Environmental and Experimental Botany xxx (2012) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Changes in root system structure, leaf water potential and gas exchange of maize and triticale seedlings affected by soil compaction

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ARTICLE INFO

Article history:
Received 29 August 2011
Received in revised form 20 January 2012
Accepted 31 January 2012

Keywords:
Biomass
Gas exchange
Maize
Root architecture
Triticale
Soil compaction
Water potential

ABSTRACT

The physiological reasons associated with differential sensitivity of C_3 and C_4 plant species to soil compaction stress are not well explained and understood. The responses of growth characteristics, changes in leaf water potential and gas exchange in maize and triticale to a different soil compaction were investigated. In the present study seedlings of triticale and maize, representative of C_3 and C_4 plants were subjected to low (L – 1.10 g cm^{-3}), moderate (M – 1.34 g cm^{-3}) and severe (S – 1.58 g cm^{-3}) soil compaction level. Distinct differences in distribution of roots in the soil profile were observed. Plants of treatments M or S in comparison to treatment L, showed a decrease in leaf number, dry mass of stem, leaves and roots, and an increase in the shoot to root ratio. A drastic decrease in root biomass in M and S treatments in the soil profile on depth from 15 to 40 cm was observed. Any level of soil compaction did not influence the number of seminal and seminal-adventitious roots but decreased their length. The number and total length of nodal roots decreased with compaction. Changes of growth traits in M and S treatments in comparison to the L were greater for maize than for triticale and were accompanied by daily changes in water potential (ψ) and gas exchange parameters (P_N, E, g_s). Differences between M and S treatments in daily changes in ψ for maize were in most cases statistically insignificant, whereas for triticale, they were statistically significant. Differences in the responses of maize and triticale to soil compaction were found in P_N, E and g_s in particular for the measurements taken at 12:00 and 16:00. The highest correlation coefficients were obtained for the relationship between leaf water potential and stomatal conductance, both for maize and triticale, which indicates the close association between stomata behavior and changes in leaf water status.

1. Introduction

Soil compaction is an abiotic stress that damages crop plants. Different level of soil compaction is caused mainly by natural processes and by the use of heavy machinery in soil cultivation (Masle, 2002; Fageria et al., 2006). The restrictive effect of soil compaction can be physically and physiologically constraining to overall plant growth and yield through poor development of the root system (Tu and Tan, 1991; Lipiec et al., 1993; Iijima et al., 1993; Grzesiak, 2009). An acquisition of water and mineral nutrients is primarily determined by the dimension of the root zone and distribution of root density and root proliferation (Iijima and Kono, 1991; Oussible et al., 1993; Yamauchi, 1993). According to Yamauchi et al. (1987) and Yamauchi (1993) cereal plants develop two types of the root system, depending on the angle of growth of side branches – lateral roots and their distribution in a soil profile. "Concentrated" type of a root system develops a greater number of densely distributed nodal roots with relatively small rooting angle. Other type designated as a "scattered" develops fewer but longer nodal roots, many of which runs obliquely in the soil profile (larger rooting angle). A maize root system belongs to a "scattered" type and a that of triticale – to a "concentrated" type. Also Kono et al. (1972) recognized heterorhizy in lateral roots development on the seminal root. Typical responses of a plant root system structure to soil compaction include reduction in number and length of roots, restriction of downward penetration of the main root axes, decrease in leaf thickness, increase in the dry mass shoot-to-root ratio and a decrease in crop grain yield (Clark et al., 2003; 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).

Abbreviations: DM_R, root dry matter; DM_S, shoot dry matter; E, transpiration rate; FWC, field water capacity; g_s, stomatal conductance; L, M, S, low, moderate and severe soil compaction, respectively; P_N, photosynthesis rate; ψ, leaf water potential.

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doi:10.1016/j.envexpbot.2012.01.010

Inhibited plant growth is mostly attributed to reduced rooting volume (Iijima and Kono, 1993; Yamauchi, 1993; Grzesiak et al., 1999, 2002; Masle, 2002; Fageria et al., 2006; Grzesiak, 2009). A hormonal signal from the roots is the cause of reduction in shoot growth on compacted soils and a hormonal mechanism may play an important role in a controlling of a root growth response to mechanical impedance on compacted soils (Jackson, 2002; Else et al., 2009).

There is a limited knowledge regarding relations between the modification in root system architecture, leaf water status and gas exchange for plants grown in different soil compaction (Materechera et al., 1992; Yamauchi, 1993; Grzesiak et al., 2002). In the research on responses of plant to abiotic stresses the influence of a soil physical parameter is not taken into consideration, whereas this factor also affects the plant growth and physiological processes (Henderson, 1991).

The physiological reasons associated with differential sensitivity of C_3 and C_4 plant species to soil compaction stress are not well explained and understood (Iijima and Kono, 1993; Nayyar and Gupta, 2006). The aim of this study was to examine the response of maize and triticale seedlings to different levels of soil compaction on the biomass production, number and length of all components of a root system and daily changes in leaf water potential and gas exchange parameters. Maize and triticale have different types of photosynthesis (C_3-triticale, C_4-maize) and a root system structure and they are important crops widely cultivated throughout the world (Iijima and Kono, 1993; Masle, 2002; Ghannoum, 2009). The responses of maize and triticale to different soil compaction may explain how these species manage their growth under soil compaction stress.

2. Materials and methods

2.1. Plant material

The research was carried out using plant material obtained from a breeding station in Choryn, Poland (triticale-breeding line, CHD-147) and from SEMPOL–Holding Trnava, Slovakia (maize single-cross hybrids, Nova).

2.2. Growth conditions

Plants were grown in air-conditioned growth cabinets under the following day/night conditions: temperature 23/18 °C (±2.5 °C), relative humidity (RH) 70/60% (±5%) and during a 14 h photoperiod from 7:00 to 21:00 (artificial irradiance from high pressure sodium lamps, *Philips SON-T AGRO*, 400 W) PAR was equal to about 350 μmol m^{-2} s^{-1}.

Plants were grown in root-boxes, which enabled the non-destructive isolation of all compartments of the root system (Kono et al., 1987). The set of a "root-box and pin board method" consists of: a plexiglass root box (width – 0.25 m, depth – 0.40 m, thickness – 0.02 m), a pin board for sampling the root system, and a polyethylene sheet (envelope) for handling and preserving the root system. Root boxes were filled with a mixture of garden soil- (loamy soil (85%)) and silt-sand loam (15%), peat and sand (1:1:3, v:v:v). Air-dried soil substrate was sieved in a 0.25 cm mesh and mixed with a compound fertilizer (N – 28 mg, P – 18 mg, K – 14 mg) at the rate per 1 kg of the soil substrate. Soil pore distribution was divided into 5 classes of pore diameter (>350, 100–350, 25–100, 10–25 and <10 μm). Total pore size, in percent of soil volume for treatments L, M and S was 53.5, 49.0 and 47.2%, respectively. Soil substrate pH was about 7.1 and percent of organic material was 0.7.

Three treatments were applied, L (low), M (moderate) and S (severe) soil compaction levels and for those treatments, the air-dried soil bulk densities throughout the 0–40 cm soil profile was set at 1.10, 1.34 and 1.58 g cm^{-3}. Mechanical impedance in soil substrate was measured with penetrometer DIK 5520 (Daiki Rika Kogyo Co. Ltd., Japan).

Field soil water capacity (FWC) for soil mixture was determined according to Kopecky methods. Air-drained soil samples (110.0, 134.0, and 158.0 g) were placed inside metal cylinders, with the 1 mm hole at the bottom. For all samples, volume was 100 cm^3. Cylinders with samples were placed inside the container with water for 30 min. After 8 h, maximal soil water content in samples was 0.47, 0.43 and 0.39 (g cm^{-3}), respectively and after 48 h decreased to 0.25, 0.21 and 0.18 (g cm^{-3}), respectively. According to Hillel and van Bavel (1976) those last values were assumed to be 100% of soil field water capacity (FWC). During experiment the root-boxes were weighted every day, and the amount of the water loss through evapotranspiration was refilled to keep the constant mass of root-boxes in each treatment at a level of 65–70% FWC. In order to limit water evaporation from a root-box, soil surface was covered with a 1 cm layer of ground styrofoam.

A single pregerminated grain was planted at a depth of 3–4 cm. On the 21st, 35th and 49th day of experiment, after measurements of leaf water potential and gas exchange parameters the sampled seedling was cut into shoots and roots. The roots were sampled after the soil in the pot had been washed away by a gentle stream of water. Root samples were preserved in a FAA (formalin, acetic acid, and ethanol) solution.

2.3. Measurements

Dry matter of above-ground plants parts (DM_S) and roots (DM_R) for three depths (0–15, 15–30 and 30–40 cm) were sampled in each root-box and were determined in 21, 35 or 49 days after sowing. Dry matter of samples were measured after drying at 65 °C for 72 h. For measurements of number and length of seedling root components (seminal, seminal adventitious, nodal), the DELTA-T SCAN (England) analyzer was used.

Measurements of leaf water potential (ψ) and leaf gas exchange parameters (P_N, E, g_s) were taken in 4 h intervals on 8:00, 12:00, 16:00 and 20:00 h. This measurement was made after 21, 35 and 49 days of growth on the 3rd, 4th or 5th leaf, respectively, this means, on most recent fully expanded leaf.

Leaf water potential (ψ) was measured with a psychrometer HR 33T (Wescor Inc., Logan, USA) in "dew point" mode, equipped with a sample chamber C-52 SF (Wescor Inc., Logan, USA) and digital multimeter *Metex M-3640 D*. Measurements were taken on leaf discs – diameter of 0.3 cm for triticale and 0.5 cm for maize, cut from the middle part of the leaves and immediately placed inside the psychrometer chamber and left to balance temperature and water vapor equilibrium for 30 min before measurements.

The rates of leaf gas exchange parameters were measured using a CO_2 IRGA analyzer (CI-301PS, CID Inc., USA) with a Parkinson's assimilation chamber and a narrow type regular with light attachment CI-301 LA. During the measurements an open system was used. A flow rate of ambient air with a constant CO_2 concentration (360 μmol mol^{-1}) through the assimilation chamber amounted to 0.5 dm^3 min^{-1}. Chamber temperature was kept below 25 °C until the photosynthesis rate had stabilized. Photosynthetic capacity at light saturation was reached by exposing leaves to photosynthetically active radiation (PAR) at 800 μmol m^{-2} s^{-1}.

For each day of plant harvest (21, 35 and 49) treatment (L, M and S) and species (maize and triticale) number of replications for all measurements were $n = 5$.

Please cite this article in press as: Grzesiak, S., et al., Changes in root system structure, leaf water potential and gas exchange of maize and triticale seedlings affected by soil compaction. Environ. Exp. Bot. (2012), doi:10.1016/j.envexpbot.2012.01.010