

Osmotic Adjustment of Roots and Shoots

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SUMMARY: A simple and reliable method for measuring the water potential components in roots of soil grown-plants was developed to allow the demonstration of root osmotic adjustment. Conventional techniques were used and adopted for measurements of single roots or whole root systems, namely the pressure chamber technique for the root water potential and osmometry to measure the osmotic potential in expressed root sap. Osmotic adjustment of roots was found in all investigated species (barley, rye, wheat, corn, soybean, sunflower). Roots had a greater capacity to adjust osmotically than did shoots. Increases in root/shoot ratios of drought stressed seedlings were correlated with a more efficient osmotic adjustment in roots as compared to shoots. Osmotic adjustment in roots was influenced by the species, the nutrient status and the stress rate.

1 INTRODUCTION: Osmotic adjustment results in higher turgor pressure and higher growth rates of shoots and roots, all of which have positive effects on photosynthesis and transpiration. However reductions in growth and photosynthesis, arising from water deficits, are not eliminated but occur at lower water potentials. Osmotic adjustment of leaves has been demonstrated for a wide range of species (Turner and Jones, 1980; Morgan, 1989). Yields were higher in osmotically adjusting cultivars (Morgan, 1983, Blum and Sullivan, 1986). In contrast to leaves, osmotic adjustment in roots has received little attention. Osmotic adjustment has been documented in the roots of peas (Greacen and Oh, 1972), English oak and silver birch (Osonubi and Davies, 1978), maize (Sharp and Davies, 1979, Sharp et al., 1990), cotton (Oosterhuis, 1987) and lupin (Turner et al., 1987). However, root water potentials of excised roots placed in thermocouple psychrometers are subject to relaxation errors and pressure probe techniques cannot be adopted for routine work. Therefore, a simple method has been developed for rapid screening of root osmotic adjustment in soil-grown plants, not subject to the above mentioned errors. The technique may be used for single roots and for whole root systems. Additionally, factors influencing osmotic adjustment in roots have been elucidated.

2 MATERIALS AND METHODS: Pre-germinated seeds of several species (corn, barley, rye, wheat, soybean, sunflower, carrot) were grown for three weeks in a silty soil (Aquic Ustifluent) at a range of initially numerically equivalent soil matric and osmotic potentials. Variations in soil matric and osmotic potentials were obtained by adding different amounts of salt solutions to the same mass of air-dried soil, based on a previously determined soil moisture release curve. Thereafter, the

soil was equilibrated for 2 weeks, put into pots (10 cm in diameter, 20 cm in height), and used for the experiments without any further watering. The experiments were conducted under controlled conditions in a growth chamber. Details are reported elsewhere (Schmidhalter and Oertli, 1990).

Comparative measurements of leaf and root pre-dawn water potentials were performed by pressure chamber and psychrometric techniques. The pressure chamber and the osmometer techniques were adapted for the whole root system or for single roots. In fewer than 30 s, the bulk of the soil was gently shaken off the roots, leaving them intact. The root was then enclosed in a split silicon rubber which had a small hole in the centre and sealed within the pressure chamber. The same results were obtained when the shoot was cut from the root shoot before removing the soil or when the shoot remained attached to the root, sealing the plant in the pressure chamber, with the shoot protruding out, and then cutting the shoot. Expressed root sap was used to measure the osmotic potential. Osmometer measurements performed either with roots used for the water potential measurements or with other roots from the same pot showed comparable results. The roots were sealed together with the adhering rhizospheric soil into bags and stored in an ice-cooled box. Cleaning of the roots was required before measuring. Therefore, the roots were spread between two circular wire nets (grid size 3 x 3 mm, 30 cm in diameter) and placed onto a box inside a humidified chamber. The adhering soil was blown off by a jet of compressed air in 30-60 s. There was no need to completely clean the roots, because small amounts of adhering soil did not affect the measurements. The roots were then enclosed in polythene bags and stored until measurement in a freezer. The cell membrane integrity was destroyed with liquid nitrogen and the root sap extracted with a hand-operated press.

Psychrometric measurements were performed in the dew point mode using disc psychrometers attached to a Wescor HR-33 T dewpoint hygrometer (Wescor Inc.) at 8 mA current and 10 s cooling time. For leaves, 8-mm diameter discs were sampled from the middle of the lamina of the youngest fully expanded leaves. Components of root water potential were measured on three root tips or three root segments (8-mm long), placed in each thermocouple cup. Roots were cleaned with a fine brush before being sealed in the chambers. This procedure required 30-60 s. Samples were kept in the cups for 4 hours for thermal and vapor equilibrium before water potential readings were taken. Solute potentials were measured after freezing the entire cup in liquid nitrogen and allowing it to equilibrate for another two hours.

3 RESULTS AND DISCUSSION: Comparable results were obtained psychrometrically and with the pressure chamber technique for leaf water potentials, but differences were observed for root water potentials (Table 1). Evaporative losses may partially account for the observed differences (Oosterhuis, 1987). Decreases in the total water potential may result from cell wall relaxation to which root tissue may be more prone than leaf tissue and decreased solute potentials may be caused by hydrolysis of organic solutes. It is known that the sample/cup geometry which is ill-defined in the case of root segments may influence the psychrometric measurements. Psychrometrically measured water potential components of root tips are compared in Table 1 with measurements made on whole roots by the pressure chamber/osmometer technique. Solute concentration for the growing root tip was greater than for the root as a

whole (Fig. 1) which agrees with results reported by Sharp and Davies (1979). We have observed that psychrometric measurements of roots as compared to shoots frequently showed more negative water potentials. This is illustrated in Table 1 and Fig. 2 and was observed more often with barley roots than with maize roots. Artifactual measurements of this type were not found with the pressure chamber measurements (Tables 1 and 2). Pressure chamber and osmometer measurements are not subject to the previously mentioned errors and are therefore preferred to psychrometric measurements. These techniques require less skill, experience and time and can easily be adapted to the screening of root osmotic adjustment in large populations. A disadvantage might be that measurements in the growth zone are not possible. Pre-dawn water potentials in roots and shoots can be higher than the average soil water potential (Fig. 2) because the plants tend to equilibrate over night with the wettest or least saline soil zone (Schmidhalter et al., 1991).

Table 1. Water (Ψ_w), solute (Ψ_o), and turgor (Ψ_p) potentials of roots and shoots of soil grown maize plants ($\Psi_{soil} = -0.19$ MPa) measured psychrometrically and with the pressure chamber/osmometer technique. Standard errors are given in parentheses.

	Ψ_w (MPa)	Ψ_o (MPa)	Ψ_p (MPa)
Psychrometrically			
Leaf potential	-0.46 (± 0.15)	-0.68 (± 0.09)	0.22 (± 0.12)
Root tip potential	-0.52 (± 0.13)	-0.92 (± 0.12)	0.40 (± 0.09)
Pressure chamber/Osmometer			
Leaf potential	-0.47 (± 0.05)	-0.66 (± 0.03)	0.19 (± 0.06)
Root potential	-0.23 (± 0.04)	-0.46 (± 0.03)	0.23 (± 0.07)

Table 2. Solute (Ψ_o), water (Ψ_w) and turgor (Ψ_p) potentials of roots and shoots of maize seedlings subjected to soil drying (θ_g = gravimetric soil water content) for 11 days. Measurements were performed with the pressure chamber/osmometer technique. SDW=shoot dry weight, RDW=root dry weight. Standard errors are given in parentheses.

	Day 8	Day 9	Day 10	Day 11
Leaf Ψ_w (MPa)	-0.20(0.02)	-0.26(0.03)	-0.36(0.01)	-0.90(0.09)
Leaf Ψ_o (MPa)	-0.58(0.02)	-0.65(0.02)	-0.72(0.01)	-0.95(0.06)
Leaf Ψ_p (MPa)	0.38	0.39	0.36	0.05
Root Ψ_w (MPa)	-0.15(0.02)	-0.14(0.01)	-0.25(0.01)	-0.98(0.03)
Root Ψ_o (MPa)	-0.87(0.04)	-0.88(0.03)	-1.11(0.03)	-1.37(0.05)
Root Ψ_p (MPa)	0.72	0.74	0.86	0.39
SDW (mg)	28.7	32.8	34.6	43.6
RDW (mg)	54.8	50.7	61.7	100.2
θ_g (%)	11.8	7.3	4.6	3.3

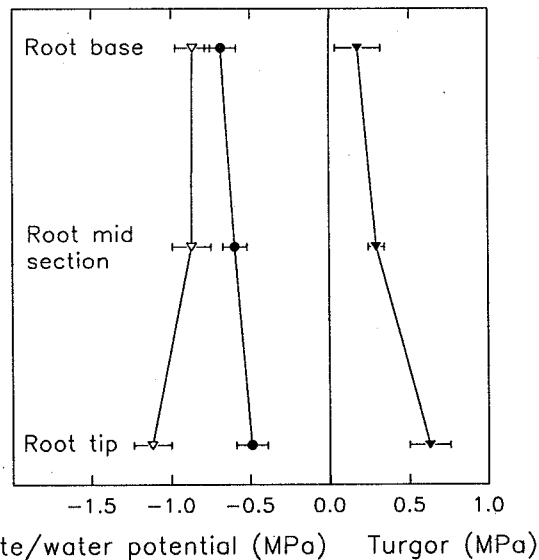


Fig. 1. Solute (▽), water (●) and turgor potentials (▼) of roots of barley plants grown at -0.2 MPa soil matric potential. Points are means \pm standard error.

The potential of the combined pressure chamber/osmometer method is further illustrated in a related paper (Schmidhalter, Besson and Oertli, 1991) which reports measurements of single and entire roots and demonstrates the gradients existing in the soil-plant continuum.

Osmotic adjustment was found in the roots of all investigated species. Roots adjusted more efficiently than did shoots (Table 2, Fig. 2). Comparative investigations to determine the effects of salt and water stress on maize (Fig. 2), barley and sunflower plants showed that shoots adjusted osmotically more efficiently under salt stress than under water stress, whereas roots did not differ to any great extent. This suggests that roots may be better adapted to water stress than shoots, which is further supported by the enhanced root growth (Table 2, Fig. 3).

Root growth was generally favored over shoot growth under water stress. Mild water stress enhanced root growth in seedlings, not only relative to shoot growth (corn and soybean seedlings), but absolutely (barley, rye, wheat, sunflower and carrot seedlings) as compared to initially well watered plants. Under the experimental conditions, the latter species showed an absolute increase in plant dry weight as a consequence of a strong promotion of root growth. It is hypothesized that increases in root/shoot ratio of water-stressed plants are due to a more efficient osmotic adjustment of roots as compared with shoots. Several other factors have been mentioned in the literature to contribute to increased root growth and hence increase the root/shoot ratio: (i) shoots are exposed to a more severe stress, (ii) roots may require a lower turgor threshold for expansive growth (Pritchard, Tomos and Wyn Jones, 1987; Hsiao and Jing, 1987), (iii) roots may have a higher cell wall extensibility, (iv) roots can maintain growth with lower tissue water potentials than shoots (Westgate and Boyer, 1985), (v) ABA accumulation may maintain root elongation and inhibit shoot elongation (Saab, Sharp, Pritchard and Voetberg, 1990). The above hypothesis does

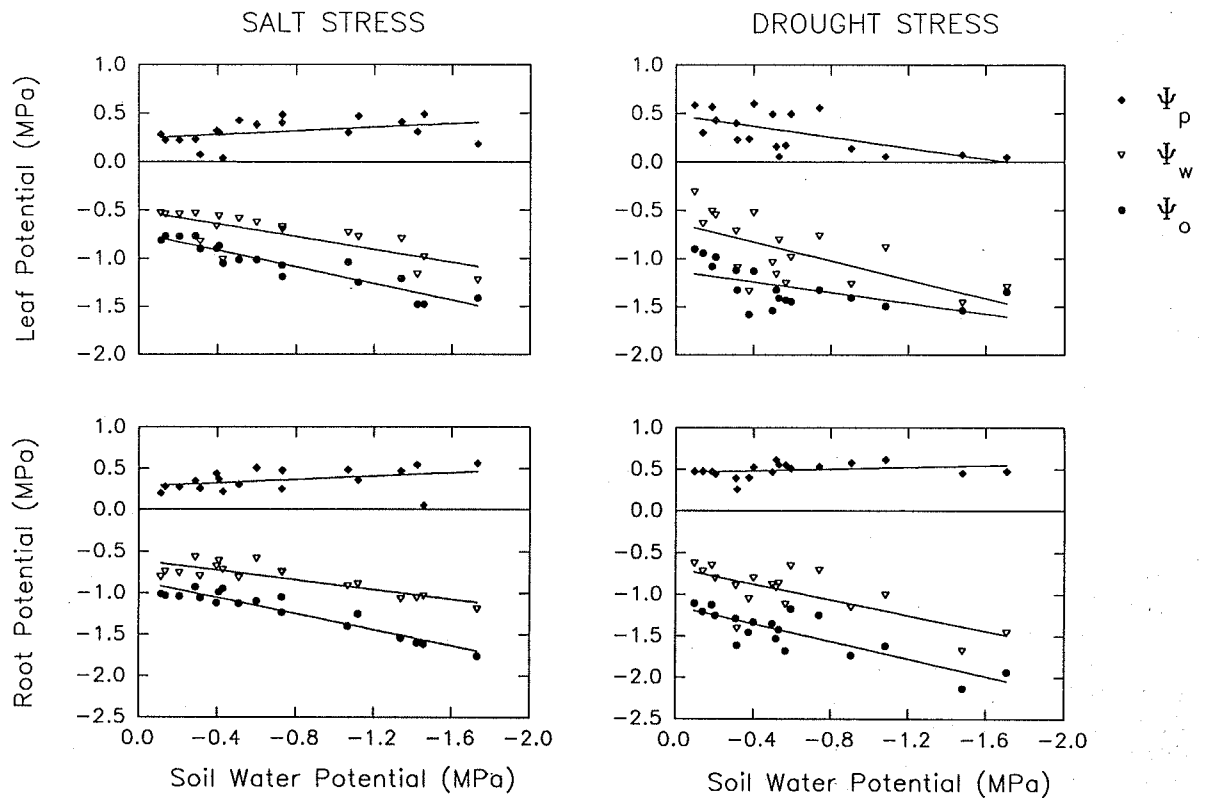


Fig. 2. Solute (Ψ_o), water (Ψ_w) and turgor (Ψ_p) potentials of roots and shoots in salt and drought stressed maize seedlings. Solute and water potentials were measured psychrometrically.

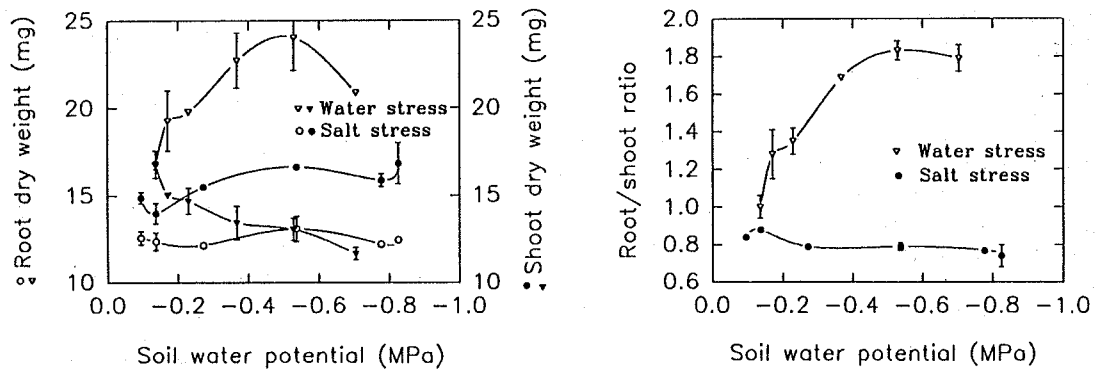


Fig. 3. Dry weights of root and shoot and root/shoot ratio of barley seedlings subjected to salt and water stress.

not preclude these factors but stresses the limiting role of osmotic adjustment in the regulation of root/shoot growth under stress.

Osmotic adjustment in roots is favored by the higher tissue elasticity in roots as compared to shoots (Evéquo, Schmidhalter and Oertli, 1991). Osmotic adjustment in roots was found to be influenced by the soil nutrient status (Studer, Schmidhalter and Oertli, 1991) and is stress rate dependent (unpublished data).

- REFERENCES:** Blum A. and C.Y. Sullivan, 1986. The comparative drought resistance of land-races of sorghum and millet from dry and humid regions. *Ann. Bot.* 57, 835-846.
- Evéquo M., U. Schmidhalter and J.J. Oertli, 1991. Osmotic and elastic properties of root and shoot tissue of four maize genotypes differing in drought sensitivity (this proceedings).
- Greacen E.L. and J.S. Oh. 1972. Physics of root growth. *Nature (London) New Biol.* 235, 24-35.
- Hsiao T.C. and J. Jing, 1987. Leaf and root expansive growth in response to water deficits. In D.J. Cosgrove and D.P. Kniewel (eds). *Physiology of cell expansion during plant growth. The Americ. Soc. of Plant Physiol.* 180-193.
- Morgan J.M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.* 34, 607-614.
- Morgan J.M. 1989. Physiological traits for drought resistance. In F.W.G. Baker. *Drought resistance in cereals. CAB International, Wallingford* 53-65.
- Oosterhuis D.M. 1987. A technique to measure the components of root water potential using screen-caged thermocouple psychrometers. *Plant and Soil* 103, 285-288.
- Osonubi O. and W.J. Davies, 1978. Solute accumulation in leaves and roots of woody plants subjected to water stress. *Oecologia* 32, 323-332.
- Pritchard M.E., A.D. Tomos and R.G. Wyn Jones, 1987. Control of wheat root elongation growth. I. Effects of ions on growth rate, wall rheology and cell water relations. *J. Exp. Bot.* 38, 948-959.
- Saab I.M., R.E. Sharp, J. Pritchard and G.S. Voetberg, 1990. Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. *Plant Phys.* 93, 1329-1336.
- Schmidhalter, U. and J.J. Oertli, 1990. Germination and seedling growth of carrots under salinity and moisture stress. *Plant and Soil* 132, 243-251.
- Schmidhalter U., A. Besson and J.J. Oertli, 1991. Water uptake by roots at spatially variable soil matric potentials (this proceedings).
- Sharp, R.E. and W.J. Davies, 1979. Solute regulation and growth by roots and shoots of water-stressed maize plants. *Planta* 147, 43-49.
- Sharp R.E., T.C. Hsiao and W.K. Silk, 1990. Growth of the maize primary root at low water potentials. II. Role of growth and deposition of hexose and potassium in osmotic adjustment. *Plant Physiol.* 93, 1337-1346.
- Studer C., U. Schmidhalter and J.J. Oertli, 1991. Interactive effects of N-, P-, K-, and water stresses on root and shoot development of young maize plants (this proceedings).
- Turner N.C. and M.M. Jones, 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. In N.C. Turner and P.J. Kramer. *Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York*, 155-172.
- Turner N.C., W.R. Stern and P. Evans, 1987. Water relations and osmotic adjustment of leaves and roots of lupins in response to water deficits. *Crop Sci.* 27, 977-983.
- Westgate M.E. and J.S. Boyer, 1985. Osmotic adjustment and the inhibition of leaf, root, stem and silk growth at low water potentials in maize. *Planta* 164, 540-549.

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