International Journal of Agricultural Science Research Vol. 3(6), pp. 089-098, June 2014 Available online at http://academeresearchjournals.org/journal/ijasr ISSN 2327-3321 ©2014 Academe Research Journals

Full Length Research Paper

Root water conductivity of some herbaceous species

Celestino Ruggiero and Massimo Fagnano*

Department of Agriculture, University of Naples Federico II, 80055 Portici (Naples) Italy.

Accepted 23 June, 2014

In this study, the values of water conductivity of roots are reported for eleven crops and grapevine. For some crops, two methods (pressure chamber and transpiration method) were compared. The effects of salt and water stress were evaluated on different crops, as the effect of chloride mercury treatment, nitrogen deprivation and the interactive effects of salt, water, nitrogen and mercury stress. Root water conductivity was evaluated, for almost all the crops, during the whole plant cycles. The transpiration method always showed values of root water conductivity higher than the pressure chamber. In almost all the species, the mercury chloride reduced root water conductivity during all the plant cycle. Nitrogen deprivation and salt stress induced higher root water conductivity reduction than mercury stress. Water stress induced also a reduction but its effect on root water conductivity was lower than that of nitrogen and salt stress. Mercury chloride treatment did not show any effect on nitrogen and salt stressed plants its effect was additive.

Key words: Roots, root water conductivity, aquaporin, mercury, nitrogen, salt stress, water stress.

INTRODUCTION

Currently, the root water uptake is the lesser known topic of the soil-plant-atmosphere (SPA) water balance. In the continuum SPA water movement, the plant is the interface between soil and atmosphere. Water moves from roots to leaves, where it is released through the stomata in the atmosphere and a balance between water root uptake and transpiration is necessary to avoid plant water stress. This movement is controlled by driving forces, by the plant water conductivity and by different resistances. The most important resistance to water flow is considered as that of the roots, which shows a large variability (Taylor and Klepper, 1975; Reicosky and Ritchie, 1976; Blizzard and Boyer, 1980). It is well known that root water conductivity changes in relation to environmental conditions (Azaizeh et al., 1991, 1992; Birner and Steudle, 1993; Carvajal et al., 1996; Peyrano et al., 1997; Clarkson et al., 2000) and during the plant ontogenesis (Zur et al., 1982; Ruggiero et al., 1999, 2003).

To explain the water flow through the roots, a "composite model" was proposed (Henzler and Steudle, 1995; Steudle, 2000a), which consider the root anatomy and two pathways, one non selective (apoplastic) and one selective (simplastic). As suggested by this model, the main water flow is dependent by transpiration level: for high transpiration levels the water flow goes through

the apoplastic pathway with hydrostatic gradient as driving force, with low resistance, while during non transpiration flow the water moves through the cells by osmotic gradient, through the simplast, which has higher resistance, because water moves through the double lipid layers of cell membranes.

The root systems have developed many strategies to adapt to environmental conditions. Many studies showed architectural and anatomical changes in the presence of adverse environmental conditions (Setia and Bala, 1994; Shannon et al., 1994; Neumann, 1995; Plant et al., 1997). The species change the resistances during plant growth. Different researches on fava bean (Ruggiero et al., 1999), pea (Ruggiero et al., 2003) and wheat (Ruggiero et al., 2007a) reported an increase of root water flow resistance until flowering, as also noted by Hailey et al. (1973) for Vigna sinensis, and Jones et al. (1982) and Zur et al. (1982) for soy bean. The water flow resistance can increase with the increase of root suberization. When the apoplastic root water flow is blocked, the only possible water pathway remains the cell-to-cell movement where the aquaporins are involved.

^{*}Corresponding author. E-mail: fagnano@unina.it.

The presence of the "composite model" (Steudle and Frensch, 1996) and the discovery of the aquaporins (Preston et al., 1992), leads to many studies on water flow through the plant. The new researches on aquaporine lead to the consideration of these proteins as very important for water flow through suberized roots (Steudle and Peterson, 1998; Steudle, 2000b). As the "composite model" suggests, water mainly moves through the apoplast. However this model does not explain how water moves through the root when some obstructions are present (Steudle and Peterson, 1998; Zimmermann and Steudle, 1998), and does not explain the fast root water conductivity changes, in relation to environmental conditions changes such as water stress, soil salinity, high transpiration rate, nutrient stress, anoxia, high temperature and heavy metals, and thus without root anatomical changes (Carvajal et al., 1996). For these reasons, the cell-to-cell pathway can have more importance than that supposed (Chaumont et al., 2000; Javot and Maurel, 2002).

The animal and vegetal aquaporins discovery is new and helped to understand the water movement through the cell membranes. These are membrane intrinsic proteins (MIPs) that are copious and diversified in the plant (Agre et al., 1998). Many different aquaporins have been identified: 36 in Zea mays and 35 in Arabidopsis (Chaumont et al., 2001; Johanson et al., 2001; Quigley et al., 2001). Many of the aquaporins present in the plant are water channels and their water transport activity has been studied in various species such as Arabidopsis (Weig et al., 1997), bean (Maurel et al., 1995), corn (Barrieu et al., 1998; Chaumont et al., 1998), spinach (Karlsson et al., 2000), tobacco (Opperman et al., 1994; Gerbeau et al., 1999), sunflower (Sarda et al., 1997), wheat (Niemietz and Tyerman, 1997; Carvajal et al., 1996), melon (Carvajal et al., 2000), grapevine (Vandeleur et al., 2009) and strawberry (Alleva et al., 2010).

The aquaporins activity should be controlled or reduced by phosphorilation, pH, osmotic pressure, salinity, heavy metals, temperature, nutrient and water stress, and anoxia (Johansson et al., 1996; Gerbeau, 2002; Steudle and Tyerman, 1983; Henzler et al., 1999). Guerrero et al. (1990) showed a higher aquaporins expression for water stressed pea plants. A reduced root water conductivity has been observed on nitrogen stressed wheat plant (Carvajal et al., 1996), and also on salt pepper stressed plants (Carvajal et al., 1999, 2000), and in the presence of anoxia on wheat plants (Birner and Steudle, 1993).

The aquaporins activity has more importance for old and suberized roots, when the aploplastic pathway is less active (Steudle, 1997; Steudle and Peterson, 1998). This activity is regulated, mainly by phosphorilation and dephosphorilation (Maurel et al., 1995; Johansson et al., 1996; Harveugt et al., 2000), but there are other mechanisms that regulate the aquaporin activity, as mercurial compounds (mercury chloride and pCMBS) (Maggio and Joly, 1995; Carvajal et al., 1996, 1999, 2000; Tazawa et al., 1997; Amodeo et al., 1999; Wan and Zwiazek, 1999; Barrowcloud et al., 2000; Martre et al., 2001; Ruggiero et al., 2007a). However, with 100-300 μ M of HgCl₂ it has been shown a turgor pressure decrease on wheat and onion roots, and this should be linked to some toxicity of these compounds (Zhang e Tyerman, 1999). The aquaporins activation or new expression can explain how root water conductivity changes during the day in relation to the transpiration changes (Daniels et al., 1994; Kammerloher et al., 1994; Kaldenhoff et al., 1998; Tyerman et al., 1999). Rodriguez et al. (2011) on poplar showed an increase of 15 AQPs when the plants are well lighted and have a high transpiration rate.

It is well known that transpiration, stomatal conductance and root water conductivity are highly influenced by nutritional stresses (Desai, 1937; Wallace and Frohlich, 1965), also without any changes on leaf water status. Some researches showed the influence of nitrogen stress on root water conductivity of cotton (Radin and Ackerson, 1981; Radin and Eidenbock, 1984; Radin and Matthews, 1989) of tomato and barley (Chapin et al., 1988; Gilbert et al., 1997) and of wheat and corn (Carvajal et al., 1996; Barthes et al., 1996). A relation between root water conductivity and sulphur uptake was also observed in barley (Karmoker et al., 1991). The root conductivity was very sensitive to mercury treatment, but the N and P deprived plants were insensible to mercury treatment. This insensitivity should be due to a low presence of PIP1, that is, mercury sensitive.

On wheat and barley N-stressed plants, Ruggiero and Angelino (2007b) found a root water conductivity decrease (49 and 66% respectively) and a lower plant growth. The shoot/root ratio was always lower as on mass area basis, and this was the effect of the lower shoot growth. On wheat, the mercury treatment caused a higher plant growth, a lower shoot/root ratio and more lignin in the root. The mercury treatment caused also a root water conductivity reduction (61 and 38% respectively for wheat and barley). In this case, the nitrogen stressed plants were considered as insensitive. Also on Pistacia vera, a reduction of shoot/root ratio and root water conductivity with N and P stress was observed (Trubat et al., 2006), whereas on tomato and melon, Gorska et al. (2008) found a higher root water conductivity.

Aim and scope

In the SPA continuum, the most relevant resistance to water movement is the root radial resistance (North and Nobel, 1996; Steudle and Peterson, 1998). As a consequence, the root tissues around the xylem, probably, play the key role in the SPA continuum water flux.

The studies on root water conductibility are relatively

	Methods for assessing root water conductivity							
Species	Pressure chambers		Transpiration					
	Samplings during the growth period	Treatments	Samplings during the growth period	Treatments				
Pepper	5	C, Hg, S	2	C, Hg				
	3	Hg, W						
Wheat	5	C, Hg, N	8	C, Hg				
Chick Pea	6	C, Hg	8	C, Hg				
Barley			4	C, Hg, S, N				
Tomato			4	C, Hg, S, W				
Bean			2	C, Hg				
Corn			2	C, Hg				
Basil			2	C, Hg				
Sunfower			2	C, Hg				
Grapevine	1	С						

Table 1. Details of the different experiments.

Note: C = control, Hg = mercury chloride, S = saline stress, W = water stress, N = Nitrogen stress.

new, becoming intense in the last years. It has been done through different methodologies: at individual root level by the "pressure probe", considering the whole root system; through the transpiration flux with intact plant or pressuring the total root system without the shoot; and through the pressure chamber. None of these studies considered the differences among root types, root age, or root system architecture, distinguishing between different root positions in the soil which can establish different soil water or oxygen availability (North and Nobel, 2000), or different soil and root contacts. And this is particularly important considering the differences on soil structure and texture. This means that the dimension of this parameter is highly variable and the average is practically not useful. In the last years, the studies considered the soil water conditions, soil salinity, the N and P availability and the aquaporin interactions.

The aim of this paper is to quantify the root water conductivity of some crops with different methods, during the plant cycle, and subject them to different stress. We report the data of root water conductivity of some crops evaluated by pressure chamber or through the transpiration method. For some crops, the root water conductivity was evaluated in salt, water or nitrogen stress conditions and in plants subjected to mercury treatment.

MATERIALS AND METHODS

For what concerns the transpiration method, the measures applied were done following the methodology used by Ruggiero et al. (2007a), and the technique reported by Ruggiero et al. (2012) was used for the pressure chamber method. For what concerns the material and methods of fava bean, pea, wheat, barley and grapevine, the methodology used by Ruggiero et al. (1999, 2003, 2007a, 2012) and Ruggiero and Angelino

(2007b) was followed.

Chick-pea, tomato, pepper, corn, sunflower, bean, and basil plants were grown on 14 L pots, filled with a sandy soil. Corn, basil, sunflower and bean were grown in 2002, while tomato was grown in 2003, and pepper and chickpea were grown in 2004. The plants were grown in open field at Portici (Southern Italy) and were subjected to usual agronomic practices in this zone for each crop. For what concerns the mercury chloride treatment, we followed the methodology reported by Ruggiero et al. (2007a), the salt stress for pepper, tomato and barley was imposed supplying salinized water at 0.25% of commercial salt, with a control irrigated at 100% ET with normal water. The water stress was imposed supplying water at 50% of ET and the nitrogen stress was imposed avoiding soil nitrogen fertilisation. The measures were made on at least three healthy plants from the growth to the beginning of fruit maturation, chosen, from a 20 plants group, for growth and age homogeneity. For grapevine, the measures were applied only once during the plant cycle, while for corn, basil, bean and sunflower it was done twice, and for the others it was done almost during the whole plant cycle.

The details (number of sampling dates, treatments and methods) of the experiments made on the different species are reported in Table 1. The average values obtained during the different samplings of all the tested species were subjected to analysis of variance and the means were separated by the Duncan method. For all the experiments, a completely randomized design with three replications was used.

RESULTS

Method comparison

Table 2 reports the data on root water conductivity

Cron	Treatment		Average					
Crop		1	2	3	4	5	6	Average
	Control	0.47	1.71	1.37	0.87	0.47		0.78 ^a
	Hg	0.20	0.44	0.43	0.27	0.37		0.34 ^b
Bonnor	S	0.34	0.14	0.44	0.11	0.12		0.23 ^c
Pepper	S + Hg	0.20	0.07	0.33	0.15	0.10		0.17 ^c
	W				0.17	0.26	0.47	0.30 ^a
	W + Hg				0.07	0.12	0.15	0.11 ^b
Wheat	Control Hg	1.40 0.80	1.80 0.60	0.80 0.20	0.40 0.18	0.40 0.14		0.96 ^a 0.38 ^b
Wheat	Ν	0.40	0.40	0.18	0.18	0.20		0.27 ^c
	N + Hg	0.26	0.30	0.20	0.20	0.20		0.23 ^c
Chick-pea	Control Hg	0.60 0.30	0.50 0.30	0.70 0.25	0.90 0.50	0.90 0.50	0.60 0.20	0.70 ^a 0.34 ^b
Grapevine	Self-rooted Grafted							4.02 ^b 5.26 ^a

Table 2. Root water conductivity values, expressed as $m^3 m^{-2} MPa^{-1} s^{-1} \times 10^{-8}$, evaluated by pressure chamber for some crop species subjected or not to different stresses.

Hg means plant treated with mercury chloride, S - salt stressed plants, W - water stressed plants, N - nitrogen stressed plant, Control - not stressed plants.

Numbers with different letters are different at 0.05 P level.

evaluated by pressure chamber, while Table 3 reports those evaluated by the transpiration method.

By comparing the data of root water conductivity obtained with the two different methods on the same crops grown without any stress (control of pepper, wheat and chickpea), it is possible to notice that values obtained by pressure chamber method (0.78, 0.96 and 0.70 m³ m⁻² MPa⁻¹ s⁻¹ x 10⁻⁸ for pepper, wheat and chickpea respectively) were lower than the corresponding values obtained by the transpiration method (1.10, 2.75 and 2.71 m³ m⁻² MPa⁻¹ s⁻¹ x 10⁻⁸ for pepper, wheat and chickpea respectively). The differences between the 2 methods were -29%, -65% and -74% for pepper, wheat and chickpea respectively.

Species comparison

Table 4 reports the data values (daily average and maximum during the day) for the different species evaluated by the transpiration method. Considering the average values, the higher root water conductivity was observed for tomato and then for grape, basil and sunflower and the lower for fava bean and then for pea and pepper. If we consider the daily maximum values, the higher values were observed again for tomato and then for grape, while the minimum was observed again for fava bean and then pea and pepper. Root water conductivity was negatively correlated with the total plant root area on the average, with a correlation coefficient of

0.65 for N = 252. For wheat and chick-pea, the root water conductivity was also negatively correlated with the root surface/leaf area surface ratio with a correlation coefficient of 0.71 for N = 71 (data not shown).

Nitrogen stress effect

The reduction of nitrogen availability caused a root water conductivity reduction as compared with control for both wheat (-66%) and barley (-40%), also if the measures were done with pressure chamber for wheat and with the transpiration method for barley.

Salt stress effect

This stress has been evaluated on pepper, barley and tomato. For these three crops, the salinity induced a root conductivity reduction that was higher on pepper (-71%) and tomato (-65%) and lower on barley (-55%).

Water stress effect

This effect was evaluated in tomato and pepper. In both cases, water stress induced a root water conductivity reduction that is higher in pepper (62%) and lower in tomato (20%).

Chloride mercury effect

In all the crops, this treatment induced a root water

Crono	Trestments	Samplings during growth period								
Crops	Treatments	1	2	3	4	5	6	7	8	Average
Wheat	Control	3.99	3.87	1.55	3.03	3.76	4.69	5.29	3.62	3.73 ^a
	Hg	2.66	2.37	1.18	2.43	2.29	2.52	3.45	2.53	2.43 ^b
Chick-pea	Control	3.99	4.62	1.09	2.47	2.39	1.91	2.47	2.73	2.71 ^a
	Hg	3.85	3.74	1.15	1.88	1.84	1.51	1.47	2.45	2.24 ^b
	Control	2.08	2.58	3.23	1.11					2.25 ^a
	Hg	1.67	1.43	2.21	0.69					1.50 ^b
Barley	Ν	1.11	1.39	1.65	0.93					1.27 ^{bc}
Daney	N + Hg	0.93	1.04	1.63	0.77					1.09 ^c
	S	1.33	0.86	1.33	0.56					1.02 ^c
	S + Hg	1.80	0.86	1.01	0.49					1.04 ^c
	Control	5.43	4.11	6.73	9.07					6.34 ^a
	W	5.34	3.44	4.10	7.50					5.10 ^b
	Hg	5.80	3.66	4.50	4.70					4.67 ^b
Tomato	W + Hg	2.05	3.51	3.18	5.85					3.65 ^c
Tomato	W + S	4.95	3.71	1.38	4.02					3.52 ^c
	S	3.18	2.26	2.14	2.39					2.20 ^d
	S + Hg	2.34	1.16	1.06	1.34					1.48 ^e
	W + S + Hg	4.19	1.96	1.54	1.71					2.35 ^d
Deen	Control	3.27	3.89							3.58 ^a
Bean	Hg	2.16	2.53							2.35 ^b
Corn	Control	2.80	3.87							3.34 ^a
	Hg	2.34	2.84							2.59 ^b
Basil	Control	2.58	5.09							3.84 ^a
	Hg	2.90	4.66							3.78 ^ª
Sunflower	Control	2.76	4.44							2.60 ^a
	Hg	1.94	2.61							2.28 ^b
Pepper	Control	0.58	1.62							1.10 ^ª
i ehhei	Hg	0.48	1.03							0.76 ^b

Table 3. Root water conductivity values, expressed as $m^3 m^{-2} MPa^{-1} s^{-1} \times 10^{-8}$, evaluated by transpiration method for some crop species subjected to different stresses.

Hg means plant treated with mercury chloride, S - salt stressed plants, W - water stressed plants, N - nitrogen stressed plant, Control - not stressed plants.

Numbers with different letters are different at 0.05 P level.

conductivity reduction that is higher in pepper (-56%) and lower in corn (-22%), with the exception of basil.

Interactive effects

In N stressed plants, the effect of mercury chloride on root water conductivity was not significant in wheat (0.23 versus 027, as shown in Table 2) and in barley (1.09

versus 1.27, as shown in Table 3).

The effect of mercury chloride on salt stressed plants was different between crops: salt stressed barley was unaffected by Hg (1.04 versus 1.02, as shown in Table 3), while root water conductivity of salt stressed pepper showed a 26% decrease with Hg (0.17 versus 0.23, as shown in Table 2) and that of salt stressed tomato significantly reduced (-37%) by Hg (1.48 versus 2.35, as

Species	Average	Species	Daily maximum
Tomato	6.34 ^a	Tomato	9.07 ^a
Vitis vinifera	4.02 ^b	Vitis Paulsen 1103	7.27 ^b
Basil	3.84 ^b	Wheat	5.29 ^c
Sunflower	3.60 ^b	Basil	4.66 ^d
Bean	3.58 ^c	Sunflower	4.44 ^d
Corn	3.34 ^c	Chick-pea	3.99 ^d
Vitis Paulsen 1103	3.31 ^c	Bean	3.89 ^d
Wheat	3.24 ^c	Corn	3.87 ^d
Chick-pea	2.71 ^d	Vitis vinifera	3.31 ^e
Barley	2.25 ^e	Barley	3.23 ^e
Pepper	1.10 ^f	Pepper	1.62 ^f
Pea	0.60 ^g	Pea	1.11 ^g
Fava bean	0.35 ^h	Fava bean	0.48 ^h

Table 4. Average and daily maximum values of root water conductivity, expressed as $m^3 m^{-2} MPa s^{-1} \times 10^{-8}$. The plants have been subjected to any stress.

Numbers with different letters are different at 0.5 P level.

shown in Table 3).

In water stressed plants, the effect of Hg was significant both on pepper (0.11 versus 0.30, as shown in Table 2) and tomato (3.52 versus 5.10, as shown in Table 1) root water conductivity, proving that these two stresses were additive.

DISCUSSION

The root water conductivity values reported in this research are of the same order of those reported by other researchers (Rieger and Litvin, 1999; Bramley, 2006; Liu et al., 2009).

The methods used showed different results: with the transpiration method the values resulted higher than those evaluated by the pressure chamber method. At this regard in literature, they are not references so the judgment is indefinite. However, considering that lower values are expected from the transpiration method because it considers, with respect to pressure chamber method, the effects of xylem and stomatal resistance, the results reported here suggest that these resistances are not influent compared to root resistances, or that the shoots influence the root activity. Also in this case, there are few data in literature (Li and Liu, 2010) that should confirm this hypothesis, while Ruggiero et al. (2012) noticed that the shoon influences the root water conductivity of grape Paulsen 1103 root system. This topic should be considered in future researches, considering that in horticulture many species are grafted with different shoons. Other explanations of these differences should be attributed to error, since with the transpiration method there are water losses, by drainage or evaporation, not carefully evaluated. The topic should worth more consideration in reason of the fact that the transpiration method is technically simpler and it works with an intact plant.

As regards the plant species evaluated, from these data it is clear that the species have different root water conductivities and this is also clear in the literature. With the exception of barley, the values agree with the plant luxuriance and with plant resistance to water stress; thus root water conductivity is higher for tomato, grapevine, wheat, corn, sunflower and chick-pea, and lower for pepper, fava bean and pea. However this parameter is linked with the root system dimension with a negative correlation. This should mean that the root water conductivity is variable not only between the species but also in relation to root age and root condition in the soil (Bramley, 2006). The fact that this relation is negative should mean that the young roots are more active than the older that usually increase as the root system growth. At this regard, Emam and Bijanzadeh (2012) observed on wheat that the seminal roots are more active than the adventitious roots, and that this difference is related to lignin content. Another explanation of this fact should be that more roots in the same soil volume determine a higher competition among the roots themselves with a lower efficiency as result. As regards this, Mu et al. (2006) observed that in the same time not all the roots are active, but only a part and the dimension of this part depends on the plant stresses. In the same vein, Vysotskaya et al. (2004) noticed on durum wheat an increase of root water conductivity after root system pruning and this means that the lower root surface stimulates the plant to increase their efficiency. This should mean that the roots, usually, take up water lesser than their total capacity and this becomes more evident when the plant is stimulated. Also on this topic, more researches are necessary, also considering that in this

research all the species showed a high root water conductivity variability during the plant cycle and this should be explained not only with root anatomy modification, but also because during the time, the ratio between total and active root area can change.

On wheat and barley, the nitrogen deficiency induced a root water conductivity decrease, and on these plants the mercury chloride treatment caused a moderate and nonsignificant effect. The effect of nitrogen stress on root water conductivity was observed by other authors (Carvajal et al., 1996, Clarkson et al., 2000) who suggested a relationship with a lower protein synthesis.

With the exception of basil, in all species the mercury chloride treatment induced a root water conductibility reduction of 35% on the average, but until to 56% in pepper. This reduction was variable during plant cycle from 10% in the first period to 69% during plant flowering. Considering that the mercury is largely considered as an aquaporins inhibitor (Maggio and Joly, 1995), it should be deduced that in all the species, these proteins have a significant rule on root water conductivity and more when the plants are more sensitive to water stress such as during flowering. However in lupin, Bramley (2006) observed that the cell to cell pathway is little used, and that the main water transport pathway is through the apoplast, so this should be also for basil. It should be observed that the nitrogen stress effect on this parameter is higher than the mercury effect and this should mean that some aquaporins are not sensible to this metal or maybe that the nitrogen stress influences other water transport pathways than the cell to cell only.

The salt stress influenced negatively the root water conductivity. This influence was of the same order of nitrogen stress. The negative effect was higher for pepper and lower for barley and this can explain the well known salt resistance of this last species. It should be observed that this effect is higher than the mercury effect, and that the mercury treatment on salt stressed plants was very low or absent and this should mean that the salt stress influences, as nitrogen stress, other pathways of the root water movement.

The water stress also induced a reduction of root water conductivity on tomato (-20%) and pepper (-62%). Also in this case, these data can explain the higher water stress resistance of tomato as compared with pepper. The mercury effect on plant subjected to water stress resulted additive to water stress effect, and this means that the two stresses should have different actions. Maybe the water stress operates mainly on apoplastic pathway, inducing more lignin and suberin synthesis. In salt stressed plant, however the water stress did not showed any effect, or on the contrary reduced the salt negative effect. This fact was observed also on salt and mercury stressed plants. In this case, the root water conductivity was of the same dimension of only salt stressed plants. The salt stress overlaps as the water is affected by the mercury, and this should mean that the salt stress

influences the apoplast, as the cell to cell pathway, while the water stress seems to reduce the negative salt effect.

In literature we do not have data to compare these results that could be of practical interest in the salinity management. These two stresses in the field are often recurring and act together, so it should be important to address the future research to this topic.

Conclusions

The collection of data on root water conductivity from different experiments carried out in Southern Italy makes possible to draw back some conclusions:

1) The transpiration method gave higher values than the pressure chamber method, maybe because of shoot influence on root activity, or errors due to non careful evaluation of water losses by drainage or evaporation. Further researches are necessary for comparing these two methods and improving their precision.

2) Root water conductivity is variable between the species and also in relation to root age and root density that can determine competition among the roots themselves thus reducing their efficiency.

3) Treatments with mercury chloride reduced root water conductivity during the entire plant cycle because it is an inhibitor of aquaporins that play a significant role on root water conductivity.

4) Mercury chloride treatments did not show any effect on nitrogen and salt stressed plants, while in the water stressed plants its effect was additive, thus suggesting that the salt stress influences, as nitrogen stress, other pathways of the root water movement: water stress may operate mainly on apoplastic pathway, inducing more lignin and suberin synthesis, while the salt stress may influence as the apoplast, as the cell to cell pathway.

5) Considering that water, salt and nutritional stresses in the field are often recurring and act together, it should be important to address the future researches to the interaction between these stresses.

REFERENCES

- Agre P, Bonhivers M, Borgnia MJ (1998). The aquaporins, blueprints for cellular plumbing systems. J. Biol. Chem., 273:14659-14662.
- Alleva K, Niemietz CM, Sutka M, Maurel C, Parisi M, Tyerman SD, Amodeo G (2010). Plasma membrane of *Beta vulgaris* storage roots shows high water channel activity regulated by cytoplasmatic pH and dual range and calcium concentrations. J. Exp. Bot., 57:609-621
- Amodeo G, Dorr R, Vallejo A, Sutka M, Parisi M (1999). Radial and axial water transport in the sugar beet storage root. J. Exp. Bot., 50:509-516.
- Azaizeh H, Steudle E (1991). Effects of salinity on water transport of excised maize roots. Plant Physiol., 97:1136-1145.

- Azaizeh H, Gunse B, Steudle E (1992). Effects of NaCl and CaCl₂ on water transport across root cells of maize (*Zea mays* L) seedlings. Plant Physiol., 99:886-894.
- Barrieu F, Chaumont F, Chrispeels MJ (1998). High expression of the tonoplast aquaporins Zm TIP1 in epidermal and conducting tissue of maize. Plant Physiol., 117:1153-1163.
- Barrowcloud DE, Peterson CA, Steudle E (2000). Radial hydraulic conductivity along developing onion roots. J. Exp. Bot., 51:547-557.
- Barthes L, Deléens E, Bousser A, Hoarau J, Prioul JL (1996). Xylem exudation is related to nitrate assimilation pathway in detopped maize seedlings: use of nitrate reductase and glutamine synthetase inhibitors as tools. J. Exp. Bot., 47:485–495.
- Birner TP, Steudle E (1993). Effects of anaerobic conditions on water and solute relations and active transport in roots of maize (*Zea Mays* L.). Planta, 190:474-483.
- Blizzard WE, Boyer JS (1980). Comparative resistance of the soil and the plant to water transport. Plant Physiol., 66:809-814.
- Bramley H (2006). Water flow in the root of three crop species: the influence of root structure, aquaporin activity and waterlogging. Thesis of School of plant biology, the University of Western Australia.
- Carvajal M, Cooke DT, Clarkson DT (1996). Responses of wheat plants to nutrient deprivation may involve the regulation of water-channel function. Planta, 199:372-381.
- Carvajal M, Martinez V, Alcaraz CF (1999). Physiological function of water channels as affected by salinity in roots of paprika pepper. Physiol. Plantarum, 105:95-101.
- Carvajal M, Cerda A, Martinez V (2000). Does calcium ameliorate the negative effect of NaCl on melon root water transport by regulating aquaporin activity? New Phytol., 145:439-447.
- Chapin FS, Walter CHS, Clarkson DT (1988). Growth response of barley and tomato to nitrogen stress and its control by abscissic acid, water relations photosynthesis. Planta, 173:352-366.
- Chaumont F, Barrieu F, Herman EM, Chrispeels MJ (1998). Characterization of maize tonoplast aquaporins expressed in zones of cell division and elongation. Plant Physiol., 117:1143-1152.
- Chaumont F, Barrieu F, Jung R, Chrispeels MJ (2000). Plasma membrane intrinsic proteins from maize cluster in two sequence subgroups with differential aquaporin activity. Plant Physiol., 122:1025-1034.
- Chaumont F, Barrieu F, Wojcik E, Chrispeels MJ, Jung R (2001). Aquaporins constitute a large and highly divergent protein family in maize. Plant Physiol., 125:1206-1215.
- Clarkson DT, Carvajal M, Menzler T, Waterhouse RN, Smyth AJ, Cooke DT, Steudle E (2000). Root hydraulic conductance: diurnal aquaporin expression and the

effects of nutrient stress J. Exp. Bot., 51:61-70.

- Daniels MJ, Mirkov TE, Chrispeels MJ (1994). The plasma membrane of *Arabidopsis thaliana* contains a mercury insensitive aquaporin that is homolog to the tonoplast water channel TIP. Plant Physiol., 106:1325-33.
- Emam Y, Bijanzadeh E (2012). Water uptake and hydraulic conductivity of seminal and adventitious roots of five wheat cultivars at early growth stage. JAST, 14:1605-1616.
- Desai MC (1937). Effect of certain nutrient deficiencies on stomatal behaviour. Plant Physiol., 12:253-283.
- Gerbeau P, Guclu J, Ripoche P, Maurel C (1999). Aquaporin Nt-TIPa can account for the high permeability of tabacco cell vacuolar membrane to small neutral solutes. Plant J. 18:577-587.
- Gerbeau P, Amodeo G, Henzler T, Santemi V, Ripoche P, Maurel C (2002). The water permeability of Arabidopsis plasma membrane is regulated by divalent cations and pH. Plant J., 30:71-81.
- Gilbert SM, Clarkson DT, Cambridge M, Lambers H, Hawkesford MJ (1997). (SO4)²⁻ deprivation has an early effect on the content of ribulose-1,5-bisphosphate carboxylase / oxygenase in young leaves of wheat. Plant Physiol., 115:1231-1239.
- Gorska A, Ye Q, Holdbrook M, Zwieniecki MA (2008). Nitrate control of root hydraulic properties in plants: translating local information to whole plant response. Plant Physiol., 148:1159-1167.
- Guerrero FD, Jones JT, Mullet JE (1990). Turgorresponsive gene transcription and RNA levels increase rapidly when pea shoots are wilted Sequence and expression of three inducible genes. Plant Mol. Biol., 15:11-26.
- Hailey JL, Hiler EA, Jordan WR, van Bavel CHM (1973). Resistance to water flow in *Vigna sinensis* L at high rates of transpiration. Crop Sci., 13:264-267.
- Harveugt P, Vlerick A, Fuks B, Wattiez R, Ruysschaert JM, Homble F (2000). Lentil seed aquaporins form a hetero-oligomer which is phosphorylated by a Mg²⁺-dependent and Ca2+- regulated kinase. Biochem J., 352:183–190.
- Henzler T, Steudle E (1995). Reversibile closing of water channels in Chara internodes provides evidence for a composite transport model of the plasma membrane. J. Exp. Bot., 46:199-209.
- Henzler T, Waterhouse RN, Smyth AJ, Carvajal M, Cooke DT, Schaffner AR, Steudle E, Clarkson DT (1999). Diurnal variation in hydraulic conductivity and root pressure can be correlated with the expression of putative aquaporins in the roots of *Lotus japonicas*. Planta, 210:50-60.
- Javot H, Maurel C (2002). The role of aquaporins in root water uptake. Ann. of Bot., 90:301-313.
- Johanson U, Karlsson M, Johansson I, Gustavsson S, Sjovall S, Fraysse L, Weig AR, Kjellbom P (2001). The complete set of genes encoding major intrinsic proteins

in *Arabidopsis* provides a framework for a new nomenclature for major intrinsic proteins in plants. Plant Physiol. 126:1358-1369.

- Johansson I, Larsson C, Ek B, Kjellbom P (1996). The major integral proteins of spinach leaf plasma membranes are putative aquaporins and are phosphorylated in response to Ca²⁺ and apoplastic water potential. The Plant Cell, 8:1181-1191.
- Jones JW, Zur B, Boote KJ, Hammond LC (1982). Plant resistance to water flow in field soybean: I Non limiting soil moisture. Agronomy J., 74:92-98.
- Kaldenhoff R, Grote K, Zhu JJ, Zimmermann U (1998). Significance of plasmalemma aquaporins for water transport in *Arabidopsis thaliana*. Plant J., 14:121-128.
- Kammerloher W, Fischer U, Piechottka GP, Schaffner AR (1994). Water channels in the plant plasma membrane cloned by immunoselection from a mammalian expression system. Plant J., 6:187-99.
- Karlsson M, Johansson I, Bush M, McCann MC, Maurel C, Larsson C, Kjellbom P (2000). An abundant TIP expressed in mature highly vacuoled cells. Plant J., 21:1-8.
- Karmoker JL, Clarkson DT, Saker LR, Rooney JM, Purves JV (1991). Sulphate deprivation depresses the transport of nitrogen to the xilem and hydraulic conductivity of barley (*Hordeum vulgare* L) roots. Planta, 185:269-278.
- Li QM, Liu BB (2010). Comparison of three methods for determination of root hydraulic conductivity of maize (*Zea mays* L) root system. Agricul. Science in China, 9:1438-1447.
- Liu BB, Steudle E, Deng XP, Zang SQ (2009). Root pressure probe can be used to measure the hydraulic properties of whole root systems of corn (*Zea mays* L). Botanical Studies, 50:303-310.
- Maggio A, Joly AJ (1995). Effects of mercuric chloride on the hydraulic conductivity of tomato root systems Evidence for a channel-mediated water pathway. Plant Physiol., 109:331-335.
- Martre P, North GB, Nobel PS (2001). Hydraulic conductance and mercury-sensitive water transport for roots of *Opuntia acanthocarpa* in relation to soil drying and rewetting. Plant Physiol., 126:352-362.
- Maurel C, Kado RT, Guern J, Chrispeels MJ (1995). Phosphorylation regulates the water channel activity of the seed-specific Aquaporin α -TIP. The EMBO J., 14:3028-3035.
- Mu Z, Zhang S, Zhang L, Liang A, Liang Z (2006). Hydraulic conductivity of whole root system is better than hydraulic conductivity of single root in correlation with the leaf water status of maize. Botanical Studies, 47:145-151.
- Neumann PM (1995). The role of cell wall adjustment in plant resistance to water deficit. Crop Sci., 35:1258-1268.
- Niemietz CM, Tyerman SD (1997). Characterization of water channels in wheat root membrane vesicles. Plant

Physiol., 115:561-567.

- North GB, Nobel PS (1996). Radial hydraulic conductivity of individual root tissues of Opuntia ficus-indica (L.) Miller as soil moisture varies. Ann Bot., 77:133-142.
- North GB, Nobel PS (2000). Heterogeneity in water availability alters cellular development and hydraulic conductivity along roots of a desert succulent. Ann Bot., 85:247-255.
- Opperman CH, Taylor CG, Conkling MA (1994). Rootknot nematode-directed expression of a plant rootspecific gene. Science, 263:221-223.
- Peyrano G, Taleisnik E, Quiroga M, De Forchetti SM, Tidier H (1997). Salinity effects on hydraulic conductance, lignin content and peroxidase activity in tomato roots. Plant Physiol. Biochem., 35:387-393.
- Plant Z, Newman M, Federman E, Grava A (1997). Response of root growth to a combination of three environmental factors. In Altman A, Waisel Y (eds). Biology of root formation and development, New York, Plenum Press, pp 243-252.
- Preston GM, Carrol TP, Guggino WB, Agre P (1992). Appearance of water channels in *Xenopus* oocytes expressing red cell CHIP28 protein. Science, 256:385-387.
- Quigley F, Rosenberg JM, Shachar-Hill Y, Bohnert HJ (2001). From genome to function: the *Arabidopsis* aquaporins. Genome Biology, 3:1-17.
- Radin JW, Ackerson RC (1981). Water relations of cotton plants under nitrogen deficiency III Stomatal conductance, photosynthesis and abscisic acid accumulation during drought. Plant Physiol., 67:115-119.
- Radin JW, Eidenbock MP (1984). Hydraulic conductance as a factor limiting leaf expansion in phosphorusdeficient cotton plants. Plant Physiol., 75:372-377.
- Radin JW, Matthews MA (1989). Water transport properties of cortical cells in roots of nitrogen and phosphorus-deficient cotton seedlings. Plant Physiol., 89:264-268.
- Reicosky DC, Ritchie JT (1976). Relative importance of soil resistance in root water absorption. Soil Sci. Am. J. 40:293-7.
- Rieger M, Litvin P (1999). Root system hydraulic conductivity in species with contrasting root anatomy. J. Exp. Bot. 50:201-209.
- Rodriguez AMA, Hacke UG, Laur J (2011). Influence of evaporative demand on aquaporin expression and root hydraulics of hybrid poplar. Plant Cell Environ., 34:1318-1331.
- Ruggiero C, De Pascale S, Fagnano M (1999). Plant and soil resistance to water flow in faba bean (*Vicia faba* L *major* Harz). Plant and Soil, 210:219-231.
- Ruggiero C, De Pascale S, Angelino G, Maggio A (2003). Developmental changes in plant resistance to water flow in *Pisum Sativum* (L). Plant and Soil, 250:121-128.
- Ruggiero C, Angelino G, Maggio A (2007a). Developmental regulation of water uptake in wheat. J.

Plant Physiol., 164:1170-1178.

- Ruggiero C, Angelino G (2007b). Changes of root hydraulic conductivity and root/shoot ratio of durum wheat and barley in relation to nitrogen availability and mercury exposure Ital. J. Agron., 3:281-290.
- Ruggiero C, Di Lorenzo R, Angelino G, Scaglione G, Gambino C, Di Vaio C (2012). Root hydraulic conductivity in three self-rooted and grafted table grape cultivars. J. Int. Sci. Vigne Vin., 45:177-183.
- Sarda X, Tousch D, Ferrare K, Legrand E, Dupuis JM, Casse-Delbart F, Lamaze T (1997). Two TIP-like genes encoding aquaporins are expressed in sunflower guard cells. Plant J., 12:1103-1111.
- Shannon MC, Grieve CM, Francois LE (1994). Whole plant response to salinity. In Wilkinson RE (ed) Plantenvironment interactions, New York, Marcel Dekker, pp 199-244.
- Setia RC, Bala R (1994). Anatomical change in root and stem of wheat (*Triticum aestivum* L) in response to heavy metals. Phytomorphology, 44:95-104.
- Steudle E, Frensch J (1996). Water transport in plants: role of the apoplast. Plant and Soil, 187:67-79.
- Steudle E (1997). Water transport across plant tissue: role of water channels. Biology of the Cell, 89:259-273.
- Steudle E, Peterson CA (1998). How does water get through roots? J. Exp. Bot., 49:775-788.
- Steudle E, Tyerman SD (1983). Determination of permeability coefficients, reflection coefficients, and hydraulic conductivity of *Chara corallina* using the pressure probe: effects of solute concentration. J. of Membrane Biology, 75:85-96.
- Steudle E (2000a). Water uptake by roots: effects of water deficit. J. Exp. Bot., 51:1531-1542.
- Steudle E (2000b). Water uptake by plant roots: an integration of views. Plant and soil, 226:45-56.
- Taylor HM, Keppler B (1975). Water uptake by cotton root system: an examination of assumption in the single root model. Soil Sci., 120:57-67.
- Tazawa M, Ohkuma E, Shibasaka M, Nakashima S (1997). Mercurial-sensitive water transport in barley roots. J. of Plant Res., 110:435-442.

- Tyerman SD, Bonhert HJ, Maurel C, Steudle E, Smith JAC (1999). Plant aquaporins: their molecular biology, biophysics and significance for plant water relations. J. Exp. Biol., 50:1055-1071.
- Trubat R, Cortina J, Vilagrosa A (2006). Plant morphology and root hydraulics are altered by nutrient deficiency in *Pistacia lentiscus* (L). Trees, 20:334-339.
- Vandeleur RK, Mayo G, Shelden MC, Gilliham M, Kaiser BN, Tyerman SD (2009). The role of plasma membrane intrinsic protein aquaporins in water transport through roots: diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. Plant Physiol., 149:445-460.
- Vysotskaya LB, Arkhipova TN, Timergalina LN, Dedov AV, Veselov SY, Kudoyarova GR (2004). Effect of partial root excision on transpiration, root hydraulic conductance and leaf growth in wheat seedlings. Plant Physiol. Biochem., 42:251-255.
- Wallace A, Frolich A (1965). Phosphrus deficiency symptoms in tobacco versus transpirational water loss. Nature, 208:123-124.
- Wan XC, Zwiazek JJ (1999). Mercuric chloride effects on root water transport in aspen seedlings. Plant Physiol., 121:939-946.
- Weig A, Deswarte C, Chrispeel MJ (1997). The major intrinsic protein family of *Arabidopsis* has 23 member that form three distinct group with functional aquaporins in each group. Plant Physiol., 114:1347-1357.
- Zhang WH, Tyerman SD (1999). Inhibition of water channels by HgCl₂ in intact wheat root cells. Plant Physiol., 120:849-858.
- Zimmermann HM, Steudle E (1998). Apoplastic transport across young maize roots: effect of the exodermis. Planta, 206:7-19.
- Zur B, Jones JW, Boote KJ, Hammond LC (1982). Total resistance to water flow in field soybeans: II Limiting soil moisture. Agron. J., 74:99-105.