

# Soil, plant and canopy resistance to water flow in bell pepper (*Capsicum annuum* L.) as affected by fertigation regimes

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## Abstract

The effect of fertigation regimes on water transport properties (soil, plant and canopy resistances) through the plant to the canopy in the Soil-Plant-Atmosphere-Continuum (SPAC) was studied in bell pepper in a Mediterranean climate. The treatments consisted of fertigated drip irrigation in factorial combinations of three levels (amounts) of water application (daily, twice and once weekly) and application frequencies (2, 6 and 10 times per fertigation event). Leaf water potential and stomatal conductance were monitored while whole plant hydraulic conductance was estimated by the evaporative flux method, using the Ohm's law analogy (the slope of the water potential difference ( $\Delta\psi$ ) versus sap fluxes). Canopy conductance (inverse of resistance) was estimated from vapour pressure deficit (vpd) and transpiration flux. Differences in the intervals between fertigation events altered the environment for root development and affected soil moisture status, stomatal conductance (gs), leaf water potential (lwp), transpiration (sap) flux, and xylem and canopy water transport capacities in bell pepper. The components of the resistance elements in the SPAC differed under the fertigation treatments. Total plant resistance (Rp) increased with transpiration flux in a linear manner in addition to a proportional decrease in stomatal (gs) and canopy conductance (gc). Canopy component constitutes the least resistance (greatest conductance) to the flow of water, estimated soil resistance was much lower than total resistance to the flow of water, and the highest within plant resistance is contained in the root system which constituted a predominant part of total plant resistance. Bell pepper has an efficient xylem sap transport system, maintains gs and plant water status under variable soil moisture regimes. Bell pepper water use is affected by soil environment, plant architectural and xylem traits. The mechanisms underlying differences in water use and plasticity of physiological functions in bell pepper under variable fertigation regimes appeared to be offered through changes in the magnitudes of component resistances of the water transport pathways in the SPAC. The implications of knowledge of the magnitudes of the resistances to water flow pathway in the SPAC to irrigation management is discussed.

**Key words:** Bell pepper, fertigation, hydraulics, stomata, canopy, leaf potential, water uptake

## Introduction

The trend to increase crop yields has led to frequent fertigation and therefore the time intervals between successive fertigation events has diminished to hours or even less. Therefore, modern agricultural systems tend to simultaneously supply water and nutrients (fertigation) mainly by drip devices (Bar-Yosef, 1999). Frequent irrigation events enhance high water fluxes from the growing medium to the root surface. The promotion of water and nutrients availability at rates that match plant requirements and reduction in the quantities of fertilizer needed to achieve optimal production contributes to the minimisation of ecological damage to environment (Silber *et al.*, 2003). In semi-arid climates, conventional daily cycle of irrigation is 1-3h per day in comparison with 10-14h of potential photosynthesis and transpiration of plants. As a result, transpiration during the day may cause significant differences between the water content in the root zone and that in the bulk soil (Silber *et al.*, 2003). Water and nutrient uptake by plants, and the formation of a depleted zone in the immediate vicinity of the roots are the driving forces for solute movement towards the roots. During fertigation events, subsequent redistribution enables frequent supply to the root surface and its vicinity with fresh nutrients in solution. These frequent replenishments eliminate the depletion zone formed at the root surface by uptake of nutrients during period between

successive irrigation events, thus decreasing the concentration gradient between the medium solution and the root surface. Frequent fertigation enhances high water fluxes from the growing medium to the root surface in contrast to non-fertigated plants where nutrients and water are supplied independently (Claassen and Steingrobe, 1999).

Soil-plant-atmosphere coupling (SPAC) explains the control exercised by the soil and atmospheric conditions (environments) on plant processes. It is reported that changes in plant water relation parameters such as leaf water potential and stomatal response can be explained in terms of changes in the hydraulic architecture of plants (Salleo *et al.*, 2000; Tyree and Zimmermann, 2002). The ease of water fluxes from the soil to the leaf (canopy) drives the architecture and physiology of plants. If a plant's hydraulic architecture is important to the maintenance of functional integrity and hence growth and productivity under soil and air drought, then, stomatal conductance and photosynthetic sensitivity to water stress may be determined by hydraulic constraints in the SPAC (Sperry *et al.*, 2002). This understanding could be a useful input in the development of prediction models for plant water requirements in regions prone to drought. The hydraulic properties of a species may influence the response of gas exchange to soil moisture deficits. Therefore, the ability of plants to maintain a favourable water status is dependent on the resistance to water

flow in the SPAC (Jones *et al.*, 1982; Stiller *et al.*, 2003). Plant hydraulic efficiency therefore regulates the diurnal and seasonal time scale of water loss and leaf water status (Stiller *et al.*, 2003; Agele *et al.*, 2005).

Under non-limiting soil water status, within plant resistance dominates soil resistance to water flow, however, soil hydraulic resistance and root densities would be the limiting resistance in dry soils (LoGullo *et al.*, 2003). Changes in soil and plant resistance in response to soil drying are important causes of changes in the overall soil to leaf hydraulic conductance ( $K_s$ -1) and water relation characteristics of plants subjected to varying cycles of drought (Sperry *et al.*, 2002). Plant resistance is not constant but according to van Honert model, it increases with decrease in transpiration (Zur *et al.*, 1982; Rieger and Motisi, 1990; Steudle, 1994). Total resistance to water flow is dependent on leaf water potential and the transpiration rate (Lascano and van Bavel, 1984), however, hydraulic resistance of plants decreased with increasing transpiration rate (Hirasawa and Ishihara, 1991; Rieger and Motisi, 1990). Baker and van Bavel (1986) opined that the conductivity of the unsaturated soil is the dominant factor controlling water flow through the soil-plant system however, Kramer and Boyer (1995) postulated the existence of higher resistance to liquid water flow in the plant than soil and the predominance of root over plant resistance. The controversial reports are due to experimental conditions which vary from differences in soil, plant and atmospheric conditions (Lafolie *et al.*, 1991; Passioura, 1988). In addition to soil water status, the need for irrigation depends also on plant water status (Hsiao, 1990). Plant water status depends on soil water status, evaporative demand of the atmosphere and other plant characters such as root distribution, and hydraulic conductance (Jones, 1990). Several physiological indicators of plant water, stem and leaf water potentials, stomatal conductance and hydraulic conductance are postulated as possible criteria for scheduling irrigation due to their sensitivity to soil water status (Jones, 1990).

Empirical relationships are commonly used to describe water flow and quantification of water uptake and plant water status in the soil-plant system. For steady state conditions, water uptake ( $Q$ ) is proportional to water potential difference. The total resistance ( $R_T$ ) to water flow can be defined as:

$$R_T = \psi_o - \psi_l / Q = \psi_s - \psi_l / Q \quad 1$$

where,  $\psi_o$  is the average water potential at sites of entry into the roots (average soil water potential) and  $\psi_l$  is the average exit potential in the leaves (average leaf water potential). The pathway of water movement can be described using the following equations;

$$T = Q = (\psi_s - \psi_r) / R_s = (\psi_r - \psi_l) / R_p = (\psi_s - \psi_l) / R_T \quad 2$$

where,  $T$  is transpiration rate,  $Q$  is the root water uptake,  $\psi_s$ ,  $\psi_r$  and  $\psi_l$  are the water potential in the soil matrix, at the root surface and in plant leaves, respectively.  $R_s$  and  $R_p$  are resistances of the soil and plant pathway, therefore,

$$R_T = R_s + R_p \quad 3$$

The diurnal time scale of plant water status and stomatal behaviour could be regulated by the hydraulic transport efficiency of sweet pepper, a herbaceous annual. It is hypothesised that in bell pepper

grown under different fertigation regimes, declines in soil water availability will be accompanied by changes in within plant water uptake and transport capacities. Such regulation will contribute to the prevention of hydraulic failure by ensuring that plant water use does not exceed supply. This is important to acclimation to water stress or adaptation to soil water availability, and these attributes could partly buffer pepper growth and survival under decreased soil water availability. Experiments were conducted to evaluate the physiological behaviour of bell pepper under fertigation regime-enhanced differences in soil moisture status. The aims were to evaluate the coupling of xylem conductance and stomatal conductance and hence the regulation of water use of bell pepper by soil, xylem and canopy hydraulics.

## Materials and methods

Bell pepper were grown on sandy soil in a net house and subjected to varying fertigation regimes. Treatments consisted of factorial combinations of three levels (amounts) of water application by different daily application frequencies. The treatments were replicated four times on 4 x 5m plots while pepper seedlings were planted at a spacing of 90 x 30 cm. Fertigation regimes were made up of daily, twice and once weekly water application, while the fertigation frequencies involved water (and nutrient) application (2, 6 and 10 times per fertigation event at 0600 and 1200h, 0600, 0800, 1000, 1200, 1400 and 1600h, and from 0600 and 1600h at 1-h intervals. Pressure compensated drippers supplying 2.0L h<sup>-1</sup> (Netafim, Inc, Israel) were used. The daily irrigation volumes per plant were 500mL during days 1-32 after transplanting, 800mL beyond days 32 to termination of experiment, and with excess at least equal to the total evapotranspiration. Irrigation scheduling was automatically implemented by a computer to deliver equal amount of water at different frequencies (time of day). Plants were individually irrigated with nutrient solution via drippers located on soil surface. The N and K concentrations were 13.5mM (constant NO<sub>3</sub>-N/NH<sub>4</sub>-N in ratio 3:1) and 6mM K<sub>2</sub>O, respectively. Micronutrients concentrations (mg L<sup>-1</sup>) were 0.6 Zn, 0.65 Mn, 0.8 Fe, 0.04 Cu, 0.4 B and 0.03 Mo, all EDTA-based (Silber personal communication). The initial pH of the irrigating solutions was 7.1, and irrigating solution was prepared in three 2500-L tanks.

**Root analysis:** The development and distribution of roots (inter-row and intra-row spaces) were monitored using cubic coring tools (10 x 10 x 10 cm). The corers were drill-inserted into the soil at 5, 15 cm circumference around 10 sampled plants/plot. The excavated roots from the samples were put in 2mm sieve and were gently washed free of soil in the laboratory using moderate jets of water. Samples were taken at 10 cm interval to a depth of 60cm. This sampling procedure was advanced at least 50 cm along the row before sampling to avoid edge effects. Measurement of root geometry characteristics by image analysis was performed as described by Costa *et al.* (2000) with minor modifications using a Delta -T Scan (Delta-T Devices Ltd, UK), an interactive scanner-based image analysis of root samples. The scanner incorporates a Hewlett-Packard Scanner (Scan Jet 3c) software set to 300 dots/inch scanning resolution in a PC system. 30-g fresh weight of root samples were stained for 15 min with 0.1% (w/v) toluidine blue prior to analysis. The stained roots were placed in Plexiglas trays on a 4mm layer of water.

## Measurements of plant water potentials and stomatal

**conductance:** Simultaneous measurement of stomatal conductance and leaf water potential (lwp) were made from 0800 to early afternoon in net house grown bell pepper which received six irrigation rates. Plant water potential was measured using a pressure chamber and stomatal conductance with a steady state porometer (model LiCor 1600; LiCOR Inc. USA). Leaf water potential ( $\psi_l$ ) was measured using pressure chamber on detached leaves from the plant and sets of measurements were taken on sunlit leaves ( $\psi_{lL}$ ), shaded leaves ( $\psi_{lS}$ ) and on leaves covered with aluminium foil ( $\psi_{lC}$ ). In order to allow leaf water potential to equilibrate with stem water potential, shaded leaves were taken from inside the canopy, cut and placed in plastic bag covered with aluminium foil for about one and a half hours before measurement of its water potential. The water potential of leaves covered with aluminium foil ( $\psi_{lC}$ ) is therefore equivalent to stem xylem water potential. It is in equilibrium with the potential of the conducting stem vessels below the transpiring canopy (Moreshet *et al.*, 1990). Total root water potential was measured at pre dawn, midday and sunset on excised root segments.

**Estimation of hydraulic resistance:** During each sampling period, the measured transpiration flux and leaf water potential measured hourly were used with daily measurements of root and soil potential to calculate total resistance using Ohm's law analogy (Moreshet *et al.*, 1996; Ruggiero *et al.*, 1999; Tsuda and Tyree, 2000). The overall relationship between difference in water potential between soil and leaf and transpiration was linear, with the slope equal to average plant resistance. Transpiration rate (E) in a plant is equal to the flow of sap through the xylem, Van den Honert equation relates sap flow to leaf and soil water potential and the hydraulic conductance between the soil and the leaf (Tardieu and Simonneau, 1998).  $K_T$  was therefore obtained as the proportionality constant between sap flux ( $E_L$ ) and the gradient in water potential ( $d\psi$ ) between the soil ( $\psi_{soil}$ ) and leaf ( $\psi_{leaf}$ ) needed to maintain the evaporative flux density (Tyree and Zimmermann, 2002).

The model used according to Ruggiero *et al.* (1999) was as follows:

$$T = Q = (\psi_s - \psi_r)/R_s = (\psi_r - \psi_l)/R_p = (\psi_s - \psi_l)/R_T \quad 4$$

$$\text{Therefore, } Q = (\psi_s - \psi_r)/R_s + R_p = \Delta\psi / R_s + R_p \quad 5$$

where, Q is the water flux,  $\Delta\psi$  is the water potential gradient between soil and root system,  $R_{s+1}$  is soil and plant resistance, respectively.

Soil water potential (weighted) was calculated as:

$$\psi_s = \sum i\psi_{si}Lvi/\sum iLvi \quad 6$$

where, Lvi is the root density in soil layer i (i=0.50cm)

Plant resistance was estimated as:

$$R_p = (\psi_r - \psi_l)/Q \quad 7$$

where,  $\psi_r$  is the time-weighted average total root water potential,  $\psi_l$  is total leaf water potential and Q is transpiration flux on a root length basis. Root resistance was estimated from the difference between plant resistance, and  $\psi_l$  is the total leaf water potential and Q is transpiration flux (on a root length basis). Soil resistance was calculated as the difference between total and plant resistance for each measurement day ( $R_s = R_T - R_p$ ).

Total resistance to water flux from the soil through the plant ( $R_T = R_p + R_s$ ) was calculated as follows:

$$R_T = (\psi_s - \psi_L)/Q \quad 8$$

where,  $\psi_s$  is the average soil water potential,  $\psi_L$  is the total leaf water potential and Q is the transpiration flux expressed on a root length basis.

Canopy conductance (gc) was estimated using Fick's law of diffusion and is based on vapour pressure deficit and plant water use (transpiration) (Nobel, 1983; Alacron *et al.*, 2003):

$$E = gsVPD \text{ therefore, } gc = E.VPD^{-1}$$

E (transpiration) and gc (canopy conductance) for gs (stomatal conductance), gc is the aggregate of gs throughout the canopy. Data collected were subjected to analysis of variance (ANOVA) and differences between means were tested with Fisher's Least Significant Test (LSD) (Steel *et al.*, 1997).

## Results and discussion

Differences in the intervals between fertigation events (daily, twice and once weekly) altered the environment for root development and affected soil moisture status, and water relations in bell pepper. The effects of fertigation regimes were significant on root morphology evaluated in terms of root mass densities. Intervals between successive irrigation events and daily fertigation frequencies modified root mass densities (Table 1). Higher root densities were obtained for pepper irrigated twice and once weekly over those irrigated daily. This result was consistent under the different fertigation frequencies at each irrigation event. However, across intervals between successive irrigation events, fertigation frequencies at 6 times per irrigation event produced significantly higher root densities over twice and ten times. The advantages of good root development (root biomass and root length densities) may reside in greater extraction and utilisation of soil water reserves located at shallow depths and possibly in the inter-row areas. Changes in root length and root diameter of bell pepper can possibly explain the observed variability in total resistance to water flow under the fertigation regimes. The rate of root water uptake and hence sap flow within a plant constitutes an important link between stomata and the atmospheric demand. Reduction in the intervals between fertigation events increased water uptake and use. Silber *et al.* (2003) postulated that frequent irrigation eliminates depletion zone at the root-soil interface by supplying fresh nutrient solution to the root surface. Decrease in the time intervals between irrigation events enhanced transpiration flux so that water uptake of plants grown under daily fertigation was about two fold of those irrigated once a week. Decreases in frequencies of irrigation from ten to two events induced a decrease of 6 and 18 % in transpiration (water use) fluxes. High fertigation frequencies especially under well watered situation (water and nutrient application at 6 and 10 times per fertigation event), produced higher midday leaf water potentials. However, under deficit water application (weekly fertigation event), high frequency deliveries (6 and 10 times) produced significant improvement in midday leaf water potentials over less frequent daily water application (2 times per fertigation event) to the rootzone.

The results of this study indicate rapid response of the hydraulic

Table 1. Effect of fertigation frequencies on bell pepper growth characters

	Mean root diameter (mm)	Root fresh weight (g plant <sup>-1</sup> )	Total root length (m plant <sup>-1</sup> )	Root length/unit root fresh weight (m g <sup>-1</sup> FW)	Water suction (K Pa)	Transpiration / unit root length (g h <sup>-1</sup> m <sup>-1</sup> )	Root water uptake (Q) (g h <sup>-1</sup> )
Means of irrigation intervals (I)							
Daily	0.889	33.7	236	7.02	-0.98	9.05	0.92
2 days interval	0.688	36.2	273	7.54	-1.07	7.89	0.69
Once weekly	0.623	38.5	297	7.71	-1.23	4.53	0.75
Means of fertigation frequencies/irrigation event (F)							
10 times	0.821	27.8	178	6.40	-0.92	8.91	0.48
6 times	0.793	24.3	211	8.68	-1.12	5.63	0.79
2 times	0.712	21.5	223	10.37	-1.19	3.06	1.04
LSD (P=0.05)							
Amount (I)	0.14	3.5	31.7	1.5	0.52	NS	0.51
Frequency (F)	0.01	4.7	21.4	NS	0.38	1.53	0.34
I x F	NS	*	*	NS	*	*	*

Table 2. Whole plant hydraulic resistance and water relation parameters of bell pepper as affected by fertigation regimes

Treatments	Leaf water potential midday (MPa)	Stomatal conductance (mmol s <sup>-1</sup> )	Hydraulic resistance (g s <sup>-1</sup> MPa <sup>-1</sup> )			Canopy resistance RGC
			RT	RS	RP	
Means of irrigation intervals (I)						
Daily	-0.61	191.3	0.13	0.08	0.05	0.24
2 days interval	-0.78	173.1	0.17	0.09	0.08	0.32
Once weekly	-0.91	161.4	0.21	0.11	0.10	0.56
Means of fertigation frequencies/irrigation event (F)						
10 times	-0.53	169.8	0.16	0.09	0.07	0.28
6 times	-0.68	155.2	0.22	0.12	0.10	0.44
2 times	-0.77	147.7	0.27	0.15	0.12	0.82
LSD (P=0.05)						
Amount (I)	0.21	25.3	0.08	0.03	0.02	NS
Frequency (F) 0.05	12.6	0.05	NS	NS		0.4
I x F	NS	*	*	NS	*	*

and stomatal apparatus in bell pepper, to rootzone water regimes. The measurements of stomatal conductance (gs) on several soil water availability treatments showed that gs is sensitive to water potentials in the soil (-0.92 to -1.23 MPa, Table 1) and leaf (-0.53 to -0.91 MPa, Table 2). Over deficit irrigation, superior within plant xylem transport and canopy resistances and plant water potentials were recorded in daily irrigated bell pepper (Table 2). Regardless of decreases in transpiration fluxes, hydraulic conductance in the vascular system ( $R_p$ ) was maintained. Thus it appears that plant water stress did not attain level of cavitation threshold and disruption of water conducting system. Although, reduced ability of the soil and within plant water transport capacity to supply water to the shoot system could have induced stomatal closure in water stressed plants, little changes in leaf water potential supported the concept of homeostasis of the hydraulic architecture under variable soil moisture conditions. The changes in transpiration fluxes indicated stomatal adjustment of transpiration under variable soil moisture status (irrigation regimes). The estimated value of  $R_t$  confirmed increased hydraulic resistance under deficit water application (Ruggiero *et al.*, 1999). Under water stress condition, the increases in resistance to water movement through plant to the canopy could have caused declined stomatal and canopy conductances. Soil drought increased the resistances (soil and plant) in the pathway of water flow in the SPAC via decreases in root water uptake and transpiration fluxes. Therefore, as water depletes in the rootzone, water uptake and transport

within the xylem system adjust as necessary. The increase in plant resistance under low soil moisture status (deficits) observed may be due to loosening of root-soil contact and an altered hydraulic properties in this interfacial region. Associated with increasing soil resistance for water uptake is decreased hydraulic conductance from soil to canopy ( $K_s-l$ ). However, root surface and its vicinity are frequently supplied with fresh water (nutrients) in solution by subsequent redistribution following fertigated drip irrigation events. Transpiration during the day may cause significant differences between the water content in the root zone and that in the bulk soil. Silber *et al.* (2003) reported that frequent replenishments eliminate the depletion zone formed at the root surface by uptake of water during period between successive irrigation events and decreases the concentration gradient between the medium solution and the root surface.

The components of the resistance elements in the SPAC changed as a function of the status of water in the root zone (RZ). When the total plant resistance was separated into its components, the trend observed was a greater water consumption in well irrigated pepper plants (Table 2). Soil resistance to water flow averaged about 30 % of the total resistance, and constituted a predominant part of the total resistance in the SPAC. In general, the magnitudes of plant resistance were smaller than those of soil system. The estimated value of soil and plant resistances confirmed greater soil and plant hydraulic resistance under deficit water application

resulting from remarkably larger root and canopy resistances. The resistance elements were normalised to the leaf area, stem cross section and root length in order to obtain resistances in relation to plant attributes (Table 3). The relative effect of treatments was similar when resistances were expressed per unit leaf and sapwood area (specific resistance). Plant attribute specific resistances (hydraulic resistance expressed on root length, leaf area and stem cross section) are in the range of those reported for herbaceous species on the field (Stuedle and Peterson, 1998; Ruggiero *et al.*, 1999). The observed trends following the scaling of the hydraulic resistance elements with root length, sapwood and leaf areas possibly explains the sufficiency of the hydraulic system in the maintenance of favourable plant water status and canopy water use. The trade-off between within plant water transport and canopy water use is an ecophysiological attribute with strong impact on the performance of a species under variable environmental conditions (Agele *et al.*, 2005). Low hydraulic resistance was responsible for greater water uptake per unit leaf and sapwood area under well watered situation. The homeostatic balance between the areas of leaf and sapwood/stem cross section (Huber value) could serve to maintain similar water potential gradients and hence water demands between the stem and canopy despite differences in soil moisture availability.

Soil drying (deficit irrigation condition) brought about declined leaf  $\Psi$  and increased soil and plant resistances. In circumstances of low soil water status, soil conductivity decreases sufficiently, leaf  $\Psi$  declines more than soil  $\Psi$  to overcome the increase in resistance to water uptake. Hence, stomata may be induced to close sufficiently by low soil  $\Psi$  or high evaporative demand causing a reduction in transpiration and hence a smaller difference in potentials between soil and leaf. Therefore, plants can suffer water stress on days of high evaporative demand even when the soil is well supplied with water (atmosphere induced water stress). This behaviour complicates the use of sole plant indicators for scheduling irrigation since these indicators would call for irrigation on days of high evaporative demand despite that soil is wet. The need to use plant indicators in addition to soil indicators cannot be over emphasized. It is therefore necessary to evaluate plant indicators in the context of evaporative demand and transpiration. There is a minimum level of soil water allowable before irrigation is intended to keep leaf  $\Psi$  at or above a given limit. For example, under high frequency fertigation, frequent replenishment of depleted water in the root zone means that the limit of soil  $\Psi$  would be extended because of smaller difference in potential needed between the soil and leaf to drive water uptake. Under

Table 4. Important relationships among water relation parameters in bell pepper

Parameters	Regression equations	r <sup>2</sup>	P
swp and lwp	y=-1.05+1.90	0.95	P<0.05
swp and gs*	y=-1.23x+304.1	0.94	P<0.05
swp and Tn	y=-16.29+21.64	0.87	
swp and Q	y=-1.42x+2.36	0.91	P>0.05
swp and gc	y=-1.63x+2.3	0.90	
swp and R <sub>T</sub>	y=-0.57x+0.84	0.93	P<0.05
Swp and R <sub>p</sub>	y=0.13x <sup>-3.57</sup>	0.79	
Lwp and Q	y=1.37x-0.22	0.97	P>0.05
Lwp and R <sub>p</sub>	y=0.29-0.12	0.97	P<0.05
Lwp and gc	y=1.55x-0.61	0.98	
gs and gc	y=2.15Ln(x)10.48	0.97	P<0.05

\*gs is stomatal conductance, swp is soil water potential, lwp is leaf water potential, R<sub>T</sub> and R<sub>p</sub> are total and plant hydraulic resistance, gc is canopy conductance, Q is root water uptake, Tn is transpiration flux

deficit irrigation (once weekly), plant can be allowed to deplete soil water to drier status under high daily frequent fertigation. Larger allowable depletion would imply fewer frequencies of irrigation and more water application per irrigation.

The relation between water potential difference and transpiration flux and hence plant resistance to water flow is influenced by soil moisture status. Our results were consistent with those reported by Stuedle (2000). Hydraulic characteristics optimizes water uptake from the soil and moderate canopy water use. The stomata regulates leaf water potential and leaf area is adjusted as necessary to maximize water uptake and avoid loss of hydraulic contact with the soil. Fertigation regimes and hence root zone water status influenced the responses of stomata and canopy conductance (gc), water uptake and within xylem transport capacity (Kh) in bell pepper. Changes in hydraulic properties and stomatal behaviour enable pepper plants to sense root zone water status and to adjust canopy water loss (transpiration) adequately. Therefore, within xylem transport capacity (Kh) could serve as a signal controlling stomatal closure under soil moisture deficit.

Significant relationships were established among physiological attributes of bell pepper and fertigation regime enhanced differences in soil water potential (Table 4). The measured physiological parameters differed in their sensitivity to irrigation regimes. The strong association among measured physiological parameters (r<sup>2</sup> ranging from 0.70 and 0.90) appeared to indicate adjustment of crop water use under variable soil moisture conditions.

Table 3. Whole plant hydraulic conductance normalized with plant attributes (root length, leaf area and stem cross section) of pepper

Treatments	Leaf area	Stem cross section	Huber value	Specific resistance					
				Root length		Leaf area		Stem section	
				R <sub>T</sub>	R <sub>p</sub>	R <sub>T</sub>	R <sub>p</sub>	R <sub>T</sub>	R <sub>p</sub>
Means of irrigation intervals (I)									
Daily	0.22	0.00011	0.00050	0.00055	0.00021	0.59	0.23	1545.5	454.6
2 days interval	0.20	0.00010	0.00050	0.00062	0.00029	0.85	0.40	1700.0	800.0
Once weekly	0.19	0.000097	0.00051	0.00071	0.00034	1.11	0.53	2164.9	1030.9
Means of fertigation frequencies/irrigation event (F)									
10 times	0.23	0.00013	0.00057	0.00090	0.00039	0.30	0.31	1230.8	438.5
6 times	0.22	0.00012	0.00055	0.0010	0.00047	0.46	0.43	1833.3	833.3
2 times	0.20	0.00010	0.00050	0.0012	0.00054	0.60	0.57	2700.0	1200.0
SE	0.02	0.00004	0.00003	0.0004	0.00005	0.12	0.21	673.7	97.5

The knowledge of water flow within the SPAC and its control of plant's physiological processes is important to the choice of plant based indicators of water status which is directly a basic component of irrigation management strategies. The model used in this study was able to explain the mechanisms involved in the changes in resistance to water flow in the SPAC as influenced by fertigation regimes in bell pepper. Soil drought increased the resistances (soil and plant) in the pathway of water flow in the SPAC via decreases in root water uptake and transpiration fluxes. Therefore, as water is depleted in the rootzone, water uptake and transport within the xylem system adjust as necessary. Under drought, leaf water potential and transpirational water loss adjusted to xylem hydraulic sufficiency and soil water status. A coupling between the canopy and the root system may mean that both systems were tightly synchronized in response to soil moisture status. Homeostatic balance was established between the areas of leaf and sapwood (stem cross sectional), and could serve to maintain similar water potential gradients and hence water demands between the stem and canopy despite differences in soil moisture availability. Sensitive physiological indicators of plant water status which integrate all plant characters are relevant to the understanding of the mechanisms by which plants sense soil water status and can be useful in irrigation scheduling. Plant and weather based tools can be integrated for the development of crop models for estimation of crop water use and productivity, irrigation and water resources management. The observed trends of transpiration fluxes, leaf water potential, soil, plant and total resistance to flow of water and canopy conductance are therefore useful in modeling pepper crop water use.

## References

- Agele, S., S. Cohen and S. Assouline, 2005. Hydraulic characteristics and water relations of net house-grown bell pepper as affected by irrigation regimes in a Mediterranean climate. *Env. Exp. Bot.*, 57: 226-235
- Alarcon, J.J., R. Domingo, S.R. Green, E. Nicolas and A. Torrecillas, 2003. Estimation of hydraulic conductance within field-grown apricot using sap flow measurements. *Plant and Soil*, 251: 125-135.
- Baker, J.M. and C.H.M. van Bavel, 1986. Resistance of plant roots to water loss. *Agronomy Journal*, 78: 641-644.
- Bar-Yosef, B. 1999. Advances in fertigation. *Advances in Agronomy*, 65: 2-77.
- Claassen, N. and B. Steingrobe, 1999. Mechanistic simulation models for a better understanding of nutrient uptake from soil. In: *Mineral Nutrition of Crops, Fundamental Mechanisms and Implications*. (Z. Rengel, ed.). Haworth Press, New York. Pp. 327-367.
- Costa, C., L.M. Dwyer, R. Hamilton, C. Hamel, L. Nantais and D.L. Smith, 2000. A sampling method for measurement of large root systems with scanner-based image analysis. *Agron. J.*, 92: 621-627.
- Hirasawa, T. and K. Ishihara, 1991. On the resistance to water transport in crop plants for estimating water uptake ability under intense transpiration. *Jap. J. Crop Sci.*, 60: 174-183.
- Hsiao, T.C. 1990. Plant-atmosphere interactions, evapotranspiration and irrigation scheduling. *Acta Hort.*, 278: 55-66.
- Jones, H.G. 1990. Plant water relations and implications for irrigation scheduling. *Acta Hort.*, 278: 67-76.
- Jones, J.W., B. Zur, K.J. Boote and L.C. Hammond, 1982. Plant resistance to water flow in field soybean : I. Non limiting soil moisture. *Agron. J.*, 74: 92-98.
- Jones, H.G. 1990. Plant water relations and implications for irrigation scheduling. *Acta Hort.*, 278: 67-76.
- Kramer, J.P. and J.S. Boyer, 1995. *Water relations of plants and soils*. Academic Press, San Diego, CA.
- Lafolie, F., L. Bruckler and F. Tardieu, 1991. Modeling root water and soil-root water transport: model presentation. *Soil Sci. Soc. Am. J.*, 55: 1203-1212.
- Lascano, R.J. and C.H.M. van Bavel, 1984. Root water uptake and soil water distribution: test of an availability concept. *Soil Sci., Soc. Am. J.*, 48: 233-237.
- LoGullo, M.A., A. Nardini, P. Trifilo and S. Salleo, 2003. Changes in leaf hydraulics and stomatal conductance following drought stress and irrigation in *Ceratonia siliqual* (Carob tree). *Physiol. Plant.*, 117: 186-194.
- Moreshet, S., M. Fuchs, Y. Cohen, S. Cohen and M. Langensiepen, 1996. Water transport characteristics of cotton as affected by drip irrigation layout. *Agron. J.*, 88: 717-722.
- Moreshet S., Y. Cohen, G.C. Green and M. Fuc, 1990. The partitioning of hydraulic conductances within mature orange trees. *J. Exp. Bot.*, 41(7): 833-839.
- Nobel, P.S. 1983. *Biophysical plant physiology and ecology*. W.H. Freeman and Co. San Francisco. 608p.
- Passioura, J.B. 1988. Water transport in and to root. *Annu. Rev. Plant Mol. Biol.*, 39: 245-265.
- Rieger, M. and A. Motisi, 1990. Estimation of root hydraulic conductivity on intact peach and citrus rootstocks. *HortScience*, 25(12): 1631-1634.
- Ruggiero, C., S. De Pascale and M. Fagnano, 1999. Plant and soil resistance to water flow in fababean (*Vicia faba*, L. major Harz.). *Plant and Soil*, 210: 219-231.
- Ruggiero, C., S. De Pascale, G. Angelino and A. Maggio, 2003. Development changes in plant resistance to water flow in *Pisum sativum* (L). *Plant and Soil*, 250: 121-128.
- Salleo, S., A. Nardini and M.A. Lo Gullo, 2000. Xylem cavitation and hydraulic control of stomatal in Laurel (*Laurel nobilis* L.). *Plant Cell Environ.*, 23: 71-79.
- Silber, A, G. Xu, I. Levkovitch, S. Soriano and A. Bilu, 2003. High fertigation: the effects on uptake of nutrients, water and plant growth. *Plant and Soil*, 253: 467-477.
- Sperry, J.S., U.G. Hacke, R. Oren and J.P. Comstock, 2002. Water deficits and hydraulic limits to leaf water supply. *Plant Cell Environ.*, 25(2): 251-263.
- Steel, R.D., J.H. Torrie and D.A. Dickey, 1997. *Principles and Procedures of Statistics. A Biometrical Approach*. 3<sup>rd</sup> Edition. New York, McGraw Hill. 665p.
- Steudle, E. 1994. Water transport across roots. *Plant and Soil*, 167: 79-90.
- Steudle, E. 2000. Water uptake by plant roots: an integration of views. *Plant and Soil*, 226: 45-56.
- Steudle E. and C.A. Peterson, 1998. How does water get through roots. *J. Exp. Bot.*, 49: 775-788
- Stiller, V., H.R. Lafitte and J.S. Sperry, 2003. Hydraulic properties of rice and the response of gas exchange to water stress. *Plant Physiol.*, 132: 1698-1706.
- Tardieu, F. and T. Simonneau, 1998. Vulnerability among species in stomatal control under fluctuating soil water status and evaporative demand: modeling isohydric and anisohydric behavior. *J. Exp. Bot.*, 49: 419-432.
- Tsuda, M. and M.T. Tyree, 2000. Plant hydraulic conductance measured by the high pressure flow meter in crop plants. *J. Exp. Bot.*, 51: 823-828.
- Tyree, M.T. and M.H. Zimmermann, 2002. *Xylem structure and the ascent of sap*. Springer Verlag, Berlin.
- Zur, B., J.W. Jones, K.J. Boote and L.C. Hammond, 1982. Total resistance to water flow in field soybeans: II. Limiting soil moisture. *Agron. J.*, 74: 99-105.