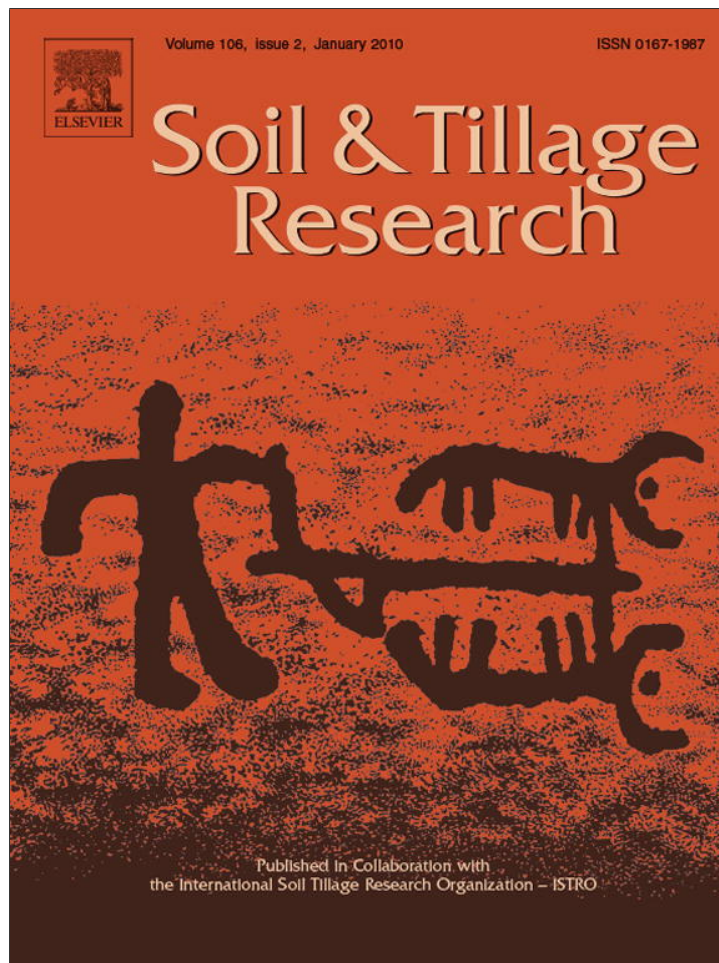


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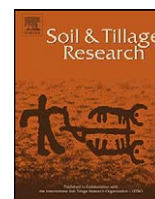
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Evaluating responses of maize (*Zea mays* L.) to soil physical conditions using a boundary line approach

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ABSTRACT

The functional relation between the decline in the rate of a physiological process and the magnitude of a stress related to soil physical conditions is an important tool for uses as diverse as assessment of the stress-related sensitivity of different plant cultivars and characterization of soil structure. Two of the most pervasive sources of stress are soil resistance to root penetration (SR) and matric potential (ψ). However, the assessment of these sources of stress on physiological processes in different soils can be complicated by other sources of stress and by the strong relation between SR and ψ in a soil. A multivariate boundary line approach was assessed as a means of reducing these complications. The effects of SR and ψ stress conditions on plant responses were examined under growth chamber conditions. Maize plants (*Zea mays* L.) were grown in soils at different water contents and having different structures arising from variation in texture, organic carbon content and soil compaction. Measurements of carbon exchange (CE), leaf transpiration (LT), plant transpiration (PT), leaf area (LA), leaf + shoot dry weight (LSDW), root total length (RTL), root surface area (RSA) and root dry weight (RDW) were determined after plants reached the 12-leaf stage. The LT, PT and LA were described as a function of SR and ψ with a double S-shaped function using the multivariate boundary line approach. The CE and LSDW were described by the combination of an S-shaped function for SR and a linear function for ψ . The root parameters were described by a single S-shaped function for SR. The sensitivity to SR and ψ depended on the plant parameter. Values of PT, LA and LSDW were most sensitive to SR. Among those parameters exhibiting a significant response to ψ , PT was most sensitive. The boundary line approach was found to be a useful tool to describe the functional relation between the decline in the rate of a physiological process and the magnitude of a stress related to soil physical conditions.

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1. Introduction

The potential growth of crops is determined by the varietal characteristics under optimal environmental conditions. However, crop growth often must occur under adverse environmental conditions. Soil physical properties, especially those controlling the availability of O₂ and water to the plant root, and the soil mechanical resistance to root penetration (SR) are among the most important limitations (Letey, 1985; Sadras and Milroy, 1996).

Diminished availability of O₂ has been found to reduce leaf growth, transpiration and photosynthesis (Meyer et al., 1987) as well as root extension (Blackwell and Wells, 1983; Huang et al., 1997). The impact of limiting availability of water on plant growth has often been assessed in relation to water potential. Increasing

matric potential (ψ) in the soil has been shown to have negative effects on stomatal conductance, photosynthesis rates, leaf expansion, and root growth (Boone et al., 1986; Dexter, 1987; Passioura, 1991; Tardieu et al., 1991; Sadras and Milroy, 1996; Ali et al., 1998; Whalley et al., 1998; Jensen et al., 2000; Zou et al., 2000; Kay et al., 2006).

Soil mechanical resistance may control plant growth by reducing root elongation rate and root dry weight (Taylor and Gardner, 1963; Taylor and Ratliff, 1969; Masle and Passioura, 1987; Veen and Boone, 1990; Misra and Gibbons, 1996; Materechera and Mloza-Banda, 1997; Zou et al., 2001), as well as leaf and shoot expansion, and stomatal conductance (Masle, 1998).

The functional relation between the rate of different physiological processes and the magnitude of a soil physical limitation is a particularly powerful tool that has been used to assess the sensitivity of species or cultivars to stress as well as to characterize soil structure (Letey, 1985; Boone et al., 1986; da Silva and Kay,

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1996). That relation is most relevant if the other limitations are either not contributing to the response of the physiological process or their contribution can be defined. However, some physical limitations are closely related creating difficulties in assessing them independently. This challenge is most obviously illustrated with ψ and SR. Both ψ and SR increase as the soil water content decreases from saturation and the increase varies with texture, organic carbon content and soil compaction (Kay et al., 2006).

Two techniques are frequently used to develop a functional relation between the rate of a physiological process and the magnitude of the physical limitations: (i) the multiple linear regression and (ii) the law of the minimum of the limiting factors (Casanova et al., 1999). However, the natural variability and the unpredictability of uncontrollable factors may mask the results making difficult the evaluation of the relationship between the two variables. An approach that may overcome those problems involves the use of the boundary line approach, which was introduced by Webb (1972).

The boundary line approach is based on the principle that biological materials have an upper limit of response in a given situation. In a scatter-gram, data appear as an array of points. The line connecting the points located at the outer margin of the array represents the functional relationship between the dependent and the independent variable when unaffected by other variables. Webb (1972) defined this line as a boundary line. Points located below the outer margin are influenced by other independent variables. Several procedures were used to select the border points and to fit the boundary line since standard statistical packages do not provide a way for fitting a curve to the maximum response (Shatar and McBratney, 2004). None have been widely adopted and all are somewhat ad hoc (Milne et al., 2006). Despite this, the fitting of boundary lines includes the following steps: (i) grouping data points according to their predictor variable, (ii) dividing data in subsets by splitting the x-axis in categories, (iii) removing outliers, (iv) identifying the maximum-yield subset, and (v) curve fitting.

The technique was successfully applied to develop soil nutrient norms for soybean production (Evanylo and Sumner, 1987), and to determine foliar nutritional standards for white spruce for all major nutrients (Quesnel et al., 2006). It was also employed to study the stomatal conductance patterns and their controlling variables of phreatophytes species (Foster and Smith, 1991), as well as to quantify the interplay between soil biochemical/physical variables and the N_2O flux (Elliot and de Jong, 1993; Bergstrom and Beauchamp, 1993; Schmidt et al., 2000; Farquharson and Baldock, 2008). Casanova et al. (1999) applied boundary line analysis to quantify the soil properties that limit rice growth. The authors derived mathematical functions to construct boundary lines, thereby making the process reproducible and more comprehensible. However, the models have been generally limited to linear regression. More recently, more flexible curves were found to be useful for the identification of causes of yield variation (Shatar and McBratney, 2004).

The boundary line approach is normally used to relate the dependent variable to one independent variable at a time. However,

this approach cannot be used when two of the independent variables are closely related to one another and a physiological process is influenced by the combination of both variables. Under these circumstances we hypothesize that a multivariate boundary line approach can be used to study the relationships between plant growth parameters and soil physical properties, with the two independent variables combined in a single function to describe the stress. Therefore the objectives of this research were to: (i) evaluate plant growth responses to soil mechanical resistance and water potential stress conditions and (ii) assess the feasibility of determining the response of different physiological parameters to those stress conditions using multivariate boundary line analyses.

2. Materials and methods

The assessment was undertaken using data collected in a study, the methodology of which was described by Kay et al. (2006). A brief summary of their methodology is provided for the benefit of readers; additional details are provided by Kay et al. (2006).

Maize (*Zea mays* L.) plants (Pionner, 3902) were grown in cylindrical plastic pots (6 l) in a growth chamber (Model PGW36, controlled environments, Winnipeg, Manitoba) providing temperatures of 26/16 °C day/night, with a 16-h photoperiod, and a relative humidity of 75%. The photosynthetic irradiance was maintained at 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the canopy, with a mixture of cool white fluorescent tubes and inside frost tungsten bulbs.

2.1. Determination of soil parameters

Variation in soil structure was achieved using four soils of different textures and organic carbon contents and similar pH and mineralogy. The soils (Table 1), collected from the A horizon (0–20 cm), were air-dried, sieved (<6 mm) and packed to a relative compaction of 0.83 and 0.91 (Håkansson, 1990). These values are commonly found under conventional till (0.83) and no-till (0.91) across a range of soil texture, organic carbon contents and climates (Kay et al., 1997). Nutrients were added at rates of 150 mg P and 50 mg K per kg of soil. Nitrogen was added at two rates (1.0 or 2.0 g N per pot) since preliminary studies indicated N contents may influence plant response to soil physical conditions. The pots were maintained at different water contents. Air content (volume air-filled pores/total volume of soil) was used as the water variable.

Soils subsamples ($n = 216$) were packed in rings (5 cm diameter, 2.5 cm height) at the required bulk densities to determine the soil resistance to root penetration (SR) and the water release curve. The samples were saturated with water for 24 h and split randomly into nine groups of 24 samples, with each sample group subjected to one of the following matric potentials (ψ): -0.001 , -0.002 , -0.004 , -0.006 , -0.01 , -0.033 , -0.1 , -0.4 , and -1.5 MPa using pressure chambers as described by Klute (1986). After equilibration, SR was measured in the center of each sample at a constant rate (2 mm min^{-1}) of penetration using an electronic penetrometer with a 30° angle cone and a 4 mm basal diameter. The readings for each ring were collected by an automated system of data acquisition throughout the 0–2.5 cm depth. The measurements

Table 1
Characteristics of the selected soils.

Soil name	Clay g kg^{-1}	Silt g kg^{-1}	Sand g kg^{-1}	Textural class	OC g kg^{-1}	Bd Mg m^{-3} RC = 0.83	Bd Mg m^{-3} RC = 0.91
Fox (Luvisol)	88	197	715	Sandy loam	13.7	1.41	1.55
Conestogo (Chernozem)	171	472	358	Loam	25.5	1.21	1.31
Perth (Luvisol)	257	560	183	Silt loam	15.6	1.28	1.40
Huron (Podzol)	363	532	106	Silty Clay loam	18.9	1.25	1.37

OC = organic carbon; Bd = soil bulk density.

were averaged across depth. The samples were then oven dried and the water content determined in order to enable the calculation of the ψ and SR at different water contents. The soil water release data were fitted to the function proposed by Van Genuchten (1980) and the soil resistance data were regressed against (θ) using a model proposed by Busscher et al. (1997).

2.2. Determination of plant parameters

The experiment was carried out as a randomized complete block design with four soils, two levels of relative compaction (RC = 0.83 and RC = 0.91), two levels of nitrogen (1 and 2 g of N/pot), three wetting treatments (10, 15 and 20% air-filled porosity), and three replications ($n = 144$). Up to the 12-leaf stage, pots were regularly weighed and plants watered to maintain the value of 10, 15 or 20% air-filled porosity. The amount of required water was calculated from the pot weight, the weight of oven dried soil in each pot, the soil volume, the density of the water and the estimated fresh weight of the plants. The plant fresh weight at different leaf stages was estimated according to previous maize physiological studies (Tollenaar and Migus, 1984).

Once the plants reached the 12-leaf stage, plant growth measurements were initiated. The pots were completely enclosed in white plastic bags and the bags tightened around the base of the stem to prevent evaporation from the soil. The pots were weighted before the end of the light period each day and water added to return the water content to that equivalent to an air content of 10, 15 and 20%. This timing maximized the opportunity for water redistribution in the pots prior to the start of the next light period. At the conclusion of the measurement period, the total plant biomass was measured and these values used to make minor adjustments to the plants weights used in estimating soil water contents. Following adjustment, the water contents after the daily addition of water were used to calculate the corresponding water potential (ψ) and soil mechanical resistance (SR) of each pot using the measured water release and soil resistance curves.

Rates of carbon exchange (CE), leaf transpiration (LT), and whole plant transpiration (PT) were measured daily at the middle of the light period for all treatments. Whole plant transpiration measurements were based on the difference in the pot weight on successive days minus the plant weight increase. Carbon exchange rate was measured using a portable, open-flow gas exchange system LI-6400 (LI-COR Inc., Lincoln, NE), on the youngest, fully expanded leaf. All carbon exchange and leaf transpiration rates were calculated by the LI-6400's operating software, which follows the method of Von Caemmerer and Farquhar (1981). Detailed information about the experiment is shown in Kay et al. (2006).

After completion of the plant growth measurements, plants were harvested and leaf area (LA) was measured. The leaf and stem dry weight (LSDW) was determined after drying at 80 °C. Roots were carefully washed free from the soil, dried at 80 °C to a constant weight and root dry weight (RDW) determined. Then, the material was placed on a scanner and root total length (RTL) and root surface area (RSA) determined using WinRHIZO (Regent Instruments Inc.).

2.3. Determination of the boundary lines

In order to use the boundary line approach, plant parameters were converted to fractional values (F -values) of their maximum according to Bergstrom and Beauchamp (1993). For each considered plant parameter, the F -values were calculated as the ratio of each measured value to the maximum measured value in the data set ($n = 144$). Then, the average F -value for the three replications of each treatment was obtained ($n = 48$). Scatter-grams of the average

F -values of all treatments for each plant parameter versus the measured values of ψ and SR were generated (as an example to see Fig. 2). After that, only the points located at the outer margin of the array in each of the ψ and SR plots (solid data points) were selected and merged in order to get a combined data set, which was used to fit a multivariate boundary line model. Points located below the outer margin (void data points) were not included because they reflect the influence of other independent variables.

In formulating the multivariate boundary line model, it was assumed that the influence of ψ and SR on a physiological process were additive (Dexter, 1987). Different functions to describe the effect on the plant parameter of the individual forms of stress were evaluated: linear, exponential and an asymmetric S-shaped function following the form of the Van Genuchten function (1980). Functions were quantified using nonlinear regression analysis with the STATISTICA software package (StatSoft, Inc., 2003). The starting form of the multivariate function was a double S-shaped function,

$$PP = \left(b_1 + \frac{1 - b_1}{1 + (b_2 \times SR)^{b_3}} \right)^{\left(1 - \frac{1}{b_5} \right)} - \left(b_4 - \frac{b_4}{(1 + (b_5 \times \psi)^{b_6})} \right)^{\left(1 - \frac{1}{b_6} \right)} \quad (1)$$

where PP is the F -values of each plant parameter and b_1 , b_2 , b_3 , b_4 , b_5 , and b_6 are constants. Values of $(b_1 - b_4)$ represent the value of PP that is approached asymptotically with increasing ψ and SR. The remaining constants regulate the shape of the curves. Subsequent analyses employed different combinations of the three functions. The function with the most complete set of statistically significant coefficients was selected as the final multivariate model.

3. Results and discussion

Values of SR and ψ varied from 0 to 5 and 0 to 0.5 MPa, respectively. Strong nonlinear relations between SR and ψ were exhibited by the different textures and compaction treatments (Fig. 1). The curves illustrate how a single value of SR can be associated with a range of values of ψ when different soil conditions are considered and this value would be expected to lead to differences in plant responses. The statistical moments for the analyzed variables are given in Table 2.

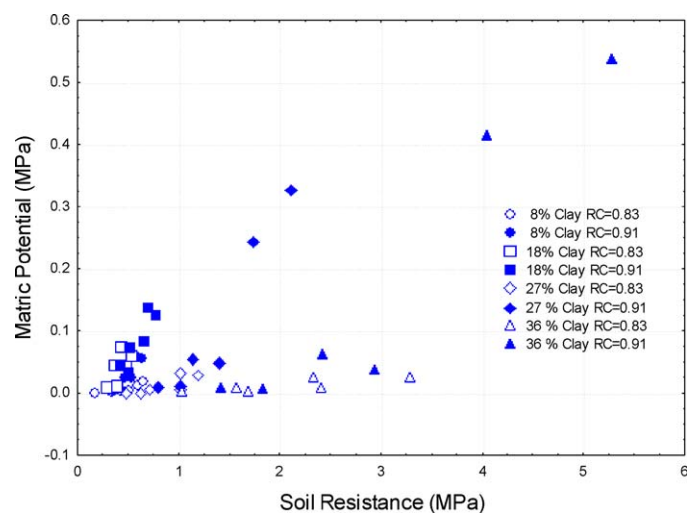


Fig. 1. Relation between soil resistance (SR) and matric potential (ψ) for soils of different clay contents and relative compaction (RC).

Table 2
Statistical moments of the analyzed variables.

Variable	Mean	Maximum	Minimum	SD	CV (%)
CE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	17.9	21.4	14.7	1.5	8.1
LT ($\text{mmol m}^{-2} \text{s}^{-1}$)	2.2	2.7	1.7	0.2	10.7
PT (g day^{-1})	222.3	323.6	107.6	58.3	26.2
LA ($\text{cm}^2 \text{plant}^{-1}$)	2539.8	3326.3	1764.7	368.5	14.5
LSDW (g plant^{-1})	24.2	34.7	14.5	4.9	20.2
RDW (g plant^{-1})	6.1	9.9	2.8	1.7	27.3
RTL (cm plant^{-1})	18418.9	33365.9	6775.2	6786.9	36.8
RSA ($\text{cm}^2 \text{plant}^{-1}$)	4067.4	6832.8	1495.2	1323.9	32.5
$ \psi $ (MPa)	0.06	0.54	0.001	0.11	180
SR (MPa)	1.15	5.27	0.17	0.92	106

CE=carbon exchange; LT=leaf transpiration; PT=plant transpiration; LA=leaf area; LSDW=leaf+shoot dry weight; RTL=root total length; RSA=root surface area; RDW=root dry weight; ψ =matric potential; SR=soil resistance.

Scatter-grams of *F*-values for PT, CE, and RDW are presented in Figs. 2–4, respectively, to illustrate the nature of the response of plant parameters to ψ and SR. The selection of the boundary points is also shown in these figures. The relation first remains almost constant, then decreases at an increasing rate and finally, half way down, begin to decrease at a decreasing rate, and eventually approaches to a limiting value. Similar behavior was verified for the other plant parameters.

The multivariate boundary line model that provided the best description of the combined effect of $|\psi|$ and SR on each plant

parameter is given in Table 3. More complex models involving double S-shaped curves were required for fitting the *F*-values of LT, PT and LA, whereas simpler models were needed for CE, LSDW and the root parameters.

The model (Table 3) for the *F*-value of PT (i.e. PT/PT_{max}) was used to predict values for all observed combinations of $|\psi|$ and SR and then the predicted values of PT/PT_{max} compared to observed values (Fig. 5). The line of best fit for the boundary points and the associated prediction limits (0.95) are also given. The prediction limits of the boundary line encompassed several points not

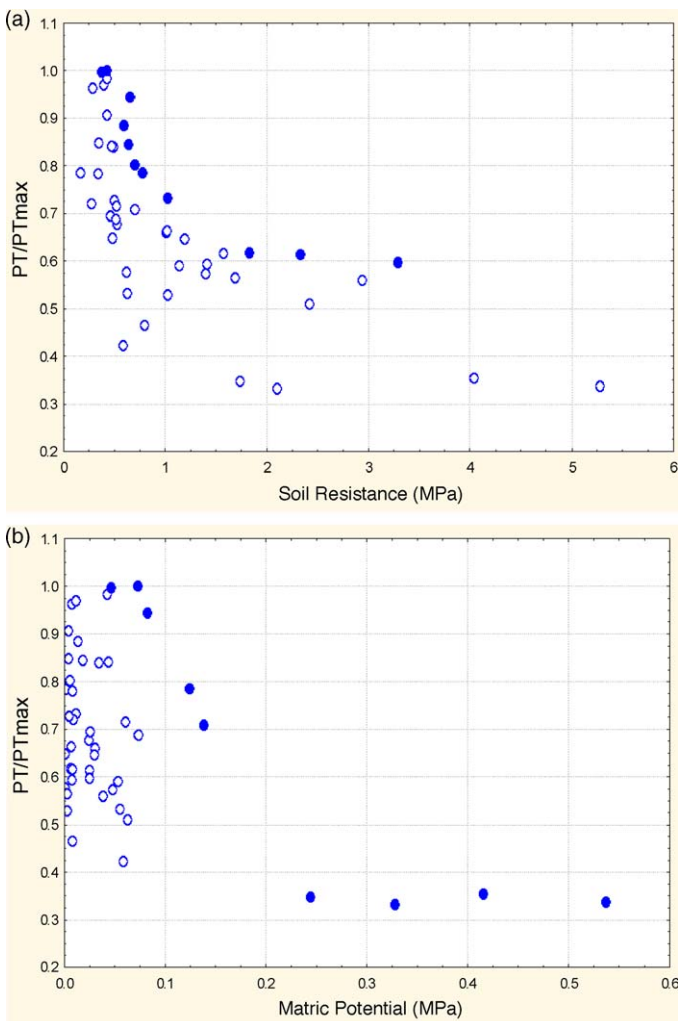


Fig. 2. Scatter-grams of standardized *F*-values for plant transpiration (PT/PT_{max}) versus soil resistance to root penetration (MPa) (a), and soil matric potential (MPa) (b). Solid data points were those selected for boundary line analysis.

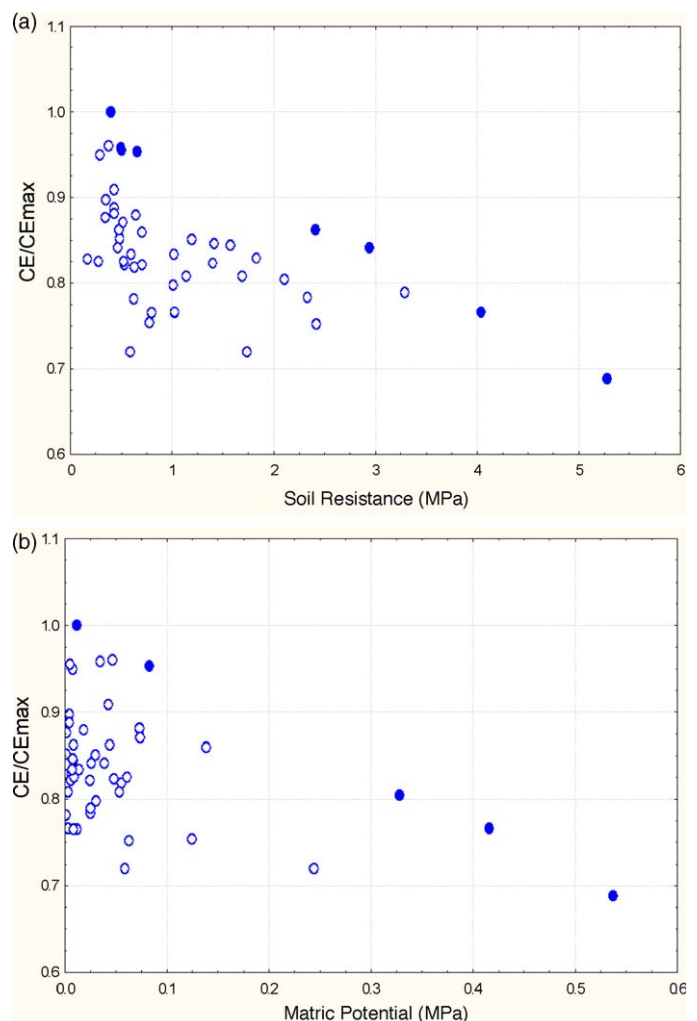


Fig. 3. Scatter-grams of standardized *F*-values for carbon exchange (CE/CE_{max}) versus soil resistance to root penetration (MPa) (a), and soil matric potential (MPa) (b). Solid data points were those selected for boundary line analysis.

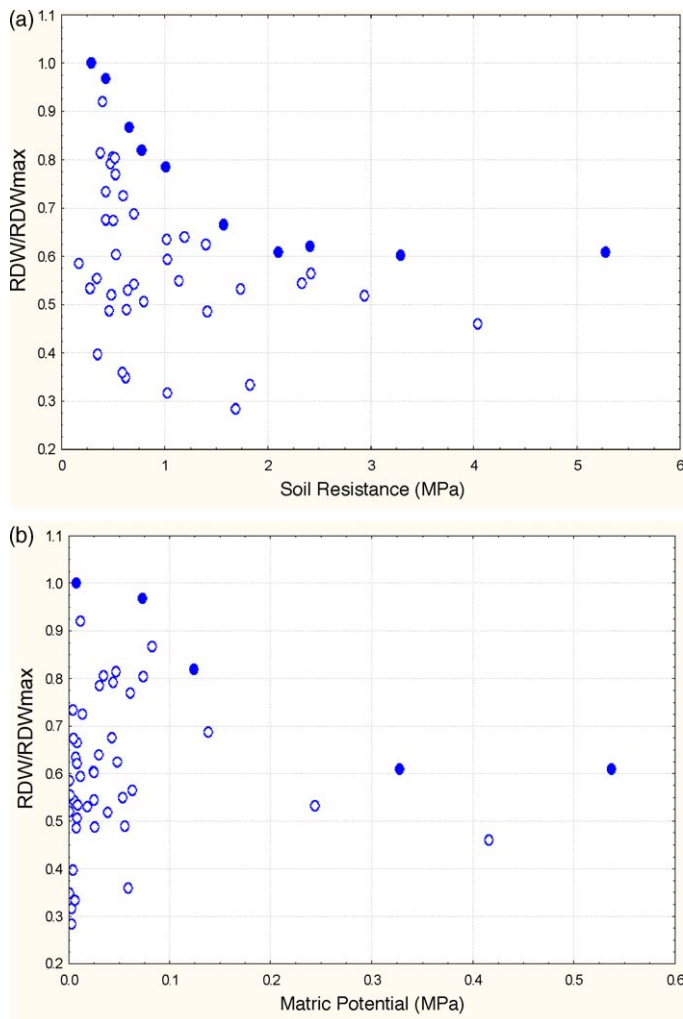


Fig. 4. Scatter-grams of standardized F -values for root dry weight (RDW/RDWM_{max}) versus soil resistance to root penetration (MPa) (a), and soil matric potential (MPa) (b). Solid data points were those selected for boundary line analysis.

included among the original boundary points. However, as expected, many points lay outside the prediction limits reflecting the impact of stresses other than ψ and SR. These stresses may be related to inadequate aeration in the treatments with the largest

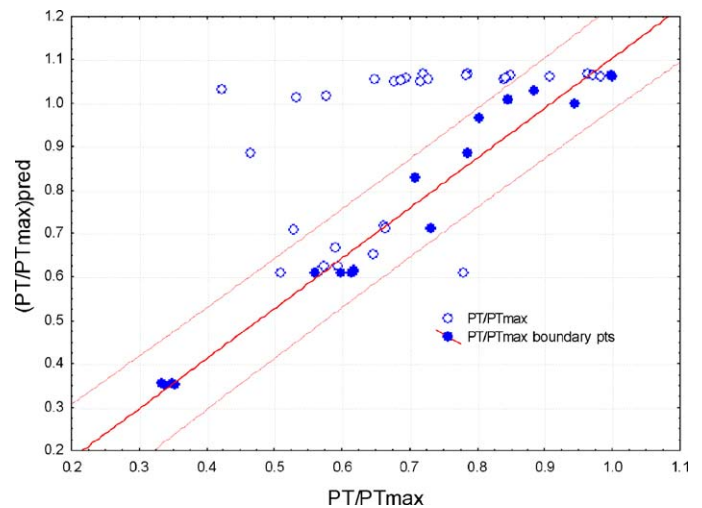


Fig. 5. Comparison of observed F -values for plant transpiration (PT/PT_{max}) with values predicted using the model given in Table 3.

water content and an adverse effect of the high N treatment in some treatments, as was mentioned by Kay et al. (2006).

The variation in PT/PT_{max} with $|\psi|$ and SR, as predicted by the double S-shaped model in Table 3, are given in Fig. 6a and b. The F -value of PT remained the same at $|\psi| \geq 0.2$ MPa and SR ≥ 1.5 MPa, respectively.

In order to quantify the sensitivity of the different plant parameters to $|\psi|$ and SR, five indicator values were selected. The first was the minimum value that the plant parameter reached at large values of SR and minimal values of $|\psi|$ (i.e., b_1 in Table 3) and large values of $|\psi|$ and minimal values of SR (i.e., $1 - b_4$ in Table 3). The second indicator, which reveals the curve shape and the processes rates, was b_2 for SR and b_5 for $|\psi|$ (Table 3). As the value of these coefficients increases, the curve is more shrunk toward the center and the decrease of the process rate is more important. The other three values were: the threshold value at which the plant parameter began to decline (0.99 of the maximum), the lower limit (1.01 of the minimum) and the midpoint between the maximum and minimum. These values were obtained from plots that were prepared for all plant parameters which corresponded to the uppermost line in Fig. 6a and b, i.e., $|\psi| = 0.03$ and variable SR, and SR = 0.01 and variable $|\psi|$. Values of $|\psi|$ and SR are summarized in Table 4.

Table 3
Regression models of the boundary lines relating plant parameters to soil resistance and matric potential.

Plant parameter (PP)	b_1	b_2	b_3	b_4	b_5	b_6
Model and coefficients						
PP = $(b_1 + (1 - b_1)/(1 + (b_2 \times SR)^{b_3})^{(1 - 1/b_3)}) - (b_4 - (b_4)/(1 + (b_5 \times \psi)^{b_6})^{(1 - 1/b_6)})$						
LT	0.829 ^a	0.940 ^b	4.778 ^b	0.148 ^b	10.187 ^a	2.557 ^a
PT	0.610 ^b	1.146 ^b	6.794 ^a	0.264 ^a	8.930 ^a	10.167 ^a
LA	0.801 ^a	1.448 ^a	7.660 ^a	0.371 ^{ab}	6.249 ^b	1.669 ^a
PP = $(b_1 + (1 - b_1)/(1 + (b_2 \times SR)^{b_3})^{(1 - 1/b_3)}) - (b_4 \times \psi)$						
CE	0.793 ^a	0.847 ^a	2.310 ^a	0.218 ^b		
LSDW	0.727 ^a	1.114 ^a	8.275 ^a	0.373 ^a		
PP = $(b_1 + (1 - b_1)/(1 + (b_2 \times SR)^{b_3})^{(1 - 1/b_3)})$						
RDW	0.591 ^a	1.331 ^a	3.264 ^a			
RSA	0.581 ^b	1.145 ^a	4.231 ^a			
RTL	0.515 ^b	1.260 ^a	4.334 ^a			

LT = leaf transpiration (mmol m⁻² s⁻¹); PT = plant transpiration (g day⁻¹); LA = leaf area (cm² plant⁻¹); CE = carbon exchange (μmol m⁻² s⁻¹); LSDW = leaf + shoot dry weight (g plant⁻¹); RDW = root dry weight (g plant⁻¹); RSA = root surface area (cm² plant⁻¹); RTL = root total length (cm plant⁻¹); SR = soil resistance (MPa); ψ = matric potential (MPa). Coefficient values followed by the same letter at each column are not significantly different (T -test, $\alpha = 0.05$).

^a Coefficient values are significant at $\alpha \leq 0.01$.
^{**} Coefficient values are significant at $\alpha \leq 0.05$.

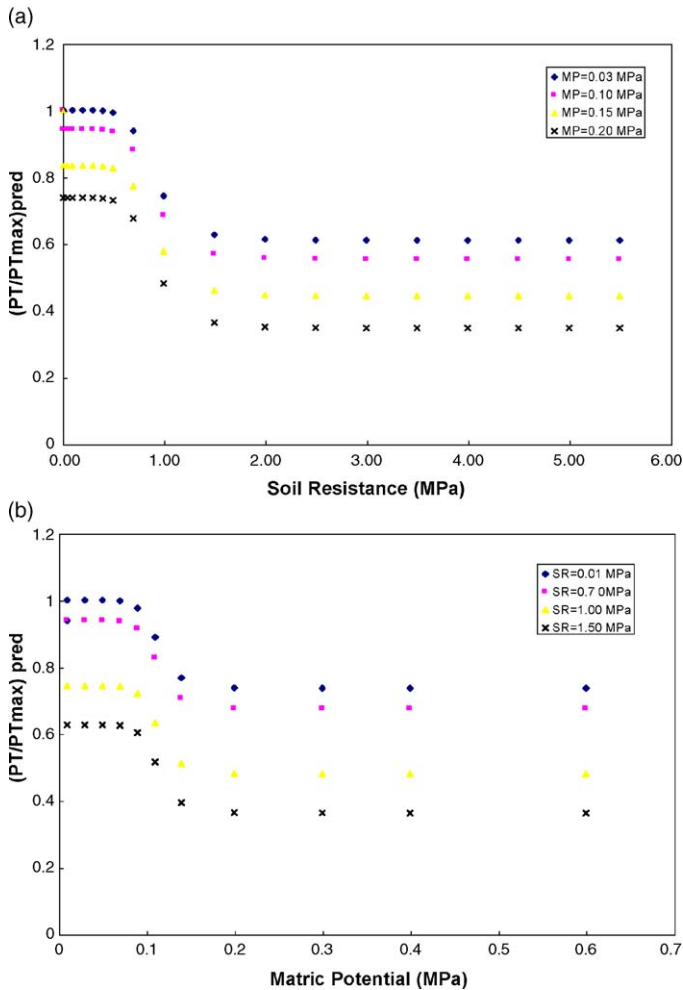


Fig. 6. Predicted variation in the F -values for plant transpiration (PT/PT_{max}) $_{pred}$ with (a) soil resistance to root penetration (SR) and different values of matric potential (ψ), and (b) soil matric potential at different values of soil resistance to root penetration.

The F -values of PT, LT and LA parameters declined quickly when SR and ψ exceeded about 0.5 MPa and 0.03–0.08 MPa respectively, but they differed in their overall extent and rates of decrease. Comparing the response of LT and LA to SR, both declined to a similar minimum value (b_1 in Table 3) but the midpoint and the limiting value occurred at a smaller SR for LA than LT (Table 4). As soon as LA has reached the threshold value, it was far more sensitive (greater b_2 value) to SR than LT. Ludlow et al. (1989) and

Table 4
Critical values of soil resistance and matric potential influencing different plant parameters.

Plant parameter	Soil resistance (MPa)			Matric potential (MPa)		
	Threshold	Midpoint	Limit	Threshold	Midpoint	Limit
LT	0.6	1.3	2.8	0.04	0.13	0.50
PT	0.5	0.9	1.4	0.08	0.11	0.19
LA	0.5	0.7	1.1	0.03	0.27	1.38
CE	0.4	1.4	4.1	0.00	0.71	1.43
LSDW	0.6	0.9	1.4	0.00	0.63	1.27
RDW	0.3	0.9	3.5	–	–	–
RSA	0.4	0.9	3.0	–	–	–
RTL	0.3	0.9	3.1	–	–	–

LT = leaf transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$); PT = plant transpiration (g day^{-1}); LA = leaf area ($\text{cm}^2 \text{plant}^{-1}$); CE = carbon exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$); LSDW = leaf + shoot dry weight (g plant^{-1}); RDW = root dry weight (g plant^{-1}); RSA = root surface area ($\text{cm}^2 \text{plant}^{-1}$); RTL = root total length (cm plant^{-1}).

Young et al. (1997) have also reported LA to be more sensitive to SR than LT. On the other hand, the F -value of PT exhibited the largest overall decline due to SR (lower b_1 in Table 3); thus reflecting the combined effects of SR on both LT and LA. Values of PT/PT_{max} reached both the midpoint and lower limit at smaller SR than LT and exhibited greater overall sensitivity to SR than either LT or LA.

Plants seem to sense the unfavorable soil conditions and start controlling their LA development, allocating the available carbon for growing the roots. This may be a mechanism to increase the chance for plants to overcome the adverse soil condition, as suggested by Masle et al. (1990).

PT and LT were the most sensitive parameters to $|\psi|$ (greater b_5 value). This fact suggests that the sensitivity of the gas exchange parameters primarily depends on the soil water availability, which in turn is conditioned by soil texture and the soil water content. Plants react to drought by closing the stomata, which reduces leaves transpiration and would prevent the development of excessive water stress.

Similar plant behavior was determined by Tardieu et al. (1991), Sadras and Milroy (1996), Jensen et al. (1998, 2000), and Ying et al. (2002). Jensen et al. (1998) determined that soil water potential rather than water content determined the stomatal closure with a critical value of 0.13 MPa. Threshold values of ψ around 0.10 MPa for gas exchange parameters were also found by Ying et al. (2002) when corn was in the 12-leaf stage.

The model that was found to give the best fit of the boundary points for CE and LSDW had the SR component described with the S-shaped function and the ψ component with a linear function (Table 3). The coefficients b_1 , b_2 , and b_3 of the two parameters were not significantly different suggesting that SR has a similar negative effect on the CO_2 assimilation and biomass accumulation. According to Beemster and Masle (1996), SR could cause a reduction in mature cell size, a decrease in the relative proportions of stomata and associated cell types, and an increase in the proportions of unspecialized cells. These modifications alter the gas exchange parameters and, consequently, influence the final plant growth. The questions of how and why these alterations on leaf organogenesis started and their relationship with the roots behavior under soil stress conditions remain unknown (Masle, 1998).

The linear relation of CE and LSDW with ψ means that the threshold occurs at 0 MPa and the impact of ψ continues until $(1 - b_4 \times \psi)$ reached the smallest value among the boundary points (0.689 and 0.527 for CE and LSDW, respectively). Although b_4 for LSDW was greater than that for CE (Table 3), the difference in their smallest value results in LSDW having only slightly smaller values of ψ at the midpoint and limit of the response curve (Table 4). Cell expansion, cell-wall synthesis, and protein synthesis in fast growing tissues are among the most sensitive processes to water stress, which would reduce the plant development (Sadras and Milroy, 1996). Saab and Sharp (1989) indicated that a non-hydraulic inhibition of plant development could act before the leaf and shoot water deficit induces the stomatal closure. It seems to be a mechanism to enhance plants survival since it allows plants to conserve water while assimilating more carbon.

The roots parameters (RDW, RSA, and RTL) were only affected by SR (Table 3). All coefficients were statistically similar but b_1 for RTL. The threshold, midpoint and limiting values of SR were also similar (Table 4), indicating that the root parameters were similarly influenced by SR. Linear and nonlinear relationships between root growth and SR have been reported (Taylor and Ratliff, 1969; Masle and Passioura, 1987; Dexter, 1987; Veen and Boone, 1990; Zou et al., 2000, 2001). Materechera and Mloza-Banda (1997) have determined that root growth started decreasing when SR was about 1 MPa and may stop at high values of SR. Boone and Veen (1982) have mentioned that maize root growth was mainly affected by SR at values between 0.9 and 1.6 MPa, which is in

agreement with the values in Table 4. Boone and Veen (1982) have also indicated that a SR value of 3 MPa strongly reduced the root growth, which is in agreement with the results of Laboski et al. (1998) as well as with our results (Table 4).

The absence of a significant relationship between root growth and ψ would initially appear to be inconsistent with the configuration of the boundary points in Fig. 4b. However, the entire set of boundary points in Fig. 4b is also included in Fig. 4a and therefore it does not contribute additional variation in SR and ψ . Furthermore, the models account for essentially all the variability in the root parameters ($R^2 = 0.99$). Consequently, we conclude that lack of significance of ψ is not an artifact of the computational procedure and that ψ has a negligible effect on RDW, RSA and RTL under the conditions of this experiment. The reasons for the lack of a significant effect of ψ are not immediately obvious. These results suggest that, in accordance with other findings, responses of above-ground plant growth might have been triggered by a signal produced in the roots in response to the soil resistance stress.

A comparison of the critical values of SR and ψ for the different plant parameters (Table 4) shows that the sensitivity to SR and ψ depended on the plant parameter. Values of PT, LA and LSDW were most sensitive to SR. Among those parameters exhibiting a significant response to ψ , PT was most sensitive.

The multivariable boundary line approach appears to be suitable for evaluating the impact on physiological processes of two variables that are strongly related. Although the results of this assessment are based on the use of functions of specific form, other functions could be selected if considered more appropriate. Similarly, the assumption that the effects of SR and ψ are additive in the multivariable model could be modified to include interactions. Models of increasing complexity would require a larger number of boundary points in the use of multiple regression analyses. The magnitude of the critical values of SR and ψ (Table 4) are most relevant to soils without an abundance of macropores (e.g., root channels, worm holes and cracks) and growing conditions with relatively low radiation and evaporative demand. Further research is necessary to determine the sensitivity of the critical values to other environmental conditions.

4. Conclusion

The multivariate boundary line approach, in combination with nonlinear multiple regression analyses, enabled the combined influence of SR and ψ on plant parameters to be successfully quantified. The resulting boundary line models could then be used to assess the threshold at which plant parameters began to respond to SR and ψ as well as the sensitivity of the plant parameters to further increases in SR and ψ . In all cases the best fit was reached with an S-shaped model, but more complex models were required to fit the above-ground plant parameters than the root parameters. Furthermore, the threshold values beyond that the plant parameter began to decrease and also its sensitivity depended on the evaluated plant component.

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