

Osmotic Adjustment and Solute Constituents in Leaves and Roots of Water-stressed Cherry (*Prunus*) Trees

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Abstract. Tissue osmotic potential (Ψ_{π}) and solute constituents were evaluated in leaves and roots of well-watered and water-stressed *Prunus avium* L. × *pseudocerasus* Lindl. 'Colt' and *Prunus cerasus* L. 'Meteor'. Osmotic potential at full turgor ($\Psi_{\pi, \text{sat}}$) decreased in response to water stress for leaves and roots of both cultivars. For 'Colt', a cultivar with an indeterminate growth habit, $\Psi_{\pi, \text{sat}}$ decreased by 0.56 MPa and 0.38 MPa for terminal expanding leaves and older expanded leaves, respectively. For 'Meteor', a cultivar with a determinate growth habit, $\Psi_{\pi, \text{sat}}$ decreased by ≈ 0.47 MPa in both terminal and older leaves. Root $\Psi_{\pi, \text{sat}}$ was alike for both cultivars and showed a similar decrease of 0.20 MPa in response to water stress. Roots had considerably higher $\Psi_{\pi, \text{sat}}$ than did leaves in both cultivars, irrespective of irrigation treatment. Soluble carbohydrates and potassium (K^+) were the major solute constituents in both cultivars. Of the soluble carbohydrates, sorbitol was found in the greatest concentration and accounted for the bulk of water stress-induced solute accumulation in both cultivars. Regardless of the irrigation treatment, mature leaves of 'Meteor' consistently had lower $\Psi_{\pi, \text{sat}}$ (typically 0.4 MPa) than 'Colt'. This variation in $\Psi_{\pi, \text{sat}}$ between *Prunus* cultivars suggests the potential for selection of cultivars with low $\Psi_{\pi, \text{sat}}$ and possibly superior drought resistance.

The capacity for osmotic adjustment via solute accumulation has been reported for many woody plants (Hinckley et al., 1981; Jones et al., 1985; Tyree and Jarvis, 1982). Higher solute concentrations contribute to lower tissue Ψ_{π} , maintenance of turgor potential, and improved tolerance of low tissue water potentials (Tyree and Jarvis, 1982). Low Ψ_{π} and the capacity for osmotic adjustment may also serve as useful criteria for selection and breeding of more drought-resistant species and cultivars (Tyree, 1976).

Tissue Ψ_{π} and the capacity for osmotic adjustment can vary among organs within a plant. In apple, mature leaves showed seasonal osmotic adjustment while shoot tips did not (Lakso, 1983; Lakso et al., 1984). Also, mature leaves of woody plants typically have lower Ψ_{π} than do expanding leaves (Knipling, 1967; Lakso et al., 1984; Syvertsen et al., 1981; Tyree et al., 1978). This variation may be important in understanding the responses of leaf gas exchange and leaf area expansion to water stress (Jones et al., 1985). Osmotic adjustment also occurs in roots of woody plants in response to water stress (Kandiko et al., 1980; Osonubi and Davies, 1978; Parker and Pallardy, 1985, 1988). However, within a plant, roots typically have higher Ψ_{π} than do leaves when compared at full turgor (Kandiko et al., 1980; Parker and Pallardy, 1985, 1988). The capacity for osmotic adjustment and turgor maintenance in roots may influence root : shoot partitioning patterns, root growth, and leaf responses to water deficits through indirect effects of root-produced plant growth regulators (Turner, 1986).

Soluble carbohydrates are often found to be important osmolytes, accumulating in response to water stress in herbaceous plants (Cutler and Rains, 1978; Ford and Wilson, 1981; Handa et al., 1983; Munns and Weir, 1981; Munns et al., 1979; Turner

et al., 1978). However, there has been little study of the solutes that contribute to Ψ_{π} and osmotic adjustment in woody plants.

Alcohol sugars, or polyols, are important osmolytes in certain lichens, yeasts, algae, and fungi accumulating in response to osmotic stress (Bielecki, 1982). In one case, the polyol sorbitol accumulates in *Plantago* in response to salt stress (Ahmad et al., 1979). Sorbitol is the primary photosynthetic product and translocated carbohydrate in many woody rosaceous species (Bielecki, 1982), including *Prunus*, where substantial diurnal accumulation of sorbitol occurs (Rom et al., 1988). Jones et al., (1985) further hypothesized that sorbitol may be an important osmolyte contributing to osmotic adjustment in rosaceous fruit trees.

Our objectives were the comparison of variations in Ψ_{π} and osmotic adjustment in response to water stress 1) between two *Prunus* cultivars, 2) between roots and leaves of different age, and 3) to determine the primary solutes that contribute to Ψ_{π} and osmotic adjustment in these plants.

Materials and Methods

Plant material and handling. *Prunus avium* × *pseudocerasus* 'Colt' and *P. cerasus* 'Meteor', 0.6 cm in caliper, were potted in 19-liter white plastic containers with a medium of 1 sphagnum peat moss : 1 vermiculite : 1 calcined clay (by volume) on 20 May 1987. Before initiation of treatments, plants were grown outside under natural conditions in Ithaca, N.Y., and were fertilized weekly with water soluble fertilizer (10N-10P₂O₅-10K₂O) at an N concentration of 200 mg·liter⁻¹. Plants were moved into the greenhouse where irrigation treatments commenced on 20 July 1987.

Treatments. The experiment was a split-unit design (Cochran and Cox, 1957) consisting of a 2 × 2 factorial with two cultivars (Meteor and Colt) and two irrigation levels (control and water-stressed) at the whole-unit level with leaves and roots within a plant treated as subunits. There were five replications per treatment combination. Plants were irrigated each evening

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Abbreviations: Ψ_{π} , osmotic potential; $\Psi_{\pi, \text{sat}}$, osmotic potential at full turgor.

either to container through-flow (control) or with only sufficient water to restore a bulk soil water potential of -1.2 MPa (water-stressed), based on a soil moisture release curve determined using a pressure chamber and ceramic plate (Soilmoisture Equipment Corp., Santa Barbara, Calif.). Imposition of water stress in this manner can result in variation in soil water content within a container at certain times. However, this method makes it possible to subject several plants to similar levels of water stress for extended periods. These irrigation treatments were imposed for 30 days.

Plant water relations. Leaf and root samples were collected before dawn to minimize variation in solute accumulation during the light period. Leaves were collected at four-node intervals along the current season's growth and at the shoot terminal. Because 'Colt' is a strongly indeterminate grower and did not set a terminal bud during the experiment, terminal leaves of 'Colt' were only partially expanded. In contrast, 'Meteor' plants had set terminal buds before sampling and terminal leaves were nearly mature (i.e., fully expanded). Roots were excised at a point where the root diameter was 5 mm and included the portion of the root system distal to the excision. Excised tissue was hydrated by recutting under water and holding for 2 h, covered with plastic, in the dark, with the cut end submerged. This method was sufficient to fully rehydrate tissue, i.e., result in a water potential of 0 MPa. $\Psi_{\pi, \text{sat}}$ was determined on expressed sap from fully hydrated tissue after freezing and thawing. Osmolality of expressed sap was determined using a vapor pressure osmometer (Wescor model 5100C, Logan, Utah). The Ψ_{π} of the expressed sap was then calculated for 20°C, based on the van't Hoff relation as given by Nobel (1983):

$$\Psi_{\pi} \text{ (MPa)} = 0.002437 \text{ (m}^3\text{·MPa·mol}^{-1}\text{)} \cdot \text{osmolality (mol·m}^{-3}\text{)}$$

The Ψ_{π} of expressed sap represents a mixture of cell contents and can yield values of Ψ_{π} slightly higher (more dilute) than would measurement of symplastic Ψ_{π} due to the dilution of symplastic solutes by apoplastic water. However, previous research has shown that measurements of $\Psi_{\pi, \text{sat}}$ of expressed sap were well correlated with measurements of $\Psi_{\pi, \text{sat}}$ determined using pressure-volume methodology for leaves of apple (Lakso et al., 1984), over a range of $\Psi_{\pi, \text{sat}}$ from 0 to -2.5 MPa, and for leaves of various ages and roots of both well-watered and water-stressed cherry trees (Ranney, 1989).

Solute analysis. Analysis for soluble carbohydrates and potassium was performed on terminal leaves, mature leaves (16th node), and roots after 30 days of irrigation treatments. Carbohydrates were extracted and then analyzed using high-performance liquid chromatography following Boersig and Negm (1985), modified by using a BioRad carbohydrate column (model HPX-87C; BioRad, Richmond, Calif.) at 85°C. Potassium was analyzed by inductively coupled argon plasma emission spectroscopy.

Osmotic contribution of solutes. The contribution of individual solutes to the osmotic potential of the expressed sap was calculated based on the relative dry weight (RDW) at saturation [dry weight/(saturated weight - dry weight)] determined for each sample, the solute concentration on a tissue dry-weight basis, the molecular weight of each solute, and the van't Hoff relation. Calculated at 20°C this gives:

$$\Psi_{\pi} \text{ (MPa)} = \text{RDW} \cdot C \text{ (mg·kg}^{-1} \text{ dry wt)} \cdot 1/\text{MW (g·mol}^{-1}\text{)} \cdot 0.002437 \text{ (m}^3\text{·MPa·mol}^{-1}\text{)},$$

where C is the solute concentration and MW is the molecular weight of a given solute.

Results

Water stress induced decreases in $\Psi_{\pi, \text{sat}}$ for leaves and roots of both cultivars (Fig. 1). For 'Colt', terminal leaves had higher $\Psi_{\pi, \text{sat}}$ than older leaves when well-watered. When stressed, all leaves of 'Colt' adjusted osmotically, with the terminal leaves showing the greatest decrease in $\Psi_{\pi, \text{sat}}$ (0.56 MPa) while expanded leaves typically decreased by 0.38 MPa. This differential response resulted in all of the leaves having similar $\Psi_{\pi, \text{sat}}$ when stressed. The roots of 'Colt' had substantially higher $\Psi_{\pi, \text{sat}}$ than leaves, with a $\Psi_{\pi, \text{sat}}$ of -0.56 and -0.74 MPa for control and stressed plants, respectively.

There was no difference in $\Psi_{\pi, \text{sat}}$ among any of the leaves of well-irrigated 'Meteor' plants that had a mean leaf $\Psi_{\pi, \text{sat}}$ of -2.02 MPa (Fig. 1). Leaves from node 12 (from the base) up to and including the terminal leaves showed similar decreases in $\Psi_{\pi, \text{sat}}$ of 0.47 MPa in response to water stress. Leaves at node 8 decreased slightly (0.17 MPa) and leaves at node 4 showed no significant osmotic adjustment. As with 'Colt', roots of 'Meteor' had higher $\Psi_{\pi, \text{sat}}$ than did leaves with a $\Psi_{\pi, \text{sat}}$ of -0.57 MPa and -0.80 MPa for control and stressed plants, respectively.

Comparison among cultivars showed that mature leaves of 'Meteor' consistently had lower $\Psi_{\pi, \text{sat}}$ (typically 0.4 MPa) than 'Colt' for plants under the same irrigation treatment except for node 4 where stress leaves of both 'Meteor' and 'Colt' had similar $\Psi_{\pi, \text{sat}}$. Roots showed very similar levels of $\Psi_{\pi, \text{sat}}$. Roots showed very similar levels of $\Psi_{\pi, \text{sat}}$ for both cultivars.

Analysis of tissue solutes showed that soluble carbohydrates and potassium were prominent solutes for 'Colt' and 'Meteor' (Table 1). Of the soluble carbohydrates, sorbitol was found in the greatest concentration regardless of cultivar, tissue, or irrigation treatment. Total soluble carbohydrates increased in response to the stress in leaves and roots of both cultivars. However, these increases in total soluble carbohydrates resulted primarily from increases in sorbitol alone. Concentrations of potassium, on a tissue dry-weight basis, did not change in response to the stress in leaves and actually decreased in roots of 'Colt' (Table 1). For 'Meteor', tissue dry-weight concentrations of potassium decreased in leaves and roots in response to stress.

The RDW at saturation increased significantly for terminal leaves and roots of both cultivars (Fig. 2). As a result, stress-induced changes in solute concentration, expressed as $\Psi_{\pi, \text{sat}}$

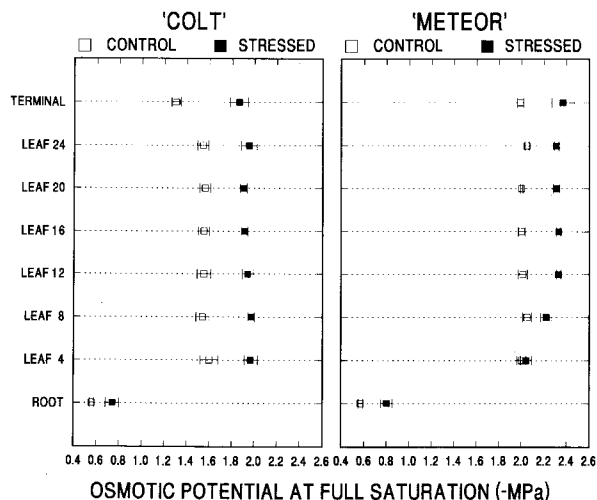


Fig. 1. $\Psi_{\pi, \text{sat}}$ for leaves and roots of control and water-stressed plants. Values are means ± 1 SEM.

varied considerably from changes in solute concentrations presented on a dry-weight basis (Table 1). It is therefore important to appreciate that comparison of solute concentrations on a dry-

Table 1. Influence of water stress on solute concentration and calculated $\Psi_{\pi, \text{sat}}$ for terminal leaves, mature leaves (16th node), and roots of 'Colt' and 'Meteor' cherry trees after 30 days of irrigation treatments.

Tissue	Solute	Concn (mmol·kg ⁻¹ dry wt)		Calculated $\Psi_{\pi, \text{sat}}$ (– MPa)	
		Control	Stressed	Control	Stressed
<i>Colt</i>					
Terminal leaves	Sugars				
	Glucose	74.76	60.34	0.06	0.07
	Sucrose	9.51	32.76	0.01	0.04*
	Sorbose	0.00	3.94	0.00	0.00
	Fructose	58.43	71.48	0.05	0.08**
	Sorbitol	193.0	488.3**	0.16	0.53**
	Total sugars	335.7	656.8**	0.28	0.72**
	K ⁺	443.0	428.8	0.37	0.46**
Mature leaves	Sugars				
	Glucose	70.90	88.10	0.06	0.08
	Sucrose	56.82	27.15	0.05	0.02*
	Sorbose	2.12	5.02	0.00	0.01
	Fructose	59.21	70.74	0.05	0.06
	Sorbitol	262.5	554.3**	0.21	0.50**
	Total sugars	451.5	745.3**	0.37	0.67**
	K ⁺	1021	919.9	0.84	0.82
Roots	Sugars				
	Glucose	47.97	54.73	0.02	0.04
	Sucrose	18.23	10.00	0.01	0.01
	Sorbose	0.00	1.11	0.00	0.00
	Fructose	34.37	44.43	0.02	0.03
	Sorbitol	83.86	166.6*	0.04	0.12**
	Total sugars	184.4	276.9*	0.08	0.20**
	K ⁺	642.8	455.6**	0.27	0.32
<i>Meteor</i>					
Terminal leaves	Sugars				
	Glucose	65.48	60.35	0.07	0.07
	Sucrose	41.52	20.40	0.04	0.02
	Sorbose	0.00	14.05**	0.00	0.02*
	Fructose	61.63	56.09	0.06	0.06
	Sorbitol	385.8	620.2**	0.40	0.70**
	Total sugars	554.5	771.1**	0.58	0.87**
	K ⁺	984.7	873.4*	1.03	0.99
Mature leaves	Sugars				
	Glucose	40.23	56.38	0.04	0.06
	Sucrose	63.24	22.00*	0.07	0.02**
	Sorbose	0.00	4.88	0.00	0.01
	Fructose	46.40	46.73	0.05	0.05
	Sorbitol	359.2	672.34**	0.38	0.73**
	Total sugars	509.0	802.34**	0.53	0.87**
	K ⁺	1081.3	919.53**	1.13	0.99*
Roots	Sugars				
	Glucose	67.96	79.12	0.04	0.06
	Sucrose	26.24	25.91	0.02	0.02
	Sorbose	0.00	0.00	0.00	0.00
	Fructose	50.53	65.72	0.03	0.05*
	Sorbitol	88.36	249.1**	0.05	0.20**
	Total sugars	233.1	419.8**	0.13	0.34**
	K ⁺	448.1	297.3**	0.25	0.24

***Significantly different from control at $P = 0.05$ and 0.01 , respectively (t test, $n = 5$).

weight basis can be misleading as solutes may be dissolved in smaller volumes of water in stress-acclimated tissues, resulting in lower $\Psi_{\pi, \text{sat}}$.

Stress-induced changes in potassium concentration contributed to a small decrease in $\Psi_{\pi, \text{sat}}$ in terminal leaves of 'Colt', but resulted in increases or no change in $\Psi_{\pi, \text{sat}}$ in all other tissues of both cultivars. The increases in total soluble carbohydrates contributed to decreases in $\Psi_{\pi, \text{sat}}$ in all tissues of both cultivars, often by >2-fold.

Estimates of the contribution of solutes to the $\Psi_{\pi, \text{sat}}$ of the expressed sap showed that the measured solutes (soluble carbohydrates and potassium) accounted for a large percentage (50% to 83%) of the measured $\Psi_{\pi, \text{sat}}$ (Table 2). Generally, the bulk of the stress-induced reduction in $\Psi_{\pi, \text{sat}}$ could be accounted for by increased levels of soluble carbohydrates, more specifically sorbitol.

Discussion

Terminal leaves of 'Colt' cherry were found to have higher $\Psi_{\pi, \text{sat}}$ than older leaves when well watered, similar to reports on apple (Lakso et al., 1984) and citrus (Syvertsen et al., 1981). Expanding leaves of 'Colt' demonstrated a significant capacity for osmotic adjustment, such that terminal leaves of water-stressed plants had $\Psi_{\pi, \text{sat}}$ similar to that of older stressed leaves. Other studies have found that sorbitol is synthesized primarily in older leaves in apple (Loescher et al., 1982) and apricot (Bieleski and Redgwell, 1985), suggesting that osmotic adjustment in expanding leaves resulted either from increased translocation of sorbitol to young leaves or from a decreased rate of sorbitol metabolism.

In 'Meteor', terminal leaves were similar to older leaves in $\Psi_{\pi, \text{sat}}$ and capacity for osmotic adjustment. This response is probably due to the determinate growth habit of 'Meteor' and the maturity of terminal leaves when sampled.

The higher osmotic potential of roots than of leaves, for both cultivars, is consistent with work done on other woody species,

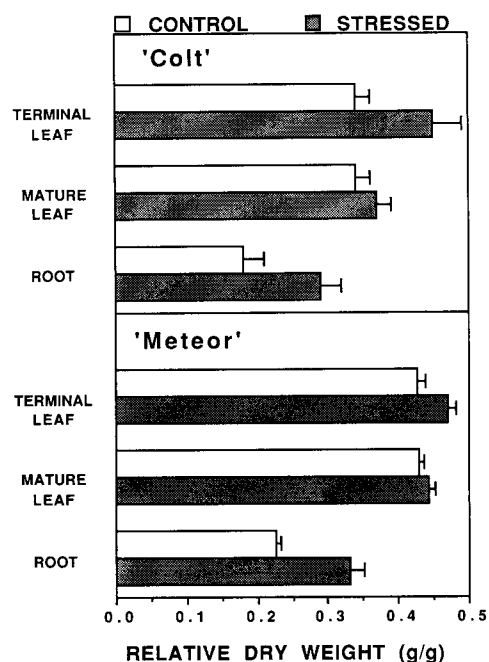


Fig. 2. Relative dry weight of saturated tissue [dry wt/(saturated wt - dry wt)] for terminal leaves, mature leaves (16th node), and roots. Values are means ± 2 SEM.

Table 2. Contribution of measured solutes to $\Psi_{\pi, \text{sat}}$.

	Terminal leaves		Mature leaves		Roots	
	Control	Stressed	Control	Stressed	Control	Stressed
<i>Colt</i>						
Measured $\Psi_{\pi, \text{sat}}$ (–MPa)	1.30	1.86	1.55	1.91	0.56	0.74
Contribution of measured solutes to $\Psi_{\pi, \text{sat}}$ (–MPa)	0.65	1.18	1.21	1.49	0.35	0.52
$\Psi_{\pi, \text{sat}}$ accounted for (%)	50	63	78	78	63	70
<i>Meteor</i>						
Measured $\Psi_{\pi, \text{sat}}$ (–MPa)	1.99	2.37	2.00	2.33	0.57	0.80
Contribution of measured solutes to $\Psi_{\pi, \text{sat}}$ (–MPa)	1.61	1.86	1.66	1.86	0.38	0.58
$\Psi_{\pi, \text{sat}}$ accounted for (%)	81	79	83	80	67	73

including *Tsuga heterophylla* (Kandiko et al., 1980), *Pseudotsuga menziesii* (Ritchie and Shula, 1984), *Juglans nigra* (Parker and Pallardy, 1985), and *Quercus* spp. (Parker and Pallardy, 1988). Although $\Psi_{\pi, \text{sat}}$ is typically higher in roots than leaves, the greater elasticity of root tissue can contribute to decreased water content and increased solute concentration as tissue water potential declines, often resulting in similar water potential at the turgor loss point for both leaves and roots (Parker and Pallardy, 1985, 1988; Ranney, 1989).

High solute concentrations can contribute to a greater capacity for turgor maintenance; however, high concentrations of electrolytes in the cytoplasm can be disruptive to organelles, enzymes, and membrane-bound processes (Wyn Jones et al., 1979). It has been proposed that polyols, such as sorbitol, may serve as more compatible solutes, being tolerated at high concentrations in the cytoplasm (Ahmad et al., 1979; Bielecki, 1982; Schobert, 1977).

Although the degree of osmotic adjustment was similar for leaves of both cultivars, 'Meteor' typically had a lower $\Psi_{\pi, \text{sat}}$ than did 'Colt' for a given irrigation treatment. In a study of reciprocal graft combinations between 'Meteor' and 'Colt', plants with 'Meteor' scions maintained higher stomatal conductance and had higher mean net assimilation rates under water-stressed conditions than plants with 'Colt' scions, regardless of the rootstock (Ranney, 1987). The greater conductance and mean net assimilation rate of 'Meteor' scions may have been due to lower $\Psi_{\pi, \text{sat}}$ and greater capacity for turgor maintenance as found for 'Meteor' in this study. Furthermore, the difference in $\Psi_{\pi, \text{sat}}$ found between these two cultivars suggests the potential for further selection of *Prunus* cultivars, particularly scions, for low $\Psi_{\pi, \text{sat}}$ and possibly superior drought resistance.

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