

Stomatal resistance, leaf water potential and hydraulic resistance of sugar beet plants

J. HUZULÁK and F. MATEJKA*

Research Institute of Irrigation, Vrakunská 29, 825 63 Bratislava, Czechoslovakia
Geophysical Institute, Dúbravská 5, 842 28 Bratislava, Czechoslovakia

Abstract

Stomatal resistance (r_L) and leaf water potential (ψ_L), soil moisture and the course of meteorological factors were measured in irrigated and non-irrigated sugar beet canopies during three years. By means of the canopy water balance equation, theoretical analysis of observed dependencies of stomatal resistance upon leaf water potential was made. The changes of r_L were not induced by the change of ψ_L but by that of external and internal factors, ψ_L correlates with. Therefore the empirical dependence of stomatal resistance upon leaf water potential cannot be generalized.

Introduction

The exact principle of the relation between leaf water potential and the behaviour of stomata is still not clear but the empirical relationship between stomatal resistance and leaf water potential was described in many works (for review see *e.g.* Pospíšilová and Solárová 1980, Jones 1988). Many of these works issue from experimental bases obtained during a single growing period. The aim of this work is to summarize the results of stomatal resistance and leaf water potential measurements of irrigated and non-irrigated sugar beet obtained during a three years period; atmospheric factors and soil moisture were also monitored. This research is a part of a larger project on mathematical modelling of sugar beet water regime.

Material and methods

Experiments were made with sugar beet (*Beta vulgaris* L. var. *saccharifera* cv. Polyna) at the Research station near Bratislava (southwest Slovakia, 48.08 north lat., 17.17 north long., 130 m above sea level) having a carbonate black soil type. Atmospheric precipitation represents the only natural water resource in the locality. One half of the experimental plot was sprinkler irrigated.

This article summarizes results of the 1987, 1988 and 1990 seasons. We may characterize the meteorological conditions of these seasons by means of Penman estimates of potential evapotranspiration, the sums of which, for the growing period of each season (April to September) were 654, 859 and 883 mm, respectively. During these same periods the total amounts of natural precipitation were 255, 224 and 245 mm, respectively, 73 to 84 % of the long term normal. Ambient air temperature, humidity and wind speeds at 25, 50, 100 and 200 cm above the effective canopy height were measured. Averages of these measurements are presented in Table 1. Soil moisture was determined by means of neutron probe at depths of 20, 40, 60 and 80 cm.

Leaf water potential (ψ_L) was measured psychrometrically with a *Wescor Dew Point Hygrometer* (a minimum of 5 replications of each measurement were made). Stomatal resistance of upper and lower leaf surfaces was measured with an automatic diffusive porometer, type *Mk 3 (Delta-T Devices)*. The total leaf resistance (r_L) was calculated in accordance with the relation $1/r_L = 1/r_{ad} + 1/r_{ab}$, where r_{ad} , r_{ab} are adaxial and abaxial resistances, respectively. For each measurement, resistances were determined for 6 to 10 leaves of approximately the same age (the youngest full-sized leaves). Averages calculated from these values are the basis for statistical analysis. Measurements were made daily at 9 a.m. and 1 p.m. except on extremely cloudy or rainy days. Boundary layer resistance values (r_a) were calculated in accordance with the method published by Hortalová and Szabó (1985).

Result and discussion

We were primarily interested in the differences in the relationship between leaf water potential and stomatal resistance between each season and between irrigated and non-irrigated plants. Stomatal resistance in sugar beet is variable between plants and even within a single plant (Brown and Rosenberg 1970). Therefore we divided measured values of ψ_L into 0.25 MPa intervals (e.g. 0.75 - 0.99 etc.). For each interval the mean values of ψ_L and r_L were calculated and plotted (Fig. 1). The relationship was approximated by exponential function (with the exception of seasons 1988 and 1990 for the irrigated variant). The applied exponential functions satisfactory describe the course of the studied dependence in non-irrigated plants. In the case of the irrigated plants this relation may be used only for the 1987 season. Testing of coefficients of these functions has shown that the differences between each season are statistically significant at the 0.05 level of significance.

In effort to explain the obtained results (Fig. 1) the canopy water balance equation stated by Choudhury and Idso (1985b) was used. This equation has after a simple algebraic modification the following form:

$$\frac{\Delta R_n r_a + \rho c_p d}{\Delta r_a + \gamma (r_a + r_c)} = \frac{(\psi_s - \psi_L) L}{g (R_s + R_p)} \quad (1)$$

where Δ is the rate of change of saturated vapour pressure with temperature [$\text{Pa } ^\circ\text{C}^{-1}$], R_n is net radiation [W m^{-2}], r_a and r_c are boundary layer and canopy resistances [s m^{-1}], ρ is the density of air [kg m^{-3}], c_p is the specific heat of air [$\text{J kg}^{-1} \text{C}^{-1}$], d is the vapour pressure deficit [Pa], ψ_s is the soil water potential [Pa], ψ_L is the leaf water potential [Pa], γ is the psychrometric constant [$\text{Pa } ^\circ\text{C}^{-1}$], L is the latent heat of vaporization of water [$2.44 \cdot 10^6 \text{ J kg}^{-1} = 2.44 \cdot 10^9 \text{ J m}^{-3}$], R_s and R_p are soil and plant resistances. The sum of R_s and R_p is sometimes denoted as hydraulic resistance (Lawlor and Milford 1975).

From equation (1) canopy resistance r_c can be expressed as follows:

$$r_c = \frac{g(\Delta R_n r_a + \rho c_p d)}{\psi_s - \psi_L} \cdot \frac{R_s + R_p}{\gamma L} - r_a \left(1 + \frac{\Delta}{\gamma}\right) \quad (2)$$

For brevity in the following discussion we will designate the first fraction on the right side of the equation (2) with the symbol A, the second fraction with the symbol B and the last term with the symbol C. Equation (2) will then have the following form:

$$r_c = A \cdot B - C \quad (3)$$

In order to use the measured values r_L in equation (2), that is to change to the canopy level, we used the procedure from the work of Choundhury and Idso (1985a) which for the given canopy leads to the following relation:

$$r_c = r_L / [1 + 0.265 (\text{LAI} - 1)] \quad (4)$$

where LAI is the leaf area index.

Considering the fact that ψ_L acts in the denominator in equation (2), canopy resistance should decrease with the descent of the value ψ_L , rather than increase as it is shown in the four diagrams of Fig. 1. This ascend of resistance r_c with decreasing ψ_L may be induced only by correlation between ψ_L and some other factor on the right side of equation (2).

Now let us analyse the importance of each term of equation (3) for the resulting value r_c . For wind speed higher than 2 m s^{-1} the term C is low (maximal values of 0.4 s cm^{-1}). The coefficient of variation of the fraction A is 27.2 % for the whole analysed period. For consideration of variability of the fraction B we calculate its values from the modified relation (1) whereby we use the measured values of r_L , soil moisture and meteorological factors. The coefficient of variation of values of fraction B calculated in this way is 69.8 %. From the comparison of coefficient of variation follows that the value of the fraction $(R_s + R_p)/L$ is of dominant importance for leaf as well as canopy resistance.

To verify the above mentioned hypothesis the relation between the values B and ψ_L was graphically expressed (Fig. 2). In non-irrigated plants there is a clear tendency of growth of B values with fall of ψ_L . This fact influences the character of

dependences in Fig. 1. In the case of irrigated canopy one may speak about this tendency only for the 1987 season.

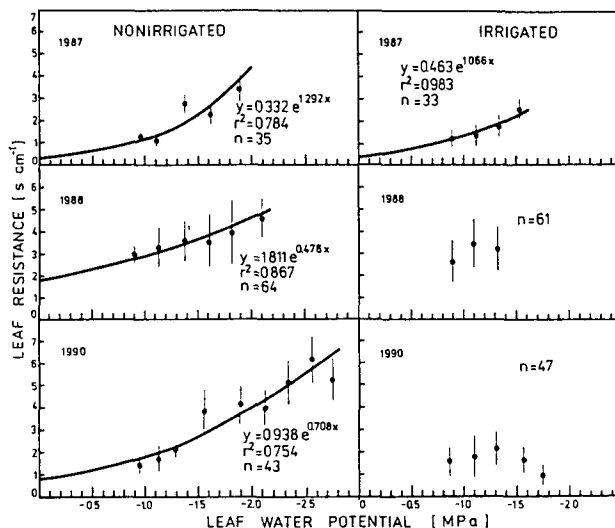


Fig. 1. The dependence of leaf stomatal resistance on leaf water potential for irrigated and non-irrigated plants (r^2 is the correlation coefficient, n is the number of measurements in the given season., bars indicate standard errors).

The values of stomatal resistance in the 1988 season are high in comparison to other seasons. Probably there are two reasons. Primarily the average value of the term A in equation (2) is approximately 1.2 times higher in the 1988 season than in that of 1987. Also the value of the term B is approximately 1.8 times higher in the 1988 season than in that of 1987.

Table 1. Mean values of measured characteristics for non-irrigated (N) and irrigated (I) fields. Q - global radiation [W m^{-2}], t - air temperature [$^{\circ}\text{C}$], d - vapour pressure deficit [Pa], v - wind speed [m s^{-1}], ψ_L - leaf water potential [MPa], ψ_S - soil water potential [MPa], B - value defined by formula (3) [$\text{s J}^{-1}\text{m}^3$], r_L , r_{LC} - measured and calculated stomatal resistances [s cm^{-1}].

Year		Q	t	d	v	ψ_L	$\psi_S - \psi_L$	B	r_L	r_{LC}
1987	N	598	23.1	1525	3.0	-1.45	0.96	0.46	2.25	2.38
	I		23.1	1463		-1.17	0.63	0.28	1.68	1.84
1988	N	539	24.3	1577	2.5	-1.48	0.84	0.65	3.65	3.91
	I		22.8	1356		-1.07	0.90	0.56	2.88	2.67
1989	N	628	23.9	1973	1.4	-1.82	1.29	0.79	3.82	4.09
	I		22.5	1610		-1.08	0.82	0.41	2.69	2.59

Apparently the high resistance values in the 1988 season are caused by a different

course of meteorological factors (Table 1), so it is not the individual elements but the total value of the numerator of the fraction A that is decisive. Also, the higher plant resistance R_p participates in the high resistance values in the 1988 season. With regard to the fact that R_p is closely related to transpiration (Choudhury and Idso 1985a) it is not due entirely to only the internal plant factors because transpiration depends also upon external factors.

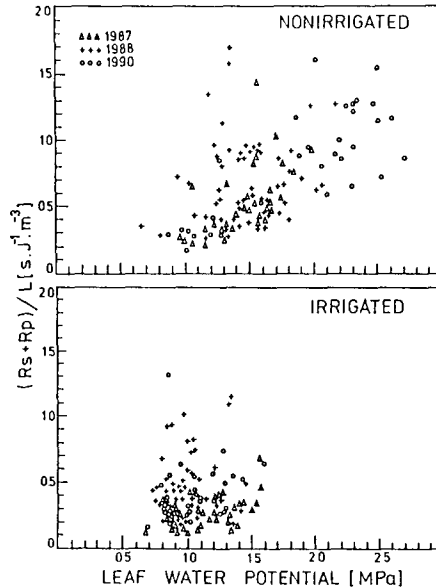


Fig. 2. Relationship between hydraulic resistance ($R_s + R_p$) normalized by latent heat (L), where R_s and R_p are soil and plant resistances, respectively and leaf water potential.

Now let us substitute the average values of input data from Table 1 into the relation (2) and calculate the corresponding average values of resistances for each season and for irrigated and non-irrigated canopy. The calculated values of resistances (the last column in Table 1) agree well with the measured values, which indicates that the relationship in equation (2) expresses the basic features of dependence of stomatal resistance upon external factors.

Let us now compare the average values of stomatal resistances of irrigated and non-irrigated canopies. From Table 1 it follows that the average stomatal resistances of irrigated canopy for the whole analysed period reached only 74 % of the average of resistances of non-irrigated canopy. This descend closely coheres with the descend of values of the fraction B in the irrigated variant. So one may say that as a consequence of irrigation application the hydraulic resistance given to water flow by soil and plant descended. Considering the fact that according to some authors (e.g. Bristow *et al.* 1984) soil resistance is generally by much lower than that of plant the B fraction value is influenced mainly by plant resistance. From Fig. 2 follows that for the irrigated variant the values $\gamma B = (R_s + R_p) / L$ are lower than those for the non-

irrigated canopy.

In irrigated plants the values $\psi_s - \psi_L$ is lower than in non-irrigated plants in the seasons 1987 and 1990 but in the season 1988 the converse is true (Table 1). Bichele *et al.* (1980) ascertained that the values of the difference $\psi_s - \psi_L$ are except of external factors influenced also by the development of plant root system. In accordance with their statements plants with a well developed root system have lower $\psi_s - \psi_L$ values than those with a slightly developed root system. The situation in the 1988 season we may explain in the way that irrigated plants had a slightly developed root system probably as a consequence of the fact that due to very intensive irrigation the average soil moisture was by 8 - 9 % higher in the above mentioned season than in those of 1987 and 1990.

The relation between stomatal resistance and leaf water potential creates a component part of several water regime models of plants and/or canopies (Bichele *et al.* 1980, Jagtap and Jones 1989). Considering the fact that the dependence between these quantities vary season by season it is necessary to calibrate these models every year.

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