

Impact of soil compaction on root architecture, leaf water status, gas exchange and growth of maize and triticale seedlings

Maciej T. Grzesiak

The Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Niezapominajek 21, PL 30-239, Cracow, Poland

Corresponding author: M.T. Grzesiak, E-mail: m.grzesiak@ifr-pan.krakow.pl

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Abstract: Triticale and maize, with different structure of the root system and type of photosynthesis were examined to know changes in shoot physiology and root architecture in response to varying degree of soil compaction. In the root-box, effects of different levels of soil compaction (1.30, 1.47 and 1.58 Mg m⁻³) on a shoot and root dry matter, leaf number and area, number and length of seminal, seminal adventitious, nodal and lateral roots, leaf water potential (ψ), maximum quantum yield of PS II (F_v/F_m) and gas exchange were studied. Severe soil compaction treatments decreased leaf number, leaf area and dry matter of shoots and roots, while increasing shoot-to-root dry matter ratio. In addition, high level of soil compaction strongly affected the length of seminal and seminal adventitious roots, and the number and length of lateral roots developed on the seminal root. Along with the restriction of root growth, significant influences were observed in ψ , F_v/F_m and gas exchange. High soil compaction treatments resulted in decreased ψ , F_v/F_m , and photosynthetic rate, transpiration rate and stomatal conductance for both triticale and maize. Maize whose root growth was more heavily restricted by the soil compaction compared to triticale showed greater damages in physiological characteristics in leaves, while the impact on triticale was relatively small. The results indicated that damages in photosynthesis, water relation and shoot growth by soil compaction would be closely related to sensitivity of root systems architecture to high mechanical impedance of soil.

Keywords: chlorophyll fluorescence, gas exchange, maize, leaf water potential, soil compaction, triticale

Introduction

Plant roots are strongly affected by physical factors in soil. Soil mechanical impedance is caused mainly by natural processes and by the use of heavy machinery for soil cultivation. Soil compaction as well as changes in soil water potential is a major factor that causes high mechanical impedance or excessive soil strength (Yamauchi 1993, Iijima et al. 1991, Masle 2002).

The root system of an individual plant consists of several component roots of different nature. Those components differ in external morphology, physiological function and genetic control. According to Yamauchi (1993), root system structure of cereal plant consists of seminal, seminal adventitious, nodal and lateral roots. The seminal and nodal roots build up the framework, while lateral roots of different orders build network of the roots in soil. The cereal species develop two types of root system, depending on the angle of growth of branches (lateral roots) and their distribution in a soil profile. A root system of “concentrated” type has a greater number of nodal roots densely distributed. Other type designated as a “scattered” type has fewer but longer nodal roots, many of which run obliquely and vertically in the soil profile. Maize root system belongs to the “scattered” type, and triticale to the “concentrated” type. Kono et al. (1972) found that there were two types of lateral roots according to their length, diameter and histological structure (L-type and S-type). In general, the L-type lateral roots are long, thick and branch into the higher order lateral roots, while S-type ones are short, slender and non-branching.

Typical responses of plant root system structure to soil compaction include reduction of number and length of roots, restriction of downward penetration of the main root axes, decrease in leaf thickness, increase in dry matter shoot-to-root ratio and decrease in crop

grain yield (Fageria et al. 2006). The degree of restriction of root growth in compact soil depends also on the species and the age of the plants (Yamauchi 1993, Masle 2002). Inhibited plant growth is mostly attributed to reduced rooting volume (Iijima and Kono 1991, Yamauchi 1993, Grzesiak et al. 1999, 2002, Masle 2002, Fageria et al. 2006). Sometimes during short-time growth under high soil impedance, temporary increase of the number and length of laterals roots was observed (Iijima and Kono 1991, Iijima et al. 1991, Yamauchi 1993).

The restrictive effect of soil compaction can be physical and physiological constraints to overall plant growth and yield through poor development of root system (Iijima and Kono 1991, Iijima et al. 1991, Grzesiak et al. 2002) since high soil impedance influences root elongation and proliferation (Tu and Tan 1991). In wheat, root length, root density and grain yield can be reduced in compacted soil compared to non-compacted one (Oussible et al. 1993). The effects of soil compaction are emphasized in drought stressed plants. In limited-rainfall areas, compacted soil can amplify these effects by reducing the ability of plants to exploit ground soil water reservoirs. Water use is primarily determined by root system density and depth during periods of soil drought (Thangraj et al. 1990). Increased root density and depth may be responsible for drought avoidance in some rice genotypes. Therefore, identification of genotypes with a greater ability to penetrate compacted soil layers is important in developing superior drought-resistant cultivars (O'Toole and De Datta 1983). In the study of Yu et al. (1995), rice cultivars from dry-land origins had greater root penetration ability than did cultivars from wetland origins.

As acquisition of water and mineral nutrients is primarily determined by dimension of root zone and distribution of root density, root proliferation and elongation would be closely related to water relation and photosynthesis of the plants in exposure to soil compaction (Iijima et al. 1991, Oussible et al. 1993, Yamauchi 1993). Although it is reported that the responses of growth in each root type and architecture of root system to compacted soil are different among plants with concentrated and scattered root system (Iijima and Kono 1991), there is limited knowledge on relationships between the modification in root system architecture and gas exchange and water relation of leaves (Yamauchi 1993, Grzesiak et al. 2002). Some researches indicated that there were genotypic differences of root growth in tolerance to soil compaction in crop species (Iijima and Kono 1993, Grzesiak et al. 2002), thus, it is important to know traits of roots and root system associating with high tolerance to soil compaction for plant breeding.

The aim of this study was to evaluate the effects of

different levels of soil compaction on plant growth characteristics, number and length of components of root system, leaf water status and gas exchange parameters in the seedlings of triticale and maize. These species have different types of photosynthesis (C_3 plant, triticale; C_4 plant, maize) and also root system structure, which is "concentrated" for triticale and "scattered" for maize. In this study, the root system structure was analyzed by separately determining traits for each component rather than dealing with the entire roots mass. The responses of these two species to soil compaction would explain how these species manage their growth.

Materials and Methods

The research was carried out on plant materials for triticale (breeding strain, CHD-147) obtained from Polish breeding station in Choryn, and maize (maize single-cross hybrids, Nova) from SAMPLO-Holding in Trnava in Slovakia. Plants were grown by 5 weeks in air-conditioned growth cabinets under the following day/night conditions: temperature at 23/18°C ($\pm 2.5^\circ\text{C}$), relative humidity (RH) at 70/60% ($\pm 5\%$) and day-length for 16 h (artificial irradiance from high pressure sodium lamps, Philips SON-T AGRO, 400 W). PAR was equal to about 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Plants were grown in root-boxes (height 0.4m \times width 0.25m \times thickness 25mm), which enabled non-destructive isolation and preservation of roots as their distribution was less disturbed. The "root pin-board method" utilizes a plexiglass root-box, a pin-board for sampling the root system and a perforated polyethylene sheet (envelope) for handling and preserving roots (Kono et al. 1987).

The root-boxes were filled with a mixture of garden soil, peat and sand (1:1:3 in volume). Air-dried soil substrate was sieved on 2.5 mm mesh and mixed with compound fertilizer at the rate N:2.8 mg, P:1.8 mg, K:1.4 mg per 1 kg of the soil substrate. Three levels of soil compaction, 1.30 Mg m^{-3} (CS1), 1.47 Mg m^{-3} (CS2), and 1.58 Mg m^{-3} (CS3) were applied to plants. Each treatment was done in 5 replications. Prior to sowing, root-boxes were soaked in water for 30 min and left to drain for 48 h. Eight hours after soaking of root-box, volumetric soil water content in CS1, CS2 and CS3 were 0.47, 0.43, and 0.39 $\text{m}^3 \text{m}^{-3}$, respectively. The soil water content decreased to 0.25, 0.21 and 0.18 $\text{m}^3 \text{m}^{-3}$ 2 days after water application. According to Hillel and van Bavel (1976), the values obtained after 8h were assumed to be 100% of soil field water capacity (FWC). The root-boxes were weighed every day, and the amount of the water loss through transpiration was refilled to keep the constant mass of root-boxes in being at 70% FWC. A pregerminated grain was planted at 3-4 cm depth.

After measurements of leaf water potential, chlorophyll fluorescence and gas exchange parameters, each sampled seedling was cut into a shoot and root system. The soil containing roots from the root-box was transferred onto pin-board and the soil was washed away with a gentle stream of water. The sample of roots was closed in a polyethylene envelope and preserved in FAA solution (formalin, 100% acetic acid, 95% ethanol and water-2:1:10:7 in volume). For measurement of the number and length of root components, a digital image root analyzer (Delta T Scan, Delta T Co., England) was used. Determination of the number and total length of L- and S-type roots was made only for seminal roots. The seminal roots were scanned and measurement was made with application of light pen of electronic planimeter Microplan II (Laboratory computer Systems, Inc., Cambridge, Massachusetts). Classification of lateral roots into L-type or S-type was made according to root length. The L-type lateral root was long and branching into the higher order lateral roots, while S-type was short and non-branching.

Leaf water potential (ψ) was measured using Dew Point Microvoltmeter (HR 33T, Wescor Inc., USA) in room temperature and in “dew point” mode, equipped with sample chamber (C-52 SF, Wescor Inc., USA) and digital multimeter (Metex M-3640 D, Metex Co., Poland). Measurements were taken on leaf discs (diameter of 3 mm for triticale and 5 mm for maize), which were cut from the middle part of the leaf, and immediately placed inside the psychrometer chamber and left for 30 min to achieve steady state condition. For each treatment the measurement of ψ was done in 30 replications (5 plants \times 2 leaves \times 3 discs).

The photochemical efficiency (F_v/F_m) of PS II photochemistry was determined with application of PSM (Plant Stress Meter-Mark II, Biomonitor AB, Sweden). Before the measurements, the plant leaves

were dark-adapted for 20 min. Fluorescence was induced by radiation $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 5 s. The F_v was calculated based on F_o (initial fluorescence in the dark-adapted state) and F_m (maximum fluorescence): $F_v = F_m - F_o$. For each treatment the measurement of F_o and F_m was done in 30 replications (5 plants \times 2 leaves \times 3 clips).

Rate of leaf gas exchange was measured using CO_2 IRGA analyzer (CI-301PS, CID Inc., USA) with Parkinson's assimilation chamber, type narrow regular with light attachment CI-301 LA. During measurement an open system was used. The flow rate of ambient air with constant CO_2 concentration ($360 \mu\text{mol mol}^{-1}$) through the assimilation chamber was $0.5 \text{ dm}^3 \text{ min}^{-1}$. Chamber temperature kept under 25°C until the photosynthesis rate had stabilized. Photosynthetic capacity at light saturation was reached by exposing leaves to photosynthetically active radiation at $800 \mu\text{mol m}^{-2} \text{s}^{-1}$. For each treatment the measurements of gas exchange rate was done in 30 replications (5 plants \times 2 leaves \times 3 measurements). Dry matter of the above-ground part and root was determined after 35 days from plant sowing and was measured after drying at 65°C for 72 h.

Analysis of obtained data was submitted to statistical analysis using Duncan's multiple range tests, upon which standard error of mean were calculated.

Results and Discussion

Five weeks of growth under conditions of moderate (CS2) or severe (CS3) soil compaction, in comparison to treatment with low soil compaction (CS1), resulted in decrease in leaf number, leaf area, dry matter of a shoot and roots, and increase in shoot-to-root (S/R) dry matter ratio (Table 1). Effects of the soil compaction on the growth parameters were greater for maize than for triticale. In CS2 and CS3, shoot dry matter decreased by 24% and 33% in triticale and by 29%

Table 1. Effect of soil compaction on leaf number and area, shoot and root dry matter and shoot-to-root ratio of triticale and maize seedlings

Treatment	Leaf number	Leaf Area ($\times 10^{-2} \text{ m}^2$)	Dry matter (g per plant)			
			Shoot	Root	Shoot + Root	Shoot/root ratio
Triticale (cv. CHD-147)						
CS1	6.7 a	43.6 a	0.76 a	0.49 a	1.25 a	1.55 b
CS2	6.1 b (0.91)#	39.1 b (0.90)	0.58 b (0.76)	0.34 b (0.69)	0.92 b (0.73)	1.71 a (1.10)
CS3	5.2 c (0.78)	32.7 c (0.75)	0.51 c (0.67)	0.31 b (0.63)	0.82 c (0.66)	1.64 a b (1.06)
Maize (cv. Nova)						
CS1	7.1 a	116.9 a	1.82 a	1.08 a	2.90 a	1.69 b
CS2	5.8 b (0.81)	96.3 b (0.82)	1.30 b (0.71)	0.67 b (0.62)	2.04 b (0.70)	2.04 a (1.21)
CS3	4.9 c (0.69)	81.4 c (0.70)	1.13 c (0.62)	0.57 c (0.53)	1.75 c (0.60)	2.07 a (1.23)

Data are means of five replicate plants. Values followed by the same alphabets within a column are not significantly different from each other ($P < 0.05$).

Figures in parentheses for CS2 and CS3 indicate relative ratio to the value in CS1.

and 38% in maize, respectively. Similarly, decrease in root dry matter for triticale was 31% and 37%, and for maize was about 38 and 47%, respectively. For both moderate and severe soil compaction levels, an increase of S/R ratio was observed in comparison with low soil compaction treatment. In CS2 and CS3, S/R ratio was 10% and 6% higher than that in CS1 for triticale, respectively. The S/R in both CS2 and CS3 ratio for maize was 20% higher than in CS1.

Results obtained in this work confirmed that moderate and severe levels of soil compaction led to reduction in shoot and root growth (Table 1). Several authors have pointed to the effects of soil impedance on reduction of plant size, dry matter and crop yield (Andrade et al. 1993, Lipiec et al. 1993, Whalley and Dexter 1994). Reduction in dry matter of maize shoots

under compacted soil conditions was mostly due to reduction in leaf area, stem diameter and plant height (Lipiec et al. 1996). In this study, there was greater reduction in dry matter of roots than dry matter of above-ground in CS2 and CS3 treatments and that explains increase in shoot-to-root ratio in those treatments (Table 1).

Moderate and severe levels of soil compaction influenced the length of seminal and seminal adventitious roots, and the number and length of L- and S-type lateral roots developed on seminal roots (Table 2, Fig.1). In CS2 and CS3, length of the seminal root decreased by 25% and 35% in triticale, and by 40% and 50% in maize, respectively. For these treatments the total length of seminal adventitious roots decreased by about 40 and 50% in triticale and

Table 2. Effects of soil compaction on number and total length of particular roots of triticale and maize seedlings

Root components	Treatment		
	CS1	CS2	CS3
Triticale (cv. CHD-147)			
Roots number			
Seminal	1.0 ± 0.0	1.0 ± 0.0 (1.00)#	1.0 ± 0.0 (1.00)
Seminal adventitious	3.0 ± 0.0	3.0 ± 0.0 (1.00)	3.0 ± 0.0 (1.00)
Nodal	6.8 ± 0.1	6.5 ± 0.2 (0.96)	6.4 ± 0.2 (0.94)
Lateral (type L) †	53.0 ± 1.9	34.4 ± 4.4 (0.65)	27.5 ± 2.8 (0.52)
Lateral (type S) †	21.3 ± 1.4	10.5 ± 1.5 (0.49)	7.6 ± 2.4 (0.36)
Roots length (×10 ⁻² m)			
Seminal	28.3 ± 1.5	21.3 ± 1.8 (0.75)	18.5 ± 1.1 (0.65)
Seminal adventitious	76.2 ± 2.2	44.6 ± 1.3 (0.59)	36.3 ± 1.5 (0.47)
Nodal	103.0 ± 3.3	93.9 ± 1.3 (0.90)	87.6 ± 2.4 (0.85)
Lateral (type L) †	194.4 ± 8.2	95.8 ± 6.0 (0.49)	75.2 ± 7.2 (0.38)
Lateral (type S) †	15.4 ± 1.5	7.1 ± 0.9 (0.46)	7.0 ± 0.7 (0.45)
Maize (cv. Nova)			
Roots number			
Seminal	1.0 ± 0.0	1.0 ± 0.0 (1.00)	1.0 ± 0.0 (1.00)
Seminal adventitious	2.0 ± 0.0	2.0 ± 0.0 (1.00)	2.0 ± 0.0 (1.00)
Nodal	8.5 ± 0.1	8.0 ± 0.1 (0.94)	7.6 ± 0.2 (0.92)
Lateral (type L) †	105.0 ± 5.2	37.1 ± 1.3 (0.35)	23.6 ± 1.1 (0.23)
Lateral (type S) †	68.1 ± 3.1	12.3 ± 0.5 (0.18)	11.8 ± 0.7 (0.17)
Roots length (×10 ⁻² m)			
Seminal	35.0 ± 2.88	20.3 ± 1.5 (0.58)	17.2 ± 2.1 (0.49)
Seminal adventitious	67.0 ± 2.01	32.4 ± 3.5 (0.48)	29.4 ± 2.4 (0.44)
Nodal	115.0 ± 1.25	92.0 ± 1.1 (0.80)	88.2 ± 1.0 (0.77)
Lateral (type L) †	339.2 ± 8.05	87.2 ± 8.1 (0.25)	50.2 ± 4.1 (0.15)
Lateral (type S) †	55.6 ± 1.41	8.1 ± 0.8 (0.15)	7.4 ± 1.4 (0.13)

Data are means from five replicate plants ± standard error

† Lateral roots only on seminal root were measured.

Figures in parentheses for CS2 and CS3 indicate relative ratio to the value in CS1.

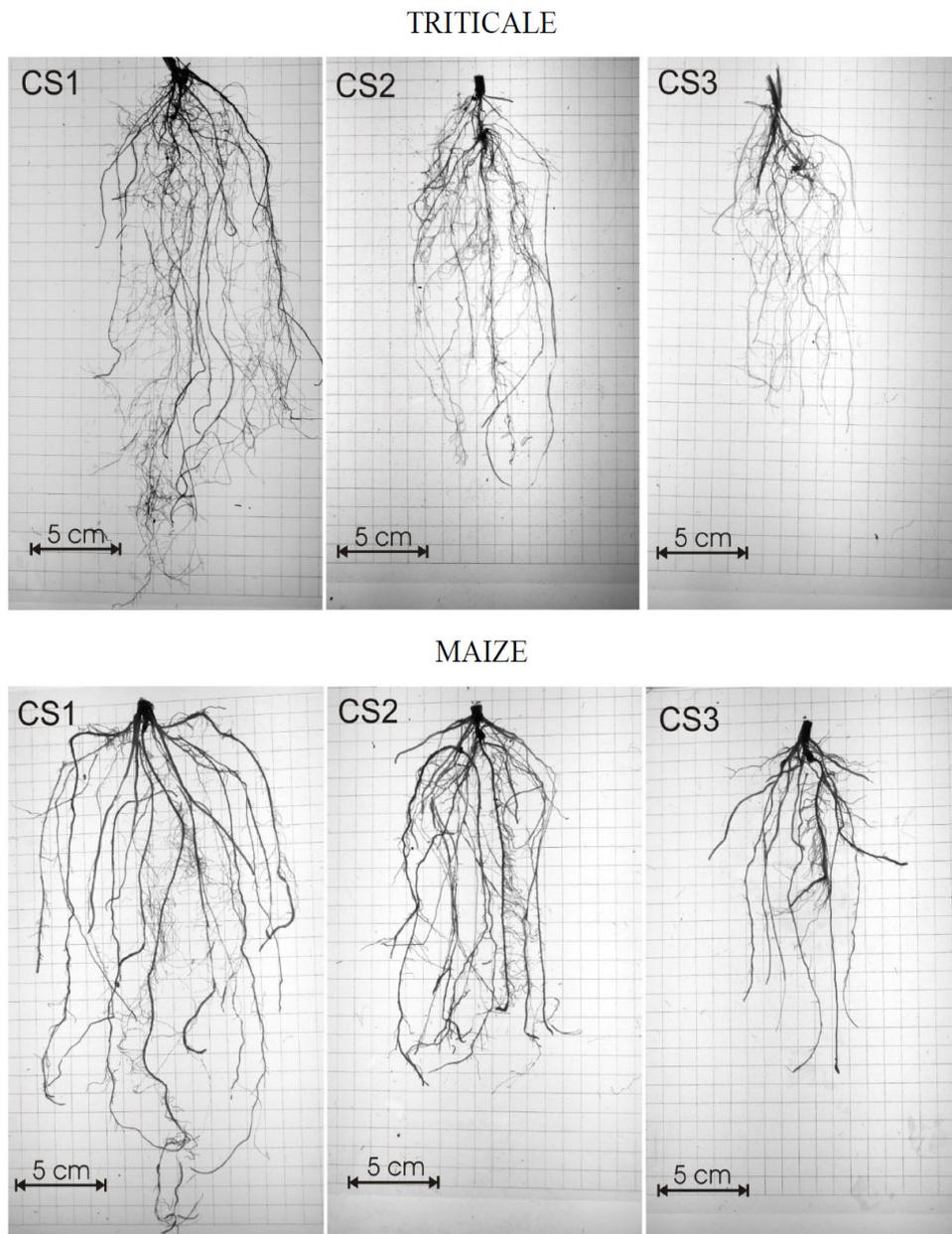


Fig. 1. Effects of soil compaction on root system profile of triticale and maize at 35 day of growth in root boxes.

about 50 and 55% in maize, respectively, in comparison to CS1. Restriction of root elongation by the soil compaction was severer in maize than in triticale. Soil compaction also reduced the number of both L- and S-type of lateral roots (Table 2). The number was more severely restricted in S-type lateral roots than in L-type roots irregardless of species. The restriction in lateral root propagation was greater in maize. The total length of L- and S-type laterals roots was also reduced by moderate and severe levels of soil compaction. For both examined species, the drastic decrease in number of lateral roots resulted in severe reduction in their total length. Iijima and Kono (1991) examined the effect of soil compaction on root growth as discrimi-

nating root components into main root axis, and L- and S-type laterals of different orders in rice and maize. In their research, responses of root types and root system to soil compaction were clearly different between rice with “concentrated” type of root system and maize with the “scattered” type. Along with the present study, a consistent trend has been found that a species with “concentrated” type of root system showed less restriction of roots growth due to high soil compaction compared to “scattered” type, as shown in a comparison between triticale and maize.

The heavy suppression of lateral root growth would affect plant nutrition and water relation because the soil compaction resulted in decreased size of root

system (Fig. 1), increased irregularity of root distribution and thus in greater distances for the transport of water and nutrients to the nearest roots (Tardieu 1991, Lipiec et al. 1996). The restriction in number and length of each root type in conditions of high soil impedance was accompanied by decrease in leaf water potential (ψ). In CS2 and CS3 treatments, the values of the leaf water potential were lower in comparison with CS1 (Table 3). In CS1 leaf water potential was -0.58 MPa in triticale and -0.52 MPa in maize, respectively. In treatments CS2 and CS3 leaf water potential was -0.80 MPa and -0.81 MPa in triticale, and -0.85 MPa and -1.07 MPa in maize, respectively. Masle and Passioura (1987) determined that increased mechanical impedance reduced water supply from root systems to shoots. This could be one of the reasons for reduction in area (Table 1).

In this study changes in root system architecture under the high soil impedance conditions were also accompanied by decrease in net photosynthetic rate (P_n), transpiration rate (E), and stomatal conductance (g_s) (Table 3). The F_v/F_m ratio was also affected by soil compaction (Table 3). The ratio of F_v/F_m has been widely used to detect perturbations in the photosynthesis apparatus induced by stress factors. Decreases of F_v/F_m in plants grown under stress conditions can occur due to development of slowly relaxing quenching processes and photodamage to PSII reaction centers (Baker and Rosenqvist 2004). In this experiment, the F_v/F_m ratio of triticale decreased by 15% in both CS2 and CS3 in comparison with CS1 (Table 3). In maize, the decrease was 25 and 36%, respectively, indicating that photosystem of maize was heavily damaged in soil compaction. The extent of reduction in P_n , E , g_s and F_v/F_m under high soil compaction coincided with restriction of root growth of triticale and maize (Table 2). A significant differ-

ence between the responses of maize and triticale to soil compaction was found in internal carbon dioxide concentration (C_i). In comparison to control C_i increased in triticale and decreased for maize under CS2 and CS3 treatments (Table 3). The differences in internal CO_2 concentration between triticale and maize under soil compaction conditions were probably caused by differences in biochemical processes for fixation of carbon dioxide (Calvin cycle in C_3 plant, and Hatch and Slace pathways in C_4 plant) and anatomical differences between C_3 and C_4 plants (Kranz syndrome).

Highlighting on water relation and gas exchange rate of plants in soil stresses, many studies indicate that leaf water status and gas exchange parameters (especially stomata behavior) are influenced through several mechanisms (Agnew and Carrow 1985, Lipiec et al. 1996). According to Masle (2002) rootborne signals affect the rate of development in the apical meristem, cell division and cell expansion in the expanding leaves and they induce stomatal behavior. Root signals are expected to be electrical and hormonal (ethylene, ABA, auxin and likely cytokinin signaling cascades) and are involved in mediating physiological effects. Understanding of processes in which the photosynthesis and gas exchange rate depressed by soil compaction requires more physiological studies on roots and shoots. Since development of a whole root system consisting of root components was closely related to productivity of triticale and maize as shown in Table 1 and Table 3, and effects of soil compaction on root growth are variable according to root types, i.e. seminal, nodal and lateral roots (Table 2), it is worthwhile to think what determines the difference in growth of roots exposed to compacted soil. The studies will encourage improvement of technology for crop production under adverse field

Table 3. Effects of different soil compaction level on leaf water potential ψ , maximum quantum yield of PS II photochemistry (F_v/F_m), net photosynthetic rate (P_n), transpiration rate (E), stomatal conductance (g_s) and internal CO_2 concentration (C_i) in triticale and maize seedlings

Treatment	ψ (MPa)	F_v/F_m	Gas exchange parameters			
			P_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)	g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	C_i (mmol mol^{-1})
Triticale (cv. CHD 147)						
CS1	-0.58 a	0.78 a	15.8 a	3.44 a	95.4 a	267.1 a
CS2	-0.80 b (1.38)#	0.67 b (0.86)	13.6 b (0.86)	3.02 b (0.87)	86.2 b (0.90)	287.3 b (1.08)
CS3	-0.81 b (1.40)	0.65 b (0.83)	12.7 b (0.80)	2.93 b (0.85)	84.8 b (0.89)	298.5 b (1.12)
Maize (cv. Nova)						
CS1	-0.52 a	0.83 a	27.6 a	2.07 a	121.5 a	175.6 a
CS2	-0.85 b (1.64)	0.62 b (0.75)	21.9 b (0.79)	1.68 b (0.81)	105.3 b (0.87)	159.2 b (0.91)
CS3	-1.07 c (2.06)	0.53 c (0.64)	19.4 c (0.70)	1.53 c (0.74)	104.0 b (0.86)	151.0 b (0.86)

Mean value for measurement on 3rd and 5th leaf. Values followed by the same alphabets within a column are not significantly different ($P < 0.05$).

Figures in parentheses for CS2 and CS3 indicate relative ratio to the value in CS1.

conditions and will contribute to the progress of breeding program aiming to improve stress tolerance of crop plants.

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References

- Agnew ML, Carrow RN 1985 Soil compaction and moisture stress preconditioning in Kentucky bluegrass. II. Stomatal resistance, leaf water potential and canopy temperature. *Agron. J.* 77: 878-884.
- Andrade A, Wolfe DW, Ferens E 1993 Leaf expansion, photosynthesis and water relations of sunflower plants grown on compacted soil. *Plant Soil* 149: 175-184.
- Baker NR 1993 Light use efficiency and photoinhibition of photosynthesis in plants under environmental stress. In: Smith JAC, Griffiths H, Eds., *Water deficits plant responses from cell to community*. BIOS Scientific Publishers Ltd., Oxford, pp. 221-235.
- Baker NR, Rosenqvist E 2004 Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. *J. Exp. Bot.* 55: 1607-1621.
- Fageria NK, Balingar VC, Clark RB 2006 *Physiology of crop production*. The Haworth Press Inc., New York, London, Oxford, pp.23-60.
- Hillel D, Bavel CHM 1976 Simulation of profile water storage as related to soil hydraulic properties. *Soil Sci. Soc. Am. J.* 40:807-815.
- Grzesiak S, Hura T, Grzesiak MT, Pieńkowski S 1999 The impact of limited soil moisture and waterlogging stress conditions on morphological and anatomical root traits in maize (*Zea mays* L.) hybrids of different drought tolerance. *Acta Physiol. Plant.* 21: 305- 315.
- Grzesiak S, Grzesiak MT, Filek W, Hura T, Stabryła J 2002 The impact of different soil moisture and soil compaction on the growth of triticale root system. *Acta Physiol. Plant.* 24: 331-342.
- Grzesiak MT, Grzesiak S, Skoczowski A 2006 Changes of leaf water potential and gas exchange during and after drought in triticale and maize genotypes differing in drought tolerance. *Photosynthetica* 44: 561-568.
- Iijima M, Kono Y 1991 Interspecific differences of the root system structures of four cereal species as affected by soil compaction. *Jpn. J. Crop Sci.* 60:130-138.
- Iijima M, Kono Y, Yamauchi A, Pardales Jr JR 1991 Effects of soil compaction on the development of rice and maize root system. *Environ. Exp. Bot.* 30: 333-342.
- Kono Y, Igeta M, Yamada N 1972 Studies on the developmental physiology of the lateral roots in the rice seminal roots. *Proc. Crop Sci. Soc. Jpn.* 41: 192-204.
- Kono Y, Yamauchi A, Nonoyama T, Tatsumi T, Kawamura N 1987 A revised system of root-soil interaction for laboratory work. *Environ. Control Biol.* 25: 141-151.
- Lipiec J, Ishioka T, Hatano R, Sakuma T 1993 Effects of soil structural discontinuity on root and shoot growth and water use in maize. *Plant Soil* 157: 65-74.
- Lipiec J, Ishioka T, Szustak A, Pietrusiewicz J, Stępniewski W 1996 Effects of soil compaction and transient oxygen deficiency on growth, water use and stomatal resistance in maize. *Acta Agric. Scand. Sect. B: Soil Plant Sci.* 46: 186-191.
- Masle J., Passioura JB 1987 The effect of soil strength on the growth of young wheat plants. *Aust. J. Plant Physiol.* 14: 643-656.
- Masle J 2002 High soil strength: mechanical forces at play on root morphogenesis and in root:shoot signaling. In: Waisel Y, Eshel A, Kafkafi U, Eds., *Plant Roots the Hidden Half*. Marcel Dekker Inc, New York, Basel, pp. 807-819.
- O'Toole JC, DeDatta SK 1983 Genotypic variation in epicuticular wax of rice. *Crop Sci.* 23:392-394.
- Oussible M, Allmaras RR, Wych RD, Crookston RK 1993 Subsurface compaction effects on tillering and nitrogen accumulation in wheat. *Agron. J.* 85: 619-625.
- Tardieu F 1991 Spatial arrangement of maize roots in the field. In: McMichael BL, Person H, Eds., *Plant roots and their environment*. Elsevier, Amsterdam, pp. 506-514.
- Thangraj M, O'Toole JC, DeDatta SK 1990 Root response to water stress in rainfed lowland rice. *Exp. Agric.* 28: 287-296.
- Tu JC, Tan CS 1991 Effect on soil compaction on growth, yield and root rots of white beans in clay loam and sand loam soil. *Soil Biol. Biochem.* 23: 233-238.
- Whalley WR, Dexter AR 1994 Root development and earthworm movement in relation to soil strength and structure. *Arch. Agron. Soil Sci.* 38: 1-40.
- Yamauchi A, Kono Y, Tatsumi J 1987 Comparison of root system structure of 13 species of cereals. *Jpn. J. Crop. Sci.* 56: 618-631.
- Yamauchi A 1993 Significance of root system structure in relation to stress tolerance in cereal crop. In: *Low-input sustainable crop production system in Asia*. Korean Soc. Crop Sci., Korea, pp. 347-360.
- Yu LX, Ray JD, O'Toole JC, Nguyen HT 1995 Use of wax-petrolatum layer for screening rice root penetration. *Crop Sci.* 35: 684-687.



Dr Maciej T. Grzesiak's research interest is focused on structure and development of plant roots and effect of different abiotic stresses (drought, waterlogging) on plant growth and productivity.