Physiological markers of stress susceptibility in maize and triticale under different soil compactions and/or soil water contents

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ABSTRACT

Differences between two maize and two triticale genotypes grown in low soil compaction (LSC), moderate soil compaction (MSC) and severe soil compaction (SSC) and with a limited (D) or excess (W) soil water content were observed as a decrease in shoot (S) and root (R) biomass, leaf greening (SPAD) and increase in membrane injury (L), root and leaf water potential (ψr, ψl), photosynthesis (Pn), transpiration (E) and stomata conductance (gS). Close correlations between ψl and ψr and between differences ψl and ψr (Δψ) were found. Drought or waterlogging with LSC conditions in both maize genotypes resulted in higher WUE than in control plants (LSC C), but under the SSC WUE declined. However, for triticale differences in WUE, between treatments were small and insignificant. In general, changes in markers were greater for genotypes sensitive to the soil compaction (Ankora, CHD-12) than in resistant ones (Tina, CHD-247) and were higher in seedlings grown under SSC conditions.

Abbreviations: ψl, ψr: root and leaf water potential; C: control; D: drought; E: transpiration rate; FWC: field water capacity; gS: stomatal conductance; LSC, MSC, SSC: low, moderate and severe soil compaction; Pn: photosynthesis rate; W: waterlogging

Introduction

The conservation of water in agriculture requires an understanding of the mechanisms of soil–plant–water relations. Drought, waterlogging and soil degradation are environmental stresses caused by the climate changes (Passioura et al. 1993; McKersie and LeShem 1994, Kozlowski 1999, Masle 2002, Ehlers and Goss 2003, Ashraf 2010). Cell dehydration caused by a soil water deficiency or excess impairs various physiological processes, especially, changes in a plant growth, development and productivity. It is known that during soil water stresses C4 plants are often more competitive than C3 plants (Colombi and Walter 2016). The responses to the decreased leaf water potential are functional and structural changes in chloroplasts, limited CO2 diffusion to chloroplasts and disturbances in accumulation and distribution of assimilation products (Cornic and Massacci 1996; Flexas and Medrano 2002; Medrano et al. 2002; Nayyar and Gupta 2006; Ripley et al. 2007; Ghannoun 2009). Physiological processes are affected also by a combination of different abiotic environmental stresses, including compacted soil and soil water deficiency or excess. Excessive soil compaction results from natural processes, past glacial ice pressure, by soil settling, slumping and the use of heavy equipment in soil cultivation. Increase in soil compaction causes changes in periodic soil mechanical impedance, hydraulic permeability, air conductivity and diffusivity and slower rates of water infiltration, resulting in risks of limited or excess soil water content (Boyer 1982; Iijima et al. 1991; Kozlowski 1999, Masle 2002; Ashraf 2010; Chan and Weil 2010; Grzesiak et al. 2014). The main effect of high compaction are changes in a root structure (number, length, thickness, direction of growth in soil) and in the above-ground plant parts (plant height, stem diameter, leaf number, leaf thickness and area, specific leaf area, thickness of epidermal cell and cell wall) (Yamauchi 1993; Clark et al. 2003; Fageria et al. 2006; Mommer et al. 2006). In the case of drought, the amount of rainfall does not compensate water loss through transpiration and evaporation, and in the case of waterlogging, the soil is inundated as a result of heavy rainfall or river floods, which cause a drastic decrease in roots’ capability for water uptake as a result of increased oxygen content in water. Excess of water in the soil destroyed the water balance in plants, resulting in oxygen limitation in plant roots (Haupt-Herting and Fock 2002; Mommer et al. 2006; Frost-Christensen and Floto 2007). With the increasing water stress, the absence of oxygen made the plant roots rotting ultimately, and the above-ground parts wilting, which even resulted in death of plants (Lawlor and Tezara 2009; Chan and Weil 2010). Negative water balance in plant tissues is one of the common consequences of environmental stresses to which plants are exposed and as such is the bottleneck of agricultural progress.

The first responses of plants to those stresses are changes of tissues’ water content, membrane permeability, chlorophyll content and gas exchange parameters (Palta 1990; Ripley et al. 2007). Exposure of roots to oxygen shortage by waterlogging induces changes in the dark respiration, use of carbohydrates, the synthesis of antioxidants and the induction of glycolysis and fermentation. Plants adapt to hypoxia by metabolic processes such as maintaining carbohydrate content, avoiding acidification of the cytoplasm and launching a defence
antioxidant system. It has also been shown that plants transition to anaerobic respiration in order to meet the demand for energy under oxygen-deficiency conditions as a result of blocking the Krebs cycle and oxidative phosphorylation (Lipiec et al. 1996; Crawford 2003; Gibbs and Greenway 2003; Tubeleh et al. 2003; Sairam et al. 2008; Rut et al. 2010; Sun et al. 2015).

Despite the amount of information about processes happening during growth under soil compaction is relatively little (Tracy et al. 2015), drought and waterlogging have been studied as separate stress factors in different plant species and cultivars. The tolerance of plants to different stresses is determined by the plants genes and the degree of plant restriction and depends on the species, variety and age of the plants. Stress susceptibility indexes are used for description and explanation of strategies implemented by plants to alleviate and/or remove an environmental stress influence (Blum 1996; Golbasy et al. 2010; Liu et al. 2010; Grzesiak et al. 2012, 2013).

The effect of stomatal or non-stomatal factors on photosynthesis and transpiration was analyzed in many studies; however, the conclusions from these studies are contradictory. Both stomatal and non-stomatal mechanism could be involved in the changes of leaf gas exchange parameters during soil water stress. Some researchers observed that stomatal behavior was the major factor limiting photosynthesis but on the other hand, other authors showed that a decrease in photosynthetic rate was due to non-stomatal factors (Berkowitz et al. 1983; Cornic and Briantais 1991; Bethenod et al. 1996; Cornic and Massacci 1996; Dubey 1997; Cornic and Fresnau 2002; Tubeleh et al. 2003; Kebbas et al. 2015). Index of water use efficiency (WUE) is defined as the ratio of dry mass accumulation to plant water use or by ratio of photosynthesis rate to transpiration rate. Improvements in the WUE of rainfall and irrigation could play a key role in agricultural practices because it often correlates with environmental stress tolerance. Also, an important factor influencing WUE is stomata because stomata play a very crucial role in mental stress tolerance. Also, an important factor influencing WUE is stomata because stomata play a very crucial role in mental stress tolerance. WUE is stomata because stomata play a very crucial role in mental stress tolerance. WUE is stomata because stomata play a very crucial role in mental stress tolerance.

Materials and methods

Plant material

Two maize single-cross hybrids (Ankora, Tina) obtained from SEMPOL-Holding Trnava, Slovakia and two and two triticale breeding form (CHD-12, CHD-247) obtained from breeding station Małyszyn (Poland) were used in the experiment. These maize and triticale genotypes had been used in our previous studies (Grzesiak et al. 2014), on the basis of which Ankora and CHD-12 were selected as susceptible to soil compaction stress and Tina and CHD-247 as resistant (Table 1).

Growth conditions and experimental treatments

Plants were grown in an air-conditioned greenhouse under the following day/night conditions: temperature 23°C/18°C (±2.5°C) and relative humidity 70%/60% (±5%), during a 14-h photoperiod from 7 am to 9 pm (artificial irradiance from high pressure sodium lamps, Philips SON-T AGRO, 400 W). Photosynthetically active radiation (PAR) was equal to about 350 µmol m⁻² s⁻¹.

One pre-germinated grain was planted per pot at a depth of 2 cm. Pots used in the experiments were PVC tubes of 11 cm diameter and 18 cm height, fitted with a window which enabled the sampling of roots. Pods were filled of quartz sand (fraction < 1 mm) as rooting medium produced by AQUAEL Ltd. (Poland). Air-dried sand was sieved with 0.25 mm mesh (to remove fraction larger than 2.5 mm) and mixed with compound fertilizer: N – 28 mg, P – 18 mg, K – 14 mg per 1 kg. Three soil substrate compaction treatments were applied – low (LSC – 1.1 g cm⁻³), medium (MSC – 1.3 g cm⁻³) and severe (SSC – 1.6 g cm⁻³). Sand was compacted in pods by using hydraulic press. Soil substrate mechanical resistance was measured with the penetrometer DIK 5520 (Daiki Rika Kogyo Co. Ltd., Japan).

Field water capacity (FWC) of soil substrate was determined according to Hillel and van Bavel (1976). Air-dried samples of 100 cm³ compacted to the three impedance values weighed 110.0, 130.0 and 160.0 g. These were placed inside metal cylinders, with a 1-mm hole at the bottom. The cylinders of sand were placed inside a container with water for 30 min. After 8 h, maximal soil water content in samples was 0.47, 0.41 and 0.39 g cm⁻³, and after 48 h it decreased to 0.25, 0.22 and 0.18 g cm⁻³, respectively. According to the latter, values were assumed to be 100% of FWC. During the experiments the PVC tubes were weighed every day, and the amount of water loss through evapotranspiration was refill to keep the constant mass in each treatment. For control treatments (LSC C, MSC C and SSC C), soil water content was maintained at 65–70% FWC from sowing to 28th day. In...
Table 1. Soil compaction stress susceptibility (SSC SI), soil root penetration ability (RPA) and the root penetration ability through a petroleum-wax layer indexes in maize and triticale genotypes according to Grzesiak et al. (2014).

| Genotype | Stress susceptibility index (SSC SI) | Root penetration ability (RPA) | Root penetration ability through a petroleum-wax layer (MPa) |
|----------|-------------------------------------|-------------------------------|-----------------------------------------------------------|
|          | Moderate*                        | Severe*                       | 0.00 | 0.52 | 1.07 | 1.58 |
| Maize    |                                    |                               |      |      |      |      |
| Ankora   | 1.40                               | 1.17                          | 0.55 | 0.51 | 17.2 | 10.2 |
| Tina     | 0.61                               | 0.69                          | 0.61 | 0.59 | 19.1 | 17.0 |
| Triticale|                                    |                               |      |      |      |      |
| CHD-12   | 1.55                               | 1.35                          | 0.59 | 0.56 | 17.0 | 11.0 |
| CHD-247  | 0.42                               | 0.56                          | 0.61 | 0.57 | 17.9 | 13.8 |

*Soil compaction level – low, moderate and severe 1.1, 1.3 and 1.6 g cm⁻³, respectively.

Measurements

Biomass

Dry matter of the above-ground parts (S) and roots (R) was determined after drying at 65°C for 72 h.

Membrane injury index (LI) was determined as relative loss of intracellular electrolytes from leaf tissues and was measured with the conductivity method using conductivity meter OK-102/1 (Radelkis, Hungary), according to the procedure described by Blum and Ebercon (1981).

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LI = \frac{1 - (T_1/T_2) - (C_1/C_2)}{1 - (C_1/C_2)} \times 100,
\]

where C and T refer to the conductivity of control and treatment solutions, respectively, and subscripts 1 and 2 refer to initial and final conductivity, respectively. Nine leaf discs (0.5 cm diameter) were cut from leaves and immersed in test tubes containing 30 cm³ redistilled water. After 24 h, initial conductivity measurements were taken. Final conductivity measurements were taken after autoclaving all tubes at 110°C for 15 min and cooling them to the room temperature.

Water potential (ψ) was measured by psychrometer HR33T (Wescor Inc., Logan, USA) in ‘dew point’ mode, equipped with sample chamber C-52 SF (Wescor Inc., Logan, USA) and digital multimeter Metex M-3640 D. Samples were placed inside the psychrometer chamber and left to balance temperature and water vapor equilibrium for 30 min before measurements. Measurements were made on the fourth, i.e. most recent fully expanded leaf.

Leaf greening in SPAD units was measured with CL 01 meter (Hansatech, Norfolk, UK).

Gas exchange

Rate of net photosynthesis (Pn), transpiration rate (E) and stomata conductivity (gs) was measured using IRGA analyser (CIRAS-2, PP System, Amesbury, USA) with a Parkinson’s assimilation chamber (narrow leaf type) and with light attachment. During the measurements, an open system was used. The flow rate of ambient air with a constant CO₂ concentration (390 µmol mol⁻¹) through the assimilation chamber amounted to 0.5 dm³ min⁻¹. Chamber temperature was kept below 25°C until the photosynthesis rate stabilized.

Photosynthetic capacity at light saturation was reached by exposing leaves to PAR at 800 µmol m⁻² s⁻¹. Index of WUE was calculated as the ratio of Pn to E. Measurements were made on the fourth leaf from 11 am to 1 pm in nine replications.

Statistical analysis

The experiments were performed in a completely randomized design. The results presented are mean values on nine (Dry matter, LI, SPAD, Pn, E, gₛ) and six (ψₛ and ψ_v) replications. Data were analyzed with the statistical package STATISTICA 12.0 (Stat-Soft Inc., Tulsa, OK, USA) using analysis of variance (ANOVA) and Duncan’s multiple range test at p ≤ 0.05.

Results

Mechanical impedance of soil substrate

For Both an air-dried and a wet soil in all soil compaction treatments (low-LSC, moderate-MSC and severe-SSC), soil mechanical impedance was increasing with soil depth, and its mean value for LSC, MSC and SSC of air-dried soil was 0.85, 1.23 and 2.01 MPa, respectively, and for wet soil (65% FWC), it was 0.74, 1.05 and 1.67 MPa, respectively. Differences between air-dried and wet soil in MSI and treatments LSC, MSC and SSC were 0.09, 0.18 and 0.34 MPa, respectively.

Effect of separate application of soil compaction stress on measured traits

Both maize and triticale seedlings’ growth under moderate (MSC) or severe (SSC) soil compaction, in comparison to low soil compaction (LSC), resulted in a decreased dry matter of S and R and changes in S/R ratio (Table 2). After 28 day of growth in MSC and SSC treatments, the dry matter of S decreased in maize hybrids Ankora to about 4% and 16% and in hybrids Tina to 3% and 14%, respectively. Similarly, in triticale, genotype CHD-12 decrease in S was found to be about 9% and 17%, respectively, and in genotype CHD-247 to 7% and 10%, respectively. Dry matter of roots (R) decreased in the MSC and SSC treatments in Ankora about 7% and 26%, respectively, while for the Tina were 4% and 16%. For CHD-12, the decrease was 14% and 29% and for CHD-247 to 7% and 16%, respectively. Significant increase in the S/R ratio to about 13% and 17% was observed only for Ankora and CHD-12 grown under SSC. Differences between resistant and sensitive genotypes were observed in membrane injury (LI) and chlorophyll content in SPAD units (Table 3). Growth under increased soil compaction...
caused a raise in LI and decrease in SPAD, and observed changes were higher in sensitive genotypes. Correlation coefficients \((r\) between total seedlings dry matter \((S + R)\) and membrane injury \((LI)\) and leaf greening \((SPAD)\) were high and statistically significant \((r = 0.769\) and 0.907 for maize and for triticale \(-0.847\) and 0.932, respectively).

Measurements of leaf \((\psi_L)\) and root \((\psi_R)\) water potential and gas exchange parameters \((Pn, E, g_s, WUE)\) were made only for low \((LSC)\) and severe \((SSC)\) soil compaction levels (Tables 4–8). In control seedlings grown under SSC treatment, decrease in \(\psi_L\) and \(\psi_R\) between 3 and 14 days were slightly larger than in seedlings grown under LSC treatments. Mean decrease of \(\psi_L\) and \(\psi_R\) in maize genotypes Ankora were about 148% and 130%, respectively, and in Tina about 132% and 124%, respectively. For triticale: CHD-12 was about 153% and 137% and in CHD-247 about 132% and 128%, respectively (Table 4). Similarly, a decrease in gas exchange parameters in genotypes grown under SSC treatments in comparison to LSC treatments was observed (Tables 5–8). Mean decrease of \(Pn\) was in Ankora about 17% and Tina 12%, CHD-12 about 13% and CHD-247 about 10%. The decrease of transpiration rate \((E)\) in Ankora and Tina was about 12% and 6%, respectively, and for CHD-12 and CHD-247 was about 10% for both genotypes. Similarly, a decrease of mean stomata conductivity \((g_s)\) was observed. Smaller differences, often not statistically significant between plants grown in the conditions of the LSC and SSC, were observed in WUE calculated as a ratio of \(Pn\) to \(E\). In general, differences between genotypes susceptible to soil compaction were only slightly greater than for resistant ones but in many cases were not statistically significant.

**Effects of soil compaction with drought (SC D) or waterlogging (SC W) on measured traits**

**Changes of biomass**

The soil compaction stress \((SC)\) combined with soil drought \((D)\) or waterlogging \((W)\) influenced a dry matter of shoot \((S)\), roots \((R)\) and shoot to roots \((S/R)\) ratio (Table 2). The obtained results show that decrease of \(S\) and \(R\) in seedlings grown under MSC and SSC soil compaction in comparison with LSC were greater in seedlings grown under drought \((D)\) than under waterlogging \((W)\) and were higher in seedlings grown under SSC for sensitive genotypes \((Ankora, CHD-12)\) than resistant genotypes \((Tina, CHD-247)\). Increase of \(S/R\) ratio was observed only in both maize hybrids \((Ankora, Tina)\) and the sensitive triticale genotype \((CHD-12)\). The ANOVA test shows significant differences for treatments \((T)\) genotypes \((G)\) for \(S, R\) and \(S/R\) ratio. Also significant differences were observed for interaction \(T \times G\), for \(S, R\) and \(S/R\) except triticale.

**Membrane injury \((LI)\) and chlorophyll content \((SPAD)\)**

Measurements of LI and SPAD were carried out in seedlings grown in three levels of soil compaction \((LSC, MSC, SSC)\) and subjected to drought \((D)\) or waterlogging \((W)\) stresses from

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**Table 2. Changes in dry weight of shoot \((S)\), root \((R)\) and ratio of dry weight of shoot to root \((S/R)\) seedlings of maize and triticale genotypes grown 28 days under three soil compaction level \((low – LSC, moderate – MSC and severe – SSC)\) and 14 days under, drought \((D)\) or waterlogging \((W)\), and ANOVA for measured traits.**

| Treatment | Maize genotype | S     | R     | S/R  | Triticale genotype | S     | R     | S/R  |
|-----------|----------------|-------|-------|------|-------------------|-------|-------|------|
| LSC C     | Ankora         | 6.86a | 3.01a | 2.3cd| CHD-12            | 3.70a | 2.00a | 1.92 |
|           | Tina           | 5.94c | 2.97ab| 2.0d | CHD-247           | 3.07cd| 1.86ab| 1.7fgh|
| Mean      |                | **6.40** | **2.99** | **2.2** | Mean              | **3.39** | **1.93** | **1.8** |
| LSC D     | Ankora         | 6.52b | 2.68bc| 2.5c | CHD-12            | 3.29bc| 1.70bcd| 2.0cde|
|           | Tina           | 5.65cd| 2.76abcd| 2.1d | CHD-247           | 2.79def| 1.67cde| 1.7fgh|
| Mean      |                | **6.09** | **2.72** | **2.3** | Mean              | **3.04** | **1.69** | **1.9** |
| LSC W     | Ankora         | 6.66ab| 2.55cde| 2.6c | CHD-12            | 3.39b | 1.72bcd| 2.0cde|
|           | Tina           | 5.70cd| 2.70bcd| 2.1d | CHD-247           | 2.91de| 1.74bc | 1.7fgh|
| Mean      |                | **6.18** | **2.63** | **2.4** | Mean              | **3.15** | **1.73** | **1.9** |
| MSC C     | Ankora         | 6.57ab| 2.81abc| 2.4d | CHD-12            | 3.38b | 1.71bcd| 2.0cde|
|           | Tina           | 5.77cd| 2.86ab | 2.1d | CHD-247           | 2.85de| 1.73  | 1.7fgh|
| Mean      |                | **6.17** | **2.84** | **2.3** | Mean              | **3.12** | **1.72** | **1.9** |
| MSC D     | Ankora         | 5.85c | 1.94h | 3.1b | CHD-12            | 2.74ef| 1.28h  | 2.1cd |
|           | Tina           | 5.06e | 2.02gh| 2.5d | CHD-247           | 2.31gh| 1.50efgh| 1.6fg |
| Mean      |                | **5.46** | **1.98** | **2.8** | Mean              | **2.53** | **1.59** | **1.9** |
| MSC W     | Ankora         | 6.17bc| 2.03gh | 3.1b | CHD-12            | 2.87de| 1.30h  | 2.2bc |
|           | Tina           | 5.26ed| 2.32ef | 2.3d | CHD-247           | 2.54fg| 1.55def| 1.7fgh|
| Mean      |                | **5.72** | **2.18** | **2.7** | Mean              | **2.71** | **1.43** | **2.0** |
| SSC C     | Ankora         | 5.78c | 2.23fg| 2.6d | CHD-12            | 3.06cd| 1.42gh | 2.2bc |
|           | Tina           | 5.07a | 2.49ef| 2.1d | CHD-247           | 2.77ef| 1.56cdef| 1.8fgh|
| Mean      |                | **5.43** | **2.36** | **2.4** | Mean              | **2.92** | **1.49** | **2.0** |
| SSC D     | Ankora         | 4.10f | 1.21i | 3.5a | CHD-12            | 1.99i | 0.82i  | 2.5ab |
|           | Tina           | 4.01f | 1.82h | 2.2d | CHD-247           | 2.05hi| 1.29h  | 1.6h |
| Mean      |                | **4.06** | **1.52** | **2.9** | Mean              | **2.02** | **1.06** | **2.1** |
| SSC W     | Ankora         | 4.49f | 1.26i | 3.6a | CHD-12            | 2.18hi| 0.86i  | 2.6a |
|           | Tina           | 4.11f | 1.77h | 2.3d | CHD-247           | 2.26hi| 1.35gh | 1.7fgh|
| Mean      |                | **4.30** | **1.53** | **3.0** | Mean              | **2.22** | **1.11** | **2.2** |

Different letters in column indicated significant differences according to Duncan test at \(p < .05\) level

**ANOVA**

| Source of variance | df | Maize | Triticale |
|--------------------|----|-------|-----------|
| Treatment (T)      | 5  | ***   | ***       |
| Genotype (G)       | 1  | ***   | **        |
| T X G              | 5  | **    | ns        |

Note: Mean value \(n = 9\); \(n s\) – not significant.

*Statistically significant at a level of probability \(p < .1\).
**Statistically significant at a level of probability \(p < .05\).
***Statistically significant at a level of probability \(p < .01\).
Table 3. The leaf membrane injury (LI)* and leaf greenness (SPAD) in maize and triticale genotypes grown from sowing to 28 day in low (LSC), moderate (MSC) and severe (SSC) levels of soil compaction and with 14 days (from 14 to 28 days) of soil drought (D) or waterlogging (W) and ANOVA test of significance for measured traits.

| Treatment | Genotype | SPAD | | Genotype | SPAD |
|-----------|----------|------|----------|----------|------|
| LSC C     | Ankora   | 6.18 ± 0.28 | | CHD-12  | 5.89 ± 0.18 |
|           | Tina     | 5.34 ± 0.20 | | CHD-247 | 5.21 ± 0.39 |
| Mean      | 5.76     | Mean 5.55  | |Mean 5.55  | |
| LSC D     | Ankora   | 5.61 ± 0.25 | | CHD-12  | 5.35 ± 0.39 |
|           | Tina     | 4.92 ± 0.20 | | CHD-247 | 4.91 ± 0.47 |
| Mean      | 5.30     | Mean 5.13  | | Mean 5.13  | |
| LSC W     | Ankora   | 5.78 ± 0.12 | | CHD-12  | 5.41 ± 0.49 |
|           | Tina     | 5.10 ± 0.20 | | CHD-247 | 5.06 ± 0.23 |
| Mean      | 5.36     | Mean 5.24  | | Mean 5.24  | |
| MSC C     | Ankora   | 4.62 ± 0.28 | | CHD-12  | 4.99 ± 0.33 |
|           | Tina     | 3.76 ± 0.18 | | CHD-247 | 4.49 ± 0.27 |
| Mean      | 4.29     | Mean 4.74  | | Mean 4.74  | |
| MSC D     | Ankora   | 3.64 ± 0.14 | | CHD-12  | 4.26 ± 0.28 |
|           | Tina     | 3.11 ± 0.05 | | CHD-247 | 4.01 ± 0.33 |
| Mean      | 3.69     | Mean 4.13  | | Mean 4.13  | |
| MSC W     | Ankora   | 4.25 ± 0.09 | | CHD-12  | 4.44 ± 0.18 |
|           | Tina     | 3.19 ± 0.17 | | CHD-247 | 4.05 ± 0.22 |
| Mean      | 3.77     | Mean 4.25  | | Mean 4.25  | |
| SSC C     | Ankora   | 2.61 ± 0.09 | | CHD-12  | 3.79 ± 0.11 |
|           | Tina     | 3.11 ± 0.18 | | CHD-247 | 3.79 ± 0.33 |
| Mean      | 2.86     | Mean 3.79  | | Mean 3.79  | |
| SSC D     | Ankora   | 1.80 ± 0.04 | | CHD-12  | 3.12 ± 0.39 |
|           | Tina     | 2.40 ± 0.06 | | CHD-247 | 3.19 ± 0.18 |
| Mean      | 2.36     | Mean 3.15  | | Mean 3.15  | |
| SSC W     | Ankora   | 1.82 ± 0.03 | | CHD-12  | 3.31 ± 0.49 |
|           | Tina     | 2.45 ± 0.09 | | CHD-247 | 3.23 ± 0.21 |
| Mean      | 2.39     | Mean 3.27  | | Mean 3.27  | |
| Mean      | 4.11     | Mean 4.51  | | Mean 4.51  | |
| T x Ankora| 13.50    | 11.68   | | T x CHD-12| 4.22  |
| T x Tina  | 9.78     | 8.66    | | T x CHD-247| 4.36  |
| T x G     | 11.64    | 10.17   | | T x G   | 4.36 |

Notes: Mean values (n = 9) ± standard error. Treatment LSC C was used as control for treatments MSC C and SSC C, respectively, and treatments LSC C, MSC C and SSC C were used as controls for treatments with drought (D) or waterlogging (W), respectively.

**Statistically significant at a level of probability p < .01.**

***Statistically significant at a level of probability p < .001.***

14th to 28th day of growth (Table 3). Membrane injury (LI) of maize and triticale seedlings grown under increased soil compaction levels and drought (D) were higher than in waterlogging (W) conditions. Differences between sensitive and resistant genotypes were observed in seedlings affected by drought or waterlogging. Membrane injury (LI) in treatments MSC D and SSC D in comparison with LSC D increased respectively in Ankora about 40% and 120%, in Tina about 15% and 85%, in CHD-12 about 40 and 135% and in CHD-247 about 40 and 160%. The ANOVA show statistically significant variance for all factors (T, G) and interactions between T x G (Table 3).

**Chlorophyll content (SPAD)**

For seedlings grown under three soil compaction levels and subjected to drought (LSC D, MSC D, SSC D) or waterlogging (LSC W, MSC W, SSC W), a decrease of chlorophyll content in SPAD units was observed (Table 3). Under control soil water content the decrease in SPAD in MSC C and SSC C treatments in comparison with LSC C was in Ankora about 25% and 58%, respectively, in Tina about 25% and 42%, in CHD-12 about 15% and 35% and in CHD-247 about 14% and 27%. Decrease in SPAD for seedlings grown under drought (D) was greater in comparison with seedlings grown under waterlogging (W). The significant differences between sensitive and resistant genotypes of maize and triticale were observed in all treatments and all soil compactions except Ankora and Tina grown under low soil compaction. Table 3 shows the ANOVA of SPAD. For all factors (T, G) and all interactions were (T x G) found statistically significant variance.

**Root (ψ₀) and leaf (ψᵢ) water potential**

Measurements of ψ₀ and ψᵢ were carried out after 3, 7, 10 and 14 days of growth under low (LSC) and severe (SSC) levels of soil compaction for seedlings grown under control conditions (LSC C, SSC C) and for drought (LSC D, SSC D) or for seedlings flooded (LSC W, SSC W). Samples of leaf and root were taken from 11 am to 13 pm in three replications. The reason for the changes of ψ₀ and ψᵢ under drought and around noon hours is that the high rate of transpiration at midday is not counterbalanced completely by the roots’ water uptake from the soil (Table 4). Under control treatments, differences between sensitive and resistant genotypes in ψ₀ and ψᵢ were small and insignificant; however, significant differences were observed between seedlings grown under low and severe soil compaction (SSC). Both in maize and triticale genotypes grown in SSC, decrease of ψ₀ and ψᵢ were greater than in seedlings grown in low soil compaction. For seedlings subjected to drought (D) or waterlogging (W), decrease of ψ₀ and ψᵢ in comparison with controls treatments was observed.
Table 4. Changes of leaf ($\psi_L$), root ($\psi_R$) and $\Delta\psi$ water potential in successive days of applied drought (D) or waterlogging (W) in two maize genotypes grown under low (LSC) or severe (SSC) soil compaction levels and the ANOVA test.

| Treatment       | Genotype     | Leaf water potential ($\psi_L$) | Root water potential ($\psi_R$) | $\Delta\psi = \psi_L - \psi_R$ |
|-----------------|--------------|--------------------------------|--------------------------------|--------------------------------|
| LSC             | CHD-12       | $-0.42c$                       | $-0.44bc$                      | $-0.47$                        |
|                 | CHD-247      | $-0.44c$                       | $-0.47a$                       | $-0.43$                        |
|                 | Mean         | $-0.39$                        | $-0.47$                        | $-0.47$                        |
| LSC             | CHD-12       | $-0.78d$                       | $-1.04c$                       | $-1.21$                        |
|                 | CHD-247      | $-1.02c$                       | $-1.18b$                       | $-1.05$                        |
|                 | Mean         | $-0.74$                        | $-1.28$                        | $-0.86$                        |
| LSC             | CHD-12       | $-0.85d$                       | $-1.10b$                       | $-0.91$                        |
|                 | CHD-247      | $-0.73b$                       | $-0.93a$                       | $-0.77$                        |
|                 | Mean         | $-0.47$                        | $-1.01$                        | $-0.64$                        |
| SSC             | CHD-12       | $-0.33c$                       | $-0.35bc$                      | $-0.37$                        |
|                 | CHD-247      | $-0.32c$                       | $-0.37b$                       | $-0.37$                        |
|                 | Mean         | $-0.33$                        | $-0.39$                        | $-0.43$                        |
| SSC             | CHD-12       | $-0.64d$                       | $-0.85c$                       | $-0.98$                        |
|                 | CHD-247      | $-0.62c$                       | $-1.03a$                       | $-0.91$                        |
|                 | Mean         | $-0.63$                        | $-1.08$                        | $-0.80$                        |
| SSC             | CHD-12       | $-0.36d$                       | $-0.90b$                       | $-0.74$                        |
|                 | CHD-247      | $-0.40c$                       | $-0.82a$                       | $-0.67$                        |
|                 | Mean         | $-0.39$                        | $-0.65$                        | $-0.59$                        |

Different letters in line indicated significant differences for genotype at $p < 0.05$ level

ANOVA

Source of variance | df | Leaf water potential ($\psi_L$) | Root water potential ($\psi_R$) | $\Delta\psi = \psi_L - \psi_R$ |
|-------------------|----|--------------------------------|--------------------------------|--------------------------------|
| Treatment (T)      | 5  | **                            | *                              | *                              |
| Genotype (G)       | 1  | **                            | **                             | **                             |
| Day (D)            | 3  | ***                           | **                             | **                             |
| T x G              | 5  | ***                           | *                              | ns                             |
| T x D              | 15 | **                            | ns                             | ns                             |
| G x D              | 5  | **                            | ns                             | ns                             |
| T x G x D          | 15 | ns                            | ns                             | ns                             |

Leaf water potential ($\psi_L$)

| Treatment       | Genotype     | Day | Mean | 3    | 7    | 10   | 14   |
|-----------------|--------------|-----|------|-----|-----|------|------|
| LSC             | Ankora       |     | $-0.45a$ | $-0.47a$ | $-0.50ab$ | $-0.56b$ | $-0.49$ |
|                 | Tina         |     | $-0.42a$ | $-0.49b$ | $-0.53c$ | $-0.52c$ | $-0.49$ |
|                 | Mean         |     | $-0.44$ | $-0.48$ | $-0.52$ | $-0.54$ | $-0.49$ |
| LSC             | Ankora       |     | $-0.85a$ | $-1.13b$ | $-1.50c$ | $-1.65d$ | $-1.28$ |
|                 | Tina         |     | $-0.77a$ | $-1.11b$ | $-1.28c$ | $-1.51d$ | $-1.17$ |
|                 | Mean         |     | $-0.81$ | $-1.12$ | $-1.39$ | $-1.58$ | $-0.57$ |
| LSC             | Ankora       |     | $-0.78a$ | $-0.92b$ | $-1.20c$ | $-1.30d$ | $-1.05$ |
|                 | Tina         |     | $-0.70a$ | $-0.87a$ | $-1.10b$ | $-1.30c$ | $-0.99$ |
|                 | Mean         |     | $-0.74$ | $-0.90$ | $-1.15$ | $-1.30$ | $-0.53$ |
| SSC             | CHD-12       |     | $-0.51a$ | $-0.61ab$ | $-0.69bc$ | $-0.76c$ | $-0.64$ |
|                 | Tina         |     | $-0.48a$ | $-0.62b$ | $-0.61b$ | $-0.61b$ | $-0.58$ |
|                 | Mean         |     | $-0.50$ | $-0.61$ | $-0.65$ | $-0.68$ | $-0.40$ |
| SSC             | CHD-12       |     | $-1.01a$ | $-1.61b$ | $-1.75c$ | $-1.91d$ | $-1.57$ |

Root water potential ($\psi_R$)

| Treatment       | Genotype     | Day | Mean | 3    | 7    | 10   | 14   |
|-----------------|--------------|-----|------|-----|-----|------|------|
| LSC             | Ankora       |     | $-0.32a$ | $-0.33a$ | $-0.35ab$ | $-0.39b$ | $-0.35$ |
|                 | Tina         |     | $-0.30a$ | $-0.35ab$ | $-0.37b$ | $-0.36b$ | $-0.34$ |
|                 | Mean         |     | $-0.31$ | $-0.34$ | $-0.36$ | $-0.38$ | $-0.31$ |
| LSC             | Ankora       |     | $-0.60a$ | $-0.79b$ | $-1.05c$ | $-1.16c$ | $-0.90$ |
|                 | Tina         |     | $-0.54a$ | $-0.79b$ | $-0.97c$ | $-1.06c$ | $-0.84$ |
|                 | Mean         |     | $-0.57$ | $-0.78$ | $-1.01$ | $-1.11$ | $-0.24$ |
| LSC             | Ankora       |     | $-0.54a$ | $-0.65b$ | $-0.84c$ | $-0.91c$ | $-0.74$ |
|                 | Tina         |     | $-0.52a$ | $-0.57a$ | $-0.81b$ | $-0.87b$ | $-0.69$ |
|                 | Mean         |     | $-0.53$ | $-0.61$ | $-0.82$ | $-0.89$ | $-0.21$ |
| SSC             | CHD-12       |     | $-0.41a$ | $-0.49b$ | $-0.55b$ | $-0.60b$ | $-0.51$ |
|                 | Tina         |     | $-0.38a$ | $-0.49b$ | $-0.49b$ | $-0.49b$ | $-0.46$ |
|                 | Mean         |     | $-0.40$ | $-0.49$ | $-0.52$ | $-0.55$ | $-0.10$ |
| SSC             | CHD-12       |     | $-0.81a$ | $-1.29b$ | $-1.40c$ | $-1.53c$ | $-1.26$ |

$\Delta\psi = \psi_L - \psi_R$
In sensitive genotypes (Ankora, CHD-12), changes were greater than for resistant genotypes (Tina, CHD-247). During successive days when drought or waterlogging stresses were applied and in both soil compaction levels differences between $\psi_L$ and $\psi_R$ were observed but under waterlogging conditions those differences were lower in comparison with drought conditions. Table 4 shows the ANOVA of root ($\psi_R$), ($\psi_L$) and ($\Delta\psi$). For all factors (T, G, D) and interactions ($T\times G$, $T\times D$, $G\times D$) statistically significant variance were found. However, interaction between ($T\times G\times D$) was significant only for ($\psi_R$) in maize.

**Gas exchange parameters (Pn, E, gs) and WUE**

Schedule of measurements of gas exchange parameters was same as measurements of water potential. Differences between sensitive and resistant of maize and triticale genotypes were observed in Pn, E and gs (Tables 5 and 7). Changes of gas exchange parameters were greater in seedlings grown under drought connected with SSC in comparison with seedlings subjected to waterlogging. In maize, decrease in Pn between 3 and 14 days in seedlings subjected to drought (D) was in treatment LSC and SSC about 20% and 57% for Ankora and about 16% and 43% for Tina, respectively. Similarly, in seedlings subjected to waterlogging (W), decrease of Pn in treatments LSC and SSC was for Ankora about 13% and 41% and for Tina 5% and 21%, respectively. In triticale, changes of Pn in this period were similar and in treatments LSC and SSC with drought (D) were in CHD-12 about 27% and 58% and in CHD-247 about 21% and 34%, respectively, and with waterlogging (W) in CHD-12 about 13% and 29% and in CHD-247 about 8% and 17%, respectively. As in the case of photosynthesis rate (Pn), similarly effects of soil compaction and soil water content on transpiration rate (E) and stomatal conductance (gs) were observed. Decrease of E between 3 and 14 days was greater in seedlings subjected to drought (D) than for seedling subjected to waterlogging (W) especially in seedling growing in SSC. In sensitive genotypes (Ankora, CHD-12), differences of E between control seedlings (LSC C, SSC C) and seedling subjected to drought (LSC D, SSC D) or waterlogging (LSC W, SSC W) were larger than in resistant genotypes (Tina, CHD-247). Similar changes were also observed in stomata conductivity (gs). In seedlings growing under drought (D) stress decrease, gs was greater than in seedlings grown under waterlogging (W) and was visible especially in sensitive genotypes. Somewhat differently proceeded changes of WUE in maize and triticale. Under conditions of low soil compaction in both genotypes of maize from 3 to 10 days, WUE was higher than in control plants but after 14 days decline of WUE was observed. However, under the SSC, WUE decline compared to control was observed after 7 days and it was particularly large in the seedling grown under drought. In both genotypes of triticale grown under low soil compaction, differences between treatments were statistically insignificant. In conditions of SSC in sensitive genotype (CHD-12), WUE decreases from 7 days especially for seedlings treated with drought, but in resistant genotype (CHD-247), differences between treatments were smaller. The results of ANOVA of gas exchange parameters and WUE are presented in Tables 5–8. For maize, the variance for Pn, E, gs, and WUE was significant for all variables (T, G, D) and for the all interactions. Similarly, for triticale, significant variances were found, except for stomata conductance ($T\times D$, $T\times G\times D$) and WUE ($T\times G\times D$).
Table 5. Changes of rate of photosynthesis (Pn) in maize and triticale genotypes grown under low or severe soil compaction (LSC, SSC) and under soil drought (D) or waterlogging (W) stresses and the ANOVA test.

| Treatment | Genotype | Day | Mean | Genotype | Day | Mean |
|-----------|----------|-----|------|----------|-----|------|
| LSC C     | Ankora   | 22.1ab | 22.9a | 21.8b | 21.3b | 22.0 |
|           | Tina     | 20.2ab | 21.1a | 19.9b | 19.6b | 20.2 |
| LSC D     | Ankora   | 20.0a  | 18.1b | 18.4b | 16.0c | 18.1 |
|           | Tina     | 18.5ab | 19.1a | 17.6b | 15.5c | 17.7 |
| LSC W     | Ankora   | 21.0a  | 19.9b | 20.1b | 18.2c | 19.8 |
|           | Tina     | 19.0ab | 19.9a | 18.5bc | 18.1c | 18.9 |
| SSC C     | Ankora   | 19.2a  | 19.0a | 18.1b | 17.2c | 18.4 |
|           | Tina     | 18.4a  | 18.1ab | 17.5b | 17.1b | 17.8 |
| SSC D     | Ankora   | 18.5a  | 14.9b | 13.2c | 7.9d | 13.6 |
|           | Tina     | 17.0a  | 16.4a | 13.2b | 9.7c | 14.1 |
| SSC W     | Ankora   | 19.1a  | 15.9b | 15.2b | 13.2c | 15.9 |
|           | Tina     | 17.0a  | 17.5a | 15.6b | 13.4c | 13.3 |
| Mean      | Ankora   | 20.0a | 19.9 | 19.3 | 18.1 | 18.1 |
|           | Tina     | 18.8 | 18.5 | 17.8 | 17.1 | 17.8 |

Different letters in line indicated significant differences according to Duncan test at $p < .05$ level.

ANOVA

| Source of variation | df | Maize | Triticale |
|---------------------|----|-------|-----------|
| Treatment (T)       | 5  | ***   | ***       |
| Genotype (G)        | 1  | **    | **        |
| Day (D)             | 3  | *     | **        |
| T x G               | 5  | *     | *         |
| T x D               | 15 | **    | *         |
| G x D               | 3  | **    | *         |
| T x G x D           | 15 | *     | *         |

Note: Mean values ($n = 9$).
*Statistically significant at a level of probability $p < 0.1$.
**Statistically significant at a level of probability $p < 0.05$.
***Statistically significant at a level of probability $p < 0.01$.
Table 6. Changes of transpiration rate (E) in maize and triticale genotypes grown under low or severe soil compaction (LSC, SSC) and under soil drought (D) or waterlogging (W) stresses and the ANOVA test.

| Treatment | Genotype | Maize | Mean | Triticale | Mean |
|-----------|----------|-------|------|-----------|------|
|           |          | Day   |      |           |      |
| Lsc C     | Ankora   | 4.0ab | 4.2a | 3.9b      | 4.1  |
|           | Tina     | 3.4a  | 3.4a | 3.4a      | 3.4  |
| Mean      | 3.7      | 3.8   | 3.8  | 3.6       | 3.2  |
| Lsc D     | Ankora   | 3.3a  | 3.2ab | 3.1b | 3.1b      | 3.2  |
|           | Tina     | 2.8ab | 2.9a | 2.7b      | 2.8  |
| Mean      | 3.1      | 3.0   | 2.9  | 2.9       | 2.8  |
| Lsc W     | Ankora   | 3.6a  | 3.5a | 3.3b      | 3.2  |
|           | Tina     | 3.2a  | 3.0b | 2.9b      | 3.0  |
| Mean      | 3.4      | 3.3   | 3.1  | 3.0       | 3.0  |
| SSC C     | Ankora   | 3.7a  | 3.7a | 3.6a      | 3.6  |
|           | Tina     | 3.2ab | 3.3a | 3.2ab     | 3.1b |
| Mean      | 3.4      | 3.5   | 3.4  | 3.2       | 3.2  |
| SSC D     | Ankora   | 2.8a  | 2.6b | 2.7b      | 1.9c |
|           | Tina     | 2.8a  | 2.6b | 2.3c      | 2.5  |
| Mean      | 3.0      | 2.6   | 2.5  | 2.2       | 2.5  |
| SSC W     | Ankora   | 3.6a  | 3.2b | 3.1bc     | 2.9c |
|           | Tina     | 2.9a  | 3.0a | 3.0a      | 2.9a |
| Mean      | 3.2      | 3.1   | 3.0  | 2.9       | 2.9  |

Different letters in line indicated significant differences according to Duncan test at p < .05 level

Mean values (n = 9).
*Statistically significant at a level of probability p < 0.1.
**Statistically significant at a level of probability p < 0.05.
***Statistically significant at a level of probability p < 0.01.

ANOVA

| Source of variation | df | Maize | Triticale |
|---------------------|----|-------|-----------|
| Treatment (T)       | 5  | **    | ***       |
| Genotype (G)        | 1  | **    | *         |
| Day (D)             | 3  | **    | **        |
| T × G               | 5  | **    | **        |
| T × D               | 15 | **    | **        |
| G × D               | 3  | *     | *         |
| T × G × D           | 15 | *     | *         |

Mean values (n = 9).
Table 7. Changes of stomata conductance ($g_s$) in maize and triticale genotypes grown under low or severe soil compaction (LSC, SSC) and under soil drought (D) or waterlogging (W) stresses and the ANOVA test.

| Treatment | Genotype | Maize Mean | 3 | 7 | 10 | 14 | 105.1 |
|-----------|----------|------------|---|---|----|----|-------|
| Lsc C     | Ankora   | 101.1b     | 106.7a | 112.4a | 100.0b | 105.1 |
|           | Tina     | 78.6b      | 79.8a  | 79.2ab  | 80.9a  | 79.6  |
|           | Mean     | 89.9d      | 93.3b  | 95.8a   | 90.5c  | 90.5c |
| Lsc D     | Ankora   | 50.5b      | 49.4b  | 51.7a   | 49.4b  | 50.3  |
|           | Tina     | 68.5a      | 62.1b  | 58.9c   | 52.4d  | 60.5  |
|           | Mean     | 59.6a      | 55.8b  | 55.3b   | 50.9c  | 50.9c |
| Lsc W     | Ankora   | 99.0ab     | 103.0a | 89.9b   | 70.0c  | 90.5c |
|           | Tina     | 84.3a      | 73.0ab | 67.4bc  | 65.2c  | 72.5  |
|           | Mean     | 91.7       | 88.0   | 78.7    | 67.6   | 72.5  |
| SSC C     | Ankora   | 91.0b      | 89.9b  | 101.1a  | 91.0b  | 93.3  |
|           | Tina     | 70.8ab     | 71.9a  | 69.7b   | 73.0a  | 71.4  |
|           | Mean     | 80.9       | 80.9   | 85.4    | 82.0   | 82.0  |
| SSC D     | Ankora   | 43.8a      | 40.7b  | 42.7ab  | 41.6b  | 42.2  |
|           | Tina     | 47.1a      | 43.9b  | 39.3c   | 33.2d  | 40.9  |
|           | Mean     | 45.5       | 42.3   | 41.0    | 37.4   | 37.4  |
| SSC W     | Ankora   | 90.0a      | 84.0b  | 87.0ab  | 83.0b  | 86.0  |
|           | Tina     | 61.8a      | 61.8a  | 50.6b   | 43.9c  | 54.5  |
|           | Mean     | 75.9       | 72.9   | 68.8    | 63.5   | 63.5  |

Different letters in line indicated significant differences according to Duncan test at $p < .05$ level.

Mean

| Treatment (T) | Maize Mean | 3 | 7 | 10 | 14 |
|---------------|------------|---|---|----|----|
| T × D (Ankora)| 79.2       | 79.0 | 80.8 | 72.5 | 77.9 |
| T × D (Tina) | 68.5       | 65.4 | 60.8 | 58.1 | 63.2 |
| T × G × D    | 73.9       | 72.2 | 70.8 | 65.3 | 70.5 |

ANOVA

| Source of variation | df | Maize | Triticale |
|---------------------|----|-------|-----------|
| Treatment (T)       | 5  | **    | **        |
| Genotype (G)        | 1  | **    | *         |
| Day (D)             | 3  | **    | **        |
| T × G               | 5  | **    | *         |
| T × D               | 15 | **    | ns        |
| G × D               | 3  | *     | *         |
| T × G × D           | 15 | *     | ns        |

Note: Mean values ($n = 9$); ns: not significant.

*Statistically significant at a level of probability $p < 0.1$.

**Statistically significant at a level of probability $p < 0.05$.

***Statistically significant at a level of probability $p < 0.01$. 
Table 8. Changes of rate of water use efficiency (WUE) in maize and triticale genotypes grown under low or severe soil compaction (LSC, SSC) and under soil drought (D) or waterlogging (W) stresses and the ANOVA test.

| Treatment | Genotype | Day | Mean |
|-----------|----------|-----|------|
| Maize     |          | 3   | 7    | 10  | 14  | Mean |
| LSC C     | Ankora   | 5.58a | 5.45ab | 5.25b | 5.45ab | 5.43 |
|           | Tina     | 5.96a | 6.16a  | 5.86b | 5.96a  | 5.99 |
| Mean      |          | 5.77 | 5.81  | 5.56  | 5.71  | 5.74 |
| LSC D     | Ankora   | 6.06a | 5.70b  | 6.00a  | 5.21c  | 5.74 |
|           | Tina     | 6.57a | 6.66a  | 6.57a  | 5.66b  | 6.37 |
| Mean      |          | 6.32 | 6.18  | 6.29  | 5.44  |      |
| LSC W     | Ankora   | 5.86b | 5.73b  | 6.16a  | 5.74b  | 5.88 |
|           | Tina     | 6.00b | 6.77a  | 6.44a  | 6.26ab | 6.32 |
| Mean      |          | 5.93 | 6.16  | 6.30  | 6.00  |      |
| SSC C     | Ankora   | 5.25a | 5.15a  | 5.05a  | 5.25a  | 5.18 |
|           | Tina     | 5.76a | 5.53a  | 5.53a  | 5.56a  | 5.60 |
| Mean      |          | 5.51 | 5.34  | 5.29  | 5.41  |      |
| SSC D     | Ankora   | 5.76a | 5.66b  | 4.95c  | 4.14d  | 5.13 |
|           | Tina     | 6.06b | 6.36a  | 5.86b  | 3.92c  | 5.55 |
| Mean      |          | 5.91 | 6.01  | 5.41  | 4.03  |      |
| SSC W     | Ankora   | 5.35a | 4.95b  | 4.96b  | 4.60c  | 4.97 |
|           | Tina     | 5.96a | 5.76a  | 5.15b  | 4.66c  | 5.38 |
| Mean      |          | 5.66 | 5.36  | 5.06  | 4.63  |      |

Different letters in line indicated significant differences according to Duncan test at p < .05 level.

ANOVA

| Source of variation | df  | Maize | Triticale |
|---------------------|-----|-------|-----------|
| Treatment (T)       | 5   | **    | ***       |
| Genotype (G)        | 1   | *     | *         |
| Day (D)             | 3   | *     | *         |
| T × G               | 5   | *     | *         |
| T × D               | 15  | *     | *         |
| G × D               | 3   | *     | *         |
| T × G × D           | 15  | *     | ns        |

Note: Mean values (n = 9); ns: not significant.
*Statistically significant at a level of probability p < 0.1.
**Statistically significant at a level of probability p < 0.05.
***Statistically significant at a level of probability p < 0.01.
Table 9. Correlation coefficients between measured traits in maize and triticale genotypes grown under low (LSC) or severe (SSC) soil compactors and under drought (D) or waterlogging (W) conditions (df = 11).

| Trait | Maize | E | WUE | $\psi_s$ | $\psi_l$ | $\Delta \psi$ | Triticale | E | WUE | $\psi_s$ | $\psi_l$ | $\Delta \psi$ |
|-------|-------|---|-----|---------|---------|-------------|-----------|---|-----|---------|---------|-------------|
| Lsc – low soil compaction | | | | | | | | | | | | |
| $\text{Pn}$ | 0.899*** | -0.071NS | 0.140 NS | 0.937*** | 0.937*** | 0.937*** | 0.807*** | -0.641** | 0.945*** | 0.945*** | 0.951*** | 0.970*** | 0.532* |
| E | -0.500* | -0.500* | 0.180 NS | 0.923*** | 0.923*** | 0.923*** | 0.814*** | 0.388 NS | 0.945*** | 0.945*** | 0.951*** | 0.970*** | 0.532* |
| $\psi_s$ | -0.124 NS | -0.124 NS | 0.204 NS | 0.924 NS | 0.924 NS | 0.924 NS | 0.675 NS | -0.571* | 0.945*** | 0.945*** | 0.951*** | 0.970*** | 0.532* |
| $\psi_l$ | 0.099*** | 0.099*** | 0.099*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** | 0.999*** |
| SSC – severe soil compaction | | | | | | | | | | | | |
| $\text{Pn}$ | 0.955*** | 0.760*** | 0.159 NS | 0.893*** | 0.893*** | 0.893*** | 0.688 NS | 0.099 NS | 0.945*** | 0.945*** | 0.951*** | 0.970*** | 0.532* |
| E | 0.540* | 0.540* | 0.196 NS | 0.947*** | 0.947*** | 0.947*** | 0.814*** | 0.099 NS | 0.945*** | 0.945*** | 0.951*** | 0.970*** | 0.532* |
| $\psi_s$ | 0.095 NS | 0.095 NS | 0.465 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS | 0.447 NS |
| $\psi_l$ | 0.227 NS | 0.227 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS | 0.212 NS |
| CHD-12 | | | | | | | | | | | | |
| Lsc – low soil compaction | | | | | | | | | | | | |
| $\text{Pn}$ | 0.528* | 0.614** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** | 0.945*** |
| E | -0.344 NS | -0.344 NS | 0.641** | 0.513* | 0.513* | 0.513* | 0.513* | 0.513* | 0.513* | 0.513* | 0.513* | 0.513* | 0.513* |
| $\psi_s$ | 0.438 NS | 0.438 NS | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* | 0.564* |
| $\psi_l$ | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** | 0.956*** |
| CHD-247 | | | | | | | | | | | | |
| SSC – severe soil compaction | | | | | | | | | | | | |
| $\text{Pn}$ | 0.798*** | 0.913*** | 0.879*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** | 0.915*** |
| E | 0.486 NS | 0.486 NS | 0.808*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** | 0.847*** |
| $\psi_s$ | 0.647** | 0.647** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** | 0.746*** |
| $\psi_l$ | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** | 0.969*** |

Note: NS: not significant.
*Statistically significant at the 0.10 probability level.
**Statistically significant at the 0.05 probability level.
***Statistically significant at 0.01 probability level.
Correlation and regression between the measured physiological markers

In this experiment, between two species, four genotypes and two levels of soil compaction conditions differences of the correlation between the studied traits were found (Table 9). In both genotypes of triticale, statistical significant correlations were observed in plants grown under SSC in all cases, except for WUE with E. On the other hand, in the seedlings grown under low soil compaction (LSC), significant coefficients were not observed at a resistant genotype (CHD-247) between WUE with Pn, gs, ψL, ψR and ψL − ψR and in sensitive genotype (CHD-12) only for WUE with E and gs. In contrast, in both maize genotypes, there has been less statistically significant correlation coefficients than in the case of triticale. This mainly concerns the associations between WUE and gs with all the cases. In experiments we found not only a close association, between ψL and ψR, but also differences between ψL and ψR (Δψ).

Soil compaction stress had a significant effect on changes in the stem and root biomass and all measured physiological traits except stomata conductance (gs), leaf and root water potential (ψL, ψR). Results presented in Figure 1 show relations between changes in total seedlings dry weight (S + R) and soil compaction, drought and waterlogging stresses. Regression coefficient ($R^2$) for relation between seedlings dry matter (S + R) and membrane injury index (LI) and leaf greening (SPAD) of maize and triticale genotypes grown under 3 levels of soil compaction (LSC, MSC, SSC) and under drought (D) or waterlogging (W) stresses. Regression coefficients (R) are shown with statistical signification by ns. non-significant; *, **, *** – statistically significant at $p < .1, .05$ and .01, respectively.

Figure 1. Relationship between seedlings dry matter (S + R) and membrane injury index (LI) and leaf greening (SPAD) of maize and triticale genotypes grown under 3 levels of soil compaction (LSC, MSC, SSC) and under drought (D) or waterlogging (W) stresses. Regression coefficients (R) are shown with statistical signification by ns. non-significant; *, **, *** – statistically significant at $p < .1, .05$ and .01, respectively.
Figure 2. Relationship between seedlings dry matter (S + R) and gas exchange parameters (Pn, E, gS, WUE) and leaf (ψL), root (ψR) water potential and Δψ (ψR − ψL) of maize and triticale genotypes grown under two levels of soil compaction (LSC, SSC) and after 14 days of drought (D) or waterlogging (W). Regression coefficients (R) are shown with statistical signification: ns: non-significant; *, **, *** – statistically significant at p < .1, .05 and .01, respectively.
the plant participates in photosynthesis and it may also perform other protective functions, with higher content often observed in plants exposed to stress. The reduction in chlorophyll content is caused by the inhibition of synthesis and accelerated decomposition of chlorophyll, and stress-resistant species have stronger chlorophyll molecules’ association with lipid–protein complex membranes of chloroplasts (Poljakoff-Mayber 1981; Smirnoff and Colombe 1988; Palta 1990). In the present paper, we show that the difference between water potential of leaf and root in seedlings subjected to different soil moisture levels lies in the limitation of water uptake by roots under drought or under waterlogging (Table 4). In the resistant genotype to compacted soil (Tina, CHD-247), the differences between \( \psi_R \) and \( \psi_L \) were smaller than in the sensitive one (Ankora, CHD-12). According to Tardieu (1993) and Ehlers and Goss (2003), in plants grown without watering under given evaporative demand of the air, water potential within the soil–plant–atmosphere continuum is dependent on the soil water potential. Extraction of water from defined soil volume in an experimental pot causes the soil matrix potential to decrease steadily from day to day. When \( \psi_R \) and \( \psi_L \) decline at noon, the tissues turgor is reduced. This will in turn affect the rate of cell enlargement, which may decline noticeably in periods of restricted water budget. Only in the night after relaxation the rates of cell enlargement and growth will increase again. Growth by cell elongation can be continued throughout the night and possibly the growth at night is greater than during the day. During the course of water extraction and soil drying in the pot, the daily amplitudes of \( \psi_R \) and \( \psi_L \) become more pronounced. In seedlings subjected to prolonged stresses, the critical value of water potential is reached and leaf wilting occurs because \( \psi_L \) does not rise above the wilting point (Passioura et al. 1993; Smith and Griffiths 1993; Lipiec et al. 1996; Bengough et al. 2011). Also, daily changes in leaf water status of seedlings grown under high soil compaction indicate damage to light-harvesting mechanisms in stressed plants and lend support to the hypothesis that early damage to PSH explains the prompt closing of stomata by stressed plants (Jackson and Ram 2003).

The relation between leaf water content and gas exchange parameters was studied in many papers as the basis for the estimation of photosynthesis limitation by stomatal or non-stomatal mechanisms in plants grown under stress conditions. The physiological mechanisms involved in stomata behavior under different soil compaction and soil water deficiency or excess are not well explained, but some studies have shown that stomata aperture controls leaf water deficit and may improve leaf WUE. Stomata play an important role in controlling \( \text{CO}_2 \) and \( \text{H}_2\text{O} \) vapor exchange and stomata aperture effects of \( \text{Pn} \) and \( E \) (Nilson and Assmann 2007, Law-son and Blatt 2014, Dodd et al. 2015). The earliest response to leaf water deficit is stomata closure, which limits \( \text{CO}_2 \) diffusion to chloroplasts. Non-stomatal mechanisms under prolonged water deficit in leaf tissues include changes in chlorophyll synthesis, functional and structural changes in chloroplasts and also disturbances in accumulation and distribution of assimilation products (Kicheva et al. 1994; Medrano et al. 2002). It has been found that both electron transfer and \( \text{CO}_2 \) fixation are affected under water stress (Chaves et al. 2002; Liu et al. 2010). Moreover, during leaf water deficit, disturbances of photosynthesis at the molecular
level are connected with low electron transport through PSII and/or with structural injuries of PSII and LHC complexes. As such, the decrease in Pn can be attributed to the influence of soil compaction on soil aeration and reduction of air transmission in the root system. Similar to our results, significant correlation coefficient was also found between stomata conductance and leaf water potential for flooded tomato plants (Tardieu et al. 1991; Tardieu 1993; Sobeih et al. 2004; Else et al. 2009).

In both maize genotypes, drought or waterlogging with LSC condition caused WUE to be higher but under the SSC, was lower than the control plants (LSC C). However, for triticale, differences in WUE between treatments were small and insignificant. Breeding of stress-resistant cereal species which apply water-saving strategies used to improve their WUE. Also, as a result of various stress factors, rapid changes occur in hormone levels of plant tissues, which alter the balance between synthesis, degradation and transport of hormones. Some of these changes may be adaptive responses to stressful conditions while others may be an expression of metabolic disorders (Chaves et al. 2002; Fageria et al. 2006; Golbashy et al. 2010; Liu et al. 2010; Sun et al. 2015).

Most research on soil compaction considers this stress in isolation; however, far less studies investigated interactions with other environmental stresses. Results obtained in our experiments show that effects of soil compaction on seedlings growth and physiological traits depend on the plant species and soil water availability. Soil compaction, soil drought and waterlogging were considered to have an effect on physiological processes; however, it is complicated to explain the impact of soil compaction (mitigation or aggravation of the harmful effects) with the presence of soil water stress factors. Our results show that changes in the dry matter of shoot and roots under different soil compaction strongly depend on soil water content and on interaction with a drought or waterlogging. Soil compaction stress decreases plant biomass, but it is not consistent with other research, which indicated that conditions of intermediate compaction stimulated a biomass growth because under these conditions there is better soil–root contact, which improves water and nutrient uptake (Masle 2002, Alameda et al. 2012, Alameda and Villar 2012).

In natural environments, we frequently have to deal with the situation of simultaneous presence of different stresses and their interactions cannot be directly extrapolated from the response of plants to a single stress. The combination of two or more stresses should be regarded as a new state of influences on plants, which requires a new defence or acclimation response Mittler (2006). Physiological markers assist the selection of plants with particular characteristics, but this task is time-consuming, requiring much experience, taking into account the different phases of growth and development of plants and reproducible environmental conditions. Our research and studies by other authors have shown that physiological markers are satisfactory for the study of populations in terms of their sensitivity to stress and they may support molecular testing (Masle 2002; Mittler 2006).

Conclusions

Tolerance to a combination of different stress conditions, particularly those that mimic field environment, should be the focus of research programs aimed at developing new crop genotypes with enhanced tolerance. The impact of combined stresses on the physiology of crop plants is key to understanding stress susceptibility mechanisms under natural field conditions. Recent studies have revealed that the response of plants to a combination of two different abiotic stresses is unique and cannot be directly extrapolated from the response of plants to each stress applied individually. Exposure of plants to more abiotic stresses causes most often a more harmful effect comparing to a single stress. In our study we found that responses of maize and triticale genotypes to soil compaction stress with drought or waterlogging are associated with plant water status, which is manifested in the changes of physiological traits such as membrane permeability, chlorophyll content and leaf gas exchange. Differences between sensitive and resistant maize and triticale genotypes indicate that resistant have more efficient protection mechanisms against water loss, cell membrane status, photosynthesis and WUE. Therefore, further studies on physiological and metabolic processes in sensitive and resistant genotypes are necessary, particularly in hydraulic and chemical signaling, sink-source relations and the supply of water and carbon.

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References

Alameda D, Anten NPR, Villar R. 2012. Soil compaction effects on growth and root traits of tobacco depend on light, water regime and mechanical stress. Soil Till Res. 120:121–129.

Alameda D, Villar R. 2012. Linking root traits to plant physiology and growth in Fraxinus angustifolia Vahl. seedlings under soil compaction conditions. Environ Exp Bot. 79:49–57.

Asch F, Bahrurn A, Jensen CR. 2009. Root-shoot communication of field-grown maize drought-stressed at different rates as modified by atmospheric conditions. J Plant Nutr Soil Sci-Z Pflanzenernahr Bodenkld. 172:678–687.

Ashraf M. 2010. Inducing drought tolerance in plants: recent advances. Biotech Adv. 28:169–183.

Ashraf M, Arfan M. 2005. Gas exchange characteristics and water relations in two cultivars of Hibiscus esculentus under waterlogging. Biol Plant. 49:459–462.

Baker NR. 1993. Light-use efficiency and photoinduction of photosynthesis in plants under environmental stress. In: Smith JAC, Griffiths H, editors. Water deficits. Plant responses from cell to community. Oxford: BIOS Scientific Publishers; p. 221–235.

Bengough AG, McKenzie BM, Hallett PD, Valentine TA. 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. J Exp Bot. 62:59–68.
Berkowitz GA, Chen C, Gibbs M. 1983. Stomatal activation mediates in vivo water stress inhibition of nonstomatal controlled photosynthesis. Plant Physiol. 72:1123–1126.

Bethenod O, Tardieu F, Katerji N. 1996. Relationship between net photosynthetic rate and stomatal conductance in leaves of field-grown maize subjected to soil compaction or soil drying. Photosynthetica. 32:367–379.

Blum A. 1996. Crop response to drought and the interpretation of adaptation. Plant Growth Regul. 20:135–148.

Blum A, Ebercon A. 1981. Cell membrane stability as a measure of drought and heat tolerance in wheat. Crop Sci. 21:43–47.

Boyer JS. 1982. Plant productivity and environment. Science. 218:443–448.

Chan G, Weil RR. 2010. Penetration of cover crop roots through compacted soil. Plant Soil. 331:31–43.

Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osorio LM, Carvalho I, Faria T, Pinheiro C. 2002. How plants cope with water stress in the field? Photosynthesis and growth. Ann Bot. 89:907–916.

Clark LJ, Whalley WR, Barralouc PR. 2003. How do roots penetrate strong soil. Plant Soil. 255:93–99.

Colombi T, Walter A. 2016. Root responses of triticale and soybean to soil compaction in the field are reproducible under controlled conditions. Funct Plant Biol. 43:114–128.

Corning C, Brantian JM. 1991. Partitioning of photosynthetic electron flow between CO2 and O2 reduction in a C3 leaf (Phascolus vulgaris L.) at different CO2 concentrations and during drought stress. Planta. 183:178–184.

Corning C, Frensel CA. 2002. Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for photosystem II activity during a mild drought. Ann Bot. 89:887–894.

Corning C, Massacci A. 1996. Leaf photosynthesis under drought stress. In: Baker NR, editor. Photosynthesis and the environment. Dordrecht: Kluwer Academic Publishers; p. 347–366.

Crawford RM. 2003. Seasonal differences in plant responses to flooding and anoxia. Can J Bot – Revue Canadienne De Botanique. 81:1224–1246.

Damanik RI, Miahziah M, Ismail MR, Ahmad S, Zain AM. 2010. Responses of the antioxidative enzymes in Malaysian rice (Oryza sativa L.) cultivars under submergence condition. Acta Physiol Plant. 32:739–747.

Dodd IC, Puértolas J, Huber K, Pérez-Pérez JG, Wright HR, Blackwell MSA. 2015. The importance of soil drying and re-wetting in crop phytohormonal and nutritional responses to deficit irrigation. J Exp Bot. 66:2239–2252.

Dubey R. 1997. Photosynthesis in plants under stressful conditions. In: Pessarakli M, editor. Handbook of photosynthesis. Tuscon: University of Arizona; p. 859–875. New York, Basel, Hong Kong: Marcel Dekker Inc.

Elahi W, Goos M. 2003. Water dynamics in plant production. Cambridge: CABI Publishing.

Else MA, Janowiak F, Atkinson CJ, Jackson MB. 2009. Long-distance signalling from roots to shoots assessed: the flooding story. J Exp Bot. 53:175–181.

Jackson MB, Ram PC. 2003. Physiological and molecular basis of susceptibility and tolerance of rice plants to complete submergence. Ann Bot. 91:227–241.

Jones HG, Flowers TJ, Jones MB. 1989. Plant under stress. Society for experimental botany, seminar series 39. Cambridge: Cambridge University Press.

Kebbas S, Latts S, Aid F. 2015. Effect of drought stress on the photosynthesis of Asacia tortilis subsp. raddiana at the young seedling stage. Photosynthetica. 53:288–298.

Kicheva MI, Tsonov TD, Popova P. 1994. Stomatal and nonstomatal limitations to photosynthesis in two wheat cultivars subjected to water stress. Photosynthetica. 30:107–116.

Kono Y, Yamadauch F, Kawamura AN, Tatsumi J. 1987. Interspecific differences of the capacities of waterlogging and drought tolerance among winter wheats. Jpn J Crop Sci. 56:115–129.

Kozlowski TT. 1999. Soil compaction and growth of woody plants. Scand J For Res. 14:596–619.

Kriedemann PE, Dowton WJS. 1981. Photosynthesis. In: Páleg LG, Aspinall D, editors. The physiology and biochemistry of drought resistance in plants. Sydney: Academic Press; p. 283–314.

Lawlor DW, Tezara W. 2009. Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: a critical evaluation of mechanisms and integration of processes. Ann Bot. 103:561–579.

Lawson T, Blatt MR. 2014. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. Plant Physiol. 164:1556–1570.

Lipiec J, Ishioka T, Szuostak 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.

Liu Y, Bin T, Zheng Y, Me K, Xu S, Qiu F. 2010. Screening methods for waterlogging tolerance at maize (Zea mays L.) seedling stage. Agr Sci China. 9:362–369.

Masle J. 2002. High soil strength: mechanical forces at play on root morphology and function. Hortscience. 37:1381–1385.

McKersie BD, Leshem YY. 1994. Stress and stress coping in cultivated plants. Dordrecht: Kluwer Academic Publishers.

Nilson SE, Assmann SM. 2007. The control of transpiration. Insights from Arabidopsis. Plant Physiol. 143:19–27.

Palta JP. 1990. Stress interactions at the cellular and membrane levels. HortsScience. 25:1377–1381.
Passioura JB, Condon AG, Richards RA. 1993. Water deficits, the development of leaf area and crop productivity. In: Smith JAC, Griffiths H, editors. Water deficits plant responses from cell to community. Oxford: BIOS Scientific Publishers; p. 253–264.

Poljakoff-Mayber A. 1981. Ultrastructural consequences of drought. In: Paleg LG, Aspinall D, editors. The physiology and biochemistry of drought resistance in plants. New York (NY): Academic Press; p. 389–403.

Ripley BS, Gilbert ME, Ibrahim D, Osborne CP. 2007. Drought constraints on C4 photosynthesis: stomatal limitation and electron sinks in C3 and C4 subspecies of *Alloteropsis semialata*. J Exp Bot. 58:1351–1363.

Rut G, Rzepka A, Krupa J. 2010. Effect of hypoxia and post-hypoxia on the fluctuations in contents of malate and citrate, the activity of malic enzyme, and on the intensity of gas exchange in moss gametophores. Photosynthetica. 48:79–86.

Sairam RK, Kumutha D, Ezhilmathi K, Deshmukh PS, Srivastava GC. 2008. Physiology and biochemistry of waterlogging tolerance in plants. Biol Plant. 52:401–412.

Smirnoff N, Colombe SV. 1988. Drought influences the activity of enzymes of the chloroplast hydrogen peroxide scavenging system. J Exp Bot. 39:1097–1108.

Smith JAC, Griffiths H. 1993. Water deficits: plant responses from cell to community. Oxford: BIOS Scientific Publishers.

Sobell W, Dodd IC, Bacon MA, Grierson DC, Davies WJ. 2004. Long-distance signals regulating stomatal conductance and leaf growth in tomato (*Lycopersicon esculentum*) plants subjected to partial root zone drying. J Exp Bot. 55:2353–2363.

Sun C, Gao X, Fu J, Zhou J. 2015. Metabolic response of maize (*Zea mays* L.) plants to combined drought and salt stress. Plant Soil. 388:99–117.

Tardieu F. 1993. Will progresses in understanding soil-root relations and root signalling substantially alter water flux models? Phil Trans R Soc. 341:57–66.

Tardieu F, Katerji N, Bethenod O, Zhang J, Davies WJ. 1991. Maize stomatal conductance in the field – its relationship with soil and plant water potentials, mechanical constraints and ABA concentration in the xylem sap. Plant Cell Environ. 14:121–126.

Tracy SR, Black CR, Roberts JA, Dodd IC, Mooney SJ. 2015. Using X-ray computed tomography to explore the role of abscisic acid in moderating the impact of soil compaction on root system architecture. Environmental and Exp Bot. 110:11–18.

Tubeileh A, Groleau-Renaud V, Plantureux S, Guckert A. 2003. Effect of soil compaction on photosynthesis and carbon partitioning within a maize-soil system. Soil Till Res. 71:151–161.

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. 347–360.

Yu H, Chen X, Youn-Hong Y, Wang Y, Xu P, Ke S, Liu H, Zhu J, Oliver DJ, Xiang C. 2008. Activated expression of an *Arabidopsis* HD-START protein confers drought tolerance with improved root system and reduced stomatal density. Plant Cell. 20:1134–1151.

Zhao HF, Zhao Y, Zhang C, Tao X, Xu XN. 2014. Growth, leaf gas exchange, and chlorophyll fluorescence responses of two cultivars of *Salix integrata* Thunb. to waterlogging stress. J Agric Sci Technol. 16:137–149.