (B_1 value)	Intercept (B_0 value)	Standard Deviation of the Slope (sd(B_1))	N-Test Statistic of slope relative to zero[†]
Water potential vs Ring width	0.023 MPa/mm	-1.22 MPa	0.019 MPa/mm	1.189
Cell osmolarity vs Ring width	-7.9 moles/m^3mm	535.0 moles/m^3	11.6 moles/m^3mm	-0.6786
Sucrose concentration vs Ring width	-3.9 g/L mm	123.2 g/L	3.8 g/L mm	-1.041
Cell diameter vs Ring width	1.4 µm/mm	88.2 µm	1.8 µm/mm	0.7699
Water potential vs # of cells across ring	3.8 X 10^{-4} MPa/#	-1.1 MPa	0.0018 MPa/#	0.2146
Cell osmolarity vs # of cells across ring	-0.13 moles/m^3#	487.8 moles/m^3	1.1 moles/m^3#	-0.1169
Sucrose concentration vs # of cells across ring	-0.16 g/L #	106.8 g/L	0.35 g/L #	0.4506

[†]Significant difference at: * 95% confidence.

Table 4. (Continued)

Items Correlated	Slope (B_1 value)	Intercept (B_0 value)	Standard Deviation of the Slope (sd(B_1))	N-Test Statistic of slope relative to zero†
Water potential vs Cell diameter	0.0045 MPa/μm	-1.5 MPa	0.0021 MPa/μm	2.139*
Sucrose concentration vs Cell diameter	-8.3 g/L μm	176.6 g/L	0.42 g/L μm	-1.955
Water potential vs Cell osmolarity	-0.00090 MPa/moles m^3	-0.63 MPa	0.00030 MPa/moles m^3	-2.963*
Sucrose concentration vs Cell osmolarity	0.18 g/L moles m^3	5.6 g/L	0.060 g/L moles m^3	3.003*
Water potential vs Sucrose concentration	-0.0024 MPa/g L	-0.84 MPa	0.00097 MPa/g L	-2.437*
Water potential vs Estimated cell turgor	0.13 MPa/MPa	-1.1 MPa	0.17 MPa/MPa	0.7584
Sucrose concentration vs Estimated cell turgor	43.3 g/L MPa	90.0 g/L	33.0 g/L MPa	1.314
Cell osmolarity vs Estimated cell turgor	352.8 moles m^3/MPa	437.0 mosM	69.8 moles m^3/MPa	5.056*

†Significant difference at: * 95% confidence.

DISCUSSION

Taken as a whole, the results of this study suggest that the apoplast of the storage parenchyma tissue in the storage organ is separate from the apoplast of the conducting xylem. This conclusion is supported by several lines of evidence. First, a water potential gradient existed, up to 0.52 MPa, between the sap in the central xylem core and the parenchyma tissue of the second intervascular ring of the storage organ (Fig. 1, and Table 1). Second, the lack of a water potential gradient between the intervascular rings of the storage organ (Table 2), suggests that this region of the storage organ may share a common apoplast. Third, preferential flow of toluidine blue was observed in the transpirational stream through the central xylem bundle but not through the xylem in the outer rings of the storage organ.

The separation of the storage tissue apoplast from that of the conducting central xylem may have implications for the ability of the storage organ to accumulate sucrose. For instance, a more negative water potential in the sink regions of a plant has been suggested as a factor that would facilitate unloading of the phloem to that region (Patrick, 1990; Wolswinkel, 1990; Beruter, 1989). To maintain this negative water potential, the storage organ must retain solutes in its apoplast such that the solutes are not pulled back into the functional xylem apoplast, and thus avoid transporting these solutes back to the leaves. The presence of an apoplastic separation of the conducting xylem from the storage parenchyma tissue is consistent with the low concentration of osmotica found in the xylem sap (Table 3). This is supported by a report by Saftner et al. (1983) that the concentration of sucrose in the free space of sugar beet storage tissue is 63 moles m^{-3}, much higher than the concentration of sucrose found in the xylem sap of red beets and close to the concentration of neutral sugars found in the storage tissue apoplastic sap samples.

The nature of this putative apoplastic separation needs further study.. The exact location is not yet known, though the movement of toluidine blue through the storage organ suggests that a barrier may be located between the central vascular bundle of the storage organ and the outer rings. Another area in need of examination has to do with the xylem in the outer rings; xylem which according to dye flow observations did not contribute significantly to the transpirational stream. Is the xylem in the outer rings of the storage organ unconnected to other xylem, or is its resistance to flow so great that little flow occurs through it. Also it would be interesting to see if these outer xylem elements become a more significant factor in conduction to the leaves in the second year of beet growth as the storage organ begins to act as a physiological source.

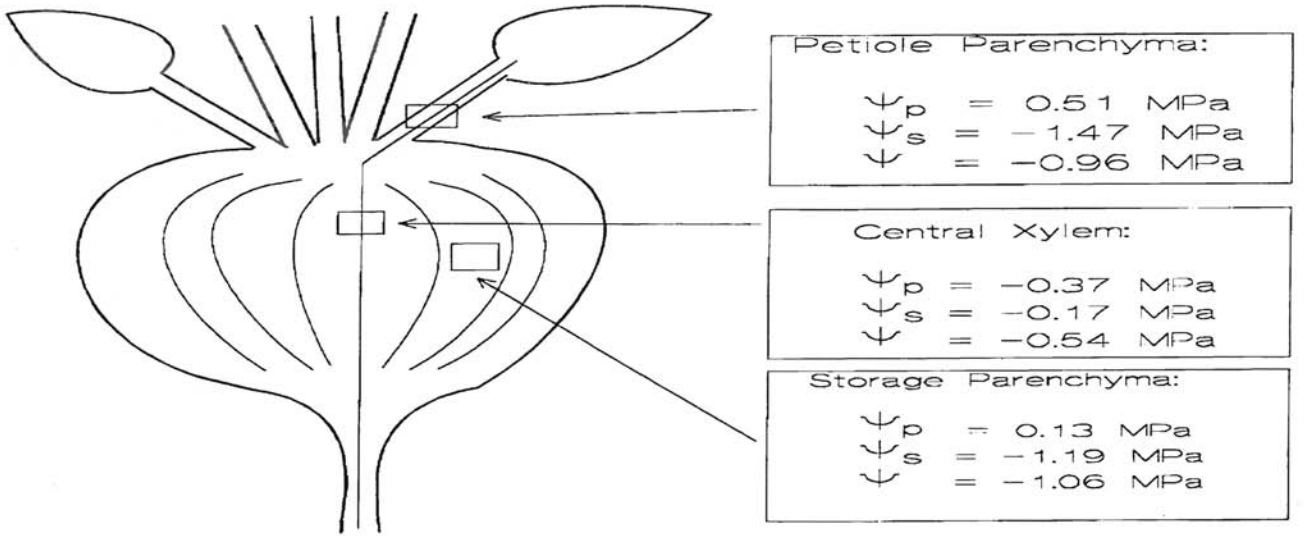

Fig. 1. Average water potential (Ψ), solute potential (Ψ s), and pressure (Ψ p) in the central xylem and in parenchyma tissue of the petiole and the second intervascular ring of the storage organ. The values given are averages obtained using six red beet plants. The water potential was estimated in parenchyma tissue, or petiole segments, by changes in percent fresh weight of tissue plugs in various concentrations of sorbitol. The solute potential was calculated using the estimate of the cellular osmolarity obtained by the use of the vacuole to cell diameter ratio of 200 cells observed in 2000 moles m^{-3} sorbitol. The pressure potential was calculated as the difference of the water potential minus the solute potential. For the xylem sap the solute potential was determined directly via an osmometer. The pressure potential of the xylem sap was estimated via a pressure bomb. The sum of the solute and pressure potential of the xylem sap gave an estimate of the water potential of the xylem sap.

One possible limitation on the ability of beet storage tissue to accumulate sucrose has been suggested to be the distance of the storage cells from the phloem (Milford and Watson, 1971; Loomis, 1979). This implies that increases in the width of the intervascular ring, and in the number of cells radially across the ring, will increase the distance the sucrose has to cross resulting in lower concentrations of sucrose accumulated in the cells at the center of the ring. However, in this work, neither the ring width nor the number of cells across the ring correlated significantly with sucrose concentration, osmolarity, or water potential (Table 4). The average diameter of the storage parenchyma cells did correlate significantly with the water potential and sugar concentration of the tissue. These results support those reported previously (Meissner and Spanswick, 1994), which suggest that, in red beets, the storage parenchyma cell diameter, rather than distance from the phloem, is closely related to the accumulation of sugar. The water potential of the storage parenchyma tissue does correlate with cell diameter and sugar concentration (Table 4), but not with the estimate of cell turgor. This implies that red beet storage parenchyma cells might accumulate osmotica to maintain a constant turgor. Thus, this work suggests that the size of the storage parenchyma cells and the ability of the storage organ to maintain a negative water potential may correlate more closely with the ability of the storage organ to accumulate sucrose than does the width of the intervascular rings or the number of cells across each ring.

ACKNOWLEDGEMENTS

Thanks to Edith Haritatos for technical help with the HPLC measurements, and Michael A. Rutzke (Dept. of Fruit and Vegetable Science, Cornell University) for the atomic emission spectrophotometric total cation analysis of the sap samples. Drs. Roger M. Spanswick, Robert Turgeon, and Randy Wayne kindly allowed me the use of equipment and materials in their laboratories. This work used equipment and supplies purchased in part through funds National Science Foundation grant DBM 8716363 to R.M. Spanswick, and by funds from the Hatch Program.

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