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Rhizosphere water repellency as affected by *Neotyphodium* endophyte-tall fescue symbiosis in calcareous soils with different clay content

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Figures 1 and 2 should be published in full color.

Summary

- To the best of the authors' knowledge, there is no document about the influence of endophyte-tall fescue symbiosis on soil water repellency and hydraulic properties so far. Our hypothesis was that presence of *Neotyphodium coenophialum* in the aboveground parts of tall fescue (*Festuca arundinacea*) may alter the chemical, biological and hydraulic properties of rhizospheric soil. A greenhouse pot experiment was conducted to characterize the effect of endophyte-tall fescue symbiosis on water repellency and hydraulic properties of rhizosphere in different soil textures.
- Endophytic symbiosis greatly enhanced soil organic carbon pools especially for the fine-textured soils and decreased the basal soil respiration. Changes in chemical and biological properties of rhizosphere *via* endophyte infection and clay content altered the soil water repellency and hydraulic properties. Lower water sorptivity (due to hydrophobic coatings) and higher ethanol sorptivity (due to altered pore structure) were responsible for the greater water repellency in the E^+ rhizosphere soil than E^- ones.
- Endophyte-tall fescue symbiosis could increase physical quality of rhizosphere soil and thus the aggregate stability. Moderate sub-critical water repellency induced by endophyte infection may provide favorable impact on soil structural stability and on plant response to water stress in the drought periods.

Key words: endophyte, hot-water soluble carbohydrates, rhizosphere, soil-water contact angle, water sorptivity, water repellency index

Introduction

Tall fescue (*Festuca arundinacea* Schreb.), as an agro-economically important forage perennial grasses is widely spread in the temperate regions of the world. In Iran, *F. arundinacea* is known as an important crop for turf uses and soil conservation in cool-season pastures of mountainous areas (Tehrani *et al*., 2009). Tall fescue has evolved symbiotic relations with fungi including mycorrhizal fungi of the roots (Smith & Read, 1997) and endophytic fungi which naturally infect plant shoots (Rodriguez *et al*., 2009).

Nonpathogenic, systemic and intercellular fungus of *Neotyphodium coenophialum* (Bacon & De Battista, 1991) usually infect *F. arundinacea* Schreb. (Morse *et al*., 2002). This infection has several positive consequences for the host plant including enhanced biomass production and tolerance to biotic (Kimmons *et al*. 1990; Clay *et al*. 1993) and abiotic stresses (Malinowski & Belesky, 2000; Swarthout *et al*., 2009; Sabzalian & Mirlohi, 2010;

Soleimani *et al.*, 2010; Ren *et al.*, 2011; Nagabhyru *et al.*, 2013). Endophytic fungi through the production of alkaloids, phenolic compounds (Iqbal *et al.*, 2012) and other secondary metabolites such as carbohydrates and proline (Malinowski & Belesky, 2000) could increase plant resistance to environmental stresses.

The release of alkaloids, phenolic compounds and other metabolites from plant roots may alter soil biological and biochemical properties (Iqbal *et al.*, 2012). Franzluebbers *et al.* (1999) and Franzluebbers & Stuedemann (2005) found that soils from E^- pastures supported lower microbial biomass and reduced basal soil respiration rates. Van Hecke *et al.* (2005) indicated that the presence of endophytic fungi may enhance rhizodeposition by tall fescue and could consequently influence microbial mineralization processes of nutrients in soil. Franzluebbers (2006) has demonstrated that the endophyte-tall fescue symbiosis may alter the dynamics of soil organic matter (SOM); total, particulate, mineralizable, and aggregate-associated C and N fractions increased during the experiment due to large rhizospheric inputs in the E^+ treatment. Also, Handayani *et al.* (2005) found that there was significant difference between E^+ and E^- tall fescue for microbial biomass C, mineralizable C, C in micro-aggregates, and aggregate-size distribution. Endophyte infection could modify chemical conditions of tall fescue rhizosphere and could regulate the root exudates (Malinowski *et al.*, 1998a; Malinowski & Belesky, 1999a,b, 2000, 2004). Presence of endophyte is also effective on litter chemistry and decomposition rates. Lemons *et al.* (2005) and Siegrist *et al.* (2010) found that E^+ tall fescue litter has been decomposed more slowly than E^- litter especially when the litter was decomposing in a pasture dominated by endophyte-infected tall fescue. Endophytic fungi through changes in the characteristics of litter, root production and exudation of host plants could affect the carbon sequestration (Franzluebbers & Stuedemann, 2002). Iqbal *et al.* (2012) observed that plant aboveground resided endophyte could enhance the carbon sequestration capacity of tall fescue stands in Southeastern US.

Soil water repellency, due to the presence of organic coatings on soil particles, is recognized as a widespread phenomenon in different climatic regions of the world (Wallis & Horne, 1992; Hallett, 2007; Leelamanie & Karube, 2007; Jordan *et al.*, 2009). The negative consequences of soil hydrophobicity including reduced infiltration, increased runoff, preferential leaching of nutrients and contaminants, reduced plant growth, and accelerated soil erosion (Chau *et al.*, 2012). However, moderate water repellency can improve the water stability of soil aggregates (Piccolo & Mbagwu, 1999; Hallett, 2007), thus might positively affect soil structure and carbon pools (Spaccini *et al.*, 2002). Both persistence and severity of water repellency are affected by land use, plant cover, soil water status, soil texture, temperature, pH and fire (Hallett *et al*., 2003; Rillig, 2005; Lichner *et al*., 2011; Vogelmann *et al*., 2013).

Sources of hydrophobic organic materials in soil may include accumulated plant-derived organic matter and waxes, microbial organic acids and polysaccharides (Kostka, 2000). Exudates produced by plant roots and some soil microbes, enhancing nutrient availability and tolerance to drought stress (Hallett *et al*., 2003), might modify soil physical, biological and chemical properties (Jones *et al*., 2009). Read *et al*. (2003) observed that plant root-released phospholipids' surfactants could significantly affect the chemical and physical environment of the rhizosphere, modifying soil hydraulic properties. Rillig *et al.* (2010) reported that the mycelium of *Glomus intradices* can significantly improve the aggregate stability through increased soil hydrophobicity. Hallett *et al*. (2003) observed that plant genotypes differently affected hydraulic properties and water repellency of the rhizosphere.

Soil texture is also effective on water repellency. Wahl (2008) reported that the hydrophobicity is influenced by the specific surface area and varies considerably with soil texture. It has been argued that soil water repellency is usually associated with coarse–textured soils (McGhie & Posner, 1980; DeBano, 1991). It is reported that the addition of clays can be very effective in reducing water repellency of sandy soils (Gonzalez-Penaloza *et al*., 2013). However, there are diverse reports about the effect of soil texture on hydrophobicity in the literature. Kawamoto *et al*. (2007) observed high water repellency in clayey soils because clay-induced aggregation could restrict available surface area for hydrophobic coatings to the outer surfaces of aggregates.

Although soil water repellency, its causes and consequences are well-known, but to the best of the authors' knowledge there is no document in literature about the influence of endophytic fungi and their symbiosis associations with tall fescue on soil hydraulic properties so far. We developed our research to fill this knowledge gap. Our hypothesis was that the presence of *N. coenophialum* in the aboveground parts of tall fescue can alter the chemical and biological properties of rhizospheric soil and as a consequence, the soil hydro-physical properties such as water repellency will be affected. The objectives of this research were to explore (i) the effect of endophyte-plant symbiosis on soil chemical and hydraulic properties and (ii) the interactive effect of the symbiosis with soil type on the mentioned soil characteristics.

Materials and Methods

Preparation of soil samples and experimental design

A greenhouse pot experiment was performed in a completely randomized design with factorial arrangement of six soil types and endophyte infection (E^+ and E^-) with three replications. The study was carried out during an 8-months period (April to November 2013) in the research greenhouse of Isfahan University of Technology. Six arable soil samples with different clay content were collected from agricultural fields of Isfahan province. The soil samples were air-dried and passed through a 6-mm sieve with minimal aggregates' destruction. Then the soils were packed in pots (25 cm internal diameter and 30 cm height) to dry bulk density (BD) of 1.25 g cm^{-3}. However, the BD of the potted soils changed over the time due to wetting-drying and settlement/consolidation. The BD values at the end of the experiment are presented in Table 1. Sufficient amounts of the soil samples were grounded and passed through a 2-mm sieve for further measurements.

Characterization of soil properties

Disturbed soil samples were used for characterization of soil properties. Soil texture with pipette method (Soil Conservation Service, 1984), the soil organic carbon (SOC) with wet-oxidation method (Walkely & Black, 1934), calcium carbonate equivalent (CCE) by back-titration with NaOH (Sims, 1996), electrical conductivity (EC) and pH in saturated soil extract were measured.

Plant materials

Clonally propagated tillers of tall fescue (genotype 75C) infected with *N. coenophialum* (E^+) or free of endophyte (E^-) were selected for the experiments (Sabzalian & Mirlohi, 2010). Prior to planting, the presence or absence of the fungus in E^+ and E^- clones, respectively, were verified by staining plant leaf tissues with Rose bengal as described by Saha *et al.* (1988). Microscopic image of endophytic fungi is shown in Fig. 1a. Five similar tillers were then transferred to each pot. During the experiment, soil water content was kept near the field capacity (FC) by daily monitoring. Field capacity (at matric suction of 330 hPa) was determined by the pressure plate apparatus. Plants were grown under natural light (>1000 µmol m^{-2} s^{-1}) and optimal temperature conditions (18−25 °C). After 8 months when plants reached the maximum vegetative growth and covering pot soil surface, the experiment was seized and shoots were carefully separated from the roots. Both roots and shoots were oven-dried at 75 °C for 72 h, then dry biomass was measured.

Collection of undisturbed soil samples from rhizosphere

After shoot-root separation, intact soil aggregates/clods (3−4 cm) adherent to plant roots were gently collected from the 5–10 cm soil layer for determination of soil hydraulic properties. Due to very high density of roots in the pots (Fig. 1b), the adhered aggregates to plant roots can be considered as rhizospheric soil (Hallett et al., 2003). The disturbed samples were collected from the rhizospheric soil for determination of SOC, hot-water soluble carbohydrates and microbial respiration rate.

INSERT FIG. 1 HERE

Measurement of hot-water soluble carbohydrates

In most soils, 5−25% of the SOM is composed of carbohydrates (Ratnayake *et al.*, 2013). Hot-water soluble carbohydrates (HWSC) are mostly originated from polysaccharides of plant exudates or microbial biomass (Bongiovanni & Lobartini, 2006) and play a major role in stability of soil aggregates. Therefore, HWSC could be used as a soil quality indicator in soil–plant ecosystems (Ghani *et al.*, 2003). The HWSC concentration of soil samples was determined as follows: 1 g of air-dried soil was mixed with 10 ml distilled water on a vortex and heated at 85 °C for 2.5 h. Afterward, the soil suspension was centrifuged at 3000 rpm for 30 min and then 2 ml of supernatant solution was used to determine the carbohydrate concentration by phenol-sulfuric acid method of Dubois *et al.* (1956). The HWSC of the extract was determined by spectrophotometric method (Spectrophotometer Model Jenway 6505 UV/Vis) with glucose as the standard and represented based on oven-dry soil mass (Brink Jr *et al.*, 1960).The absorbance of solution was read at 490 nm.

Measurement of basal soil respiration

Basal soil respiration (BSR) of the soil samples was determined by the method introduced by Chen *et al.* (2000). The air-dried soils were moisturized to FC by distilled water, followed by incubation at 25°C in a sealed glass jar for 1 week and CO_2 evolved from soil was trapped in alkali solution (1 N NaOH). The residual of alkali solution was titrated with 0.5 N H_2SO_4 to a phenolphthalein endpoint. Produced CO_2 was calculated from the difference between acid volumes used for neutralizing NaOH blanks and soil samples.

Characterization of soil water repellency

The intact oven-dried soil aggregates/clods were used for sorptivity measurements. The sorptivity of aggregates to distilled water and 95% ethanol were determined with a tension micro-infiltrometer device according to Hallett & Young (1999) (Fig. 2). Soil pore structure and water repellency are effective on water sorptivity, whereas ethanol sorptivity is affected only by pore structure (Tillman *et al*., 1989; Hallett & Young, 1999; Hallett *et al*., 2003; Cosentino *et al*., 2010). The micro-infiltrometer consists of a tube with one end connected to a reservoir with the fluid and the other one is covered with a nylon mesh that makes contact with the aggregate.

INSERT FIG. 2 HERE

Fluids were supplied to the aggregates through nylon-mesh tip with a 2 mm radius from reservoir at constant hydraulic head. In order to supply the water and ethanol with similar near-saturated scaled suction (h^*), the water and ethanol levels (h) in the bottle were set, respectively, at 2.0 and 0.7 cm lower than the tip contact with the aggregate, which were calculated using the following equation (Philip, 1957; Tillman *et al*., 1989):

$$h^* = \frac{\rho g h}{\eta} \qquad (1)$$

where h^* is the scaled suction head (cm^{-1}), h is the suction head (cm), ρ and η are the density ($g\ cm^{-3}$) and dynamic viscosity ($g\ cm^{-1}\ s^{-1}$) of the fluid, respectively, and g is the acceleration due to gravity ($cm\ s^{-2}$). This equation shows that for the same value of h^*, there should be different values of h for different wetting fluids.

Water sorption was measured followed by measurement of ethanol sorption on the same aggregate. Fluid absorption was monitored using a digital balance (with an accuracy of 0.001 g) at 5 s intervals for 180 s to reach a steady-state flow. The sorptivity (S) characterizes the soil's capability of adsorbing water/ethanol by capillary forces. Intrinsic sorptivity (S^*), which is independent of the absorbing fluid, could be related to S using the following equation (Philip, 1969):

$$S^{*}=\left[\frac{\mu}{\gamma}\right]^{0.5}S \qquad (2)$$

where μ and γ are dynamic viscosity (g cm^{-1} s^{-1}) and surface tension (g s^{-2}) of the fluid, respectively. The sorptivity (S, cm s$^{-0.5}$) was obtained from Equation 3:

$$S=\sqrt{\frac{Qf}{4br}} \qquad (3)$$

where Q is the steady-state liquid flow rate (cm^{3} s^{-1}), b is a constant parameter that depends on the soil–water diffusivity function, being 0.55, according to White & Sully (1987), r is the infiltrometer tip radius (i.e. 2 mm), and f is the air-filled porosity equal to total porosity for oven-dry aggregates (cm^{3} cm^{-3}). The infiltration data were drawn as cumulative liquid volume, I (cm^{3}) *vs*. time, t (s) and the Q was obtained from the slope of the linear section (see Fig. 6) which was usually observed in the range 30−140 s (Leeds-Harrison *et al*., 1994; Hallett *et al*., 2003). All of the measurements were done at constant temperature of 20 °C.

The water repellency index (RI) was calculated by the following equation (Tillman *et al*., 1989; Hallett & Young, 1999):

$$\mathrm{RI}=\frac{S_{\mathrm{E}}^{*}}{S_{\mathrm{W}}^{*}}=\left[\frac{(\mu_{\mathrm{E}}/\gamma_{\mathrm{E}})}{(\mu_{\mathrm{W}}/\gamma_{\mathrm{W}})}\right]^{0.5}\times\frac{S_{\mathrm{E}}}{S_{\mathrm{W}}} \qquad (4)$$

where the S_{E}^{*} and S_{W}^{*} are intrinsic ethanol and water sorptivities, respectively, S_{E} and S_{w} are the ethanol and water sorptivities, μ_{E}, γ_{E} and μ_{W}, γ_{W} are the ethanol and water viscosities and surface tensions, respectively. At 20 °C, μ_{E} and μ_{w} are 0.012 and 0.01 g cm^{-1} s^{-1}, and γ_{E}, and γ_{w} are 22 and 72 g s^{-2}, respectively. Substitution of these values reduces Equation 4 to:

$$\mathrm{RI}=1.95\times\frac{S_{\mathrm{E}}}{S_{\mathrm{W}}} \qquad (5)$$

The soil-water contact angle (θ) was calculated using the RI values as follows (Gryze *et al*., 2006):

$$\theta=\arccos\left(\frac{1}{\mathrm{RI}}\right) \qquad (6)$$

According to Tillman *et al*. (1989), Hallett & Young (1999) and Lipiec *et al.* (2009), the RI values of 1, >1.95 and >50 indicate no water repellency, sub-critical water repellency and high water repellency, respectively.

Statistical analysis

Analysis of variance (ANOVA) was performed using the SAS software (version 9.1). Mean values of treatments were compared using the LSD test at $P<0.05$. The individual linear relations between soil water repellency indices and hydraulic properties (i.e. S_E, S_w, RI, θ) and physical and chemical properties including sand content, clay content (CC), SOC, HWSC, BSR, and SOC:CC, HWSC:SOC and HWSC:CC ratios were studied. The figures were drawn using MS Excel (Microsoft Corporation, Washington State, US).

Results

Measured soil physical and chemical properties

Physical and chemical properties of the studied soils are summarized in Table 1. Soils were commonly calcareous with relatively low organic carbon (Table 1). The clay and sand contents were in broad ranges while they were similar in terms of silt content and other properties. This allowed us to demonstrate the effect of clay content on soil hydraulic properties and water repellency induced by endophyte-plant symbiosis.

INSERT TABLE 1 HERE

Effect of endophyte infection and soil clay content on root dry matter

The differences in root dry matter between E^+ and E^- tall fescue were not statistically significant (P□0.05) although E^+ plants had consistently higher root dry matter values than E^- plants (Fig. 3a). Mean values of root biomass in different soil types (i.e. clay contents) are presented in Fig. 3b. Soil clay content (CC) had significant effect on the root dry biomass ($P<0.05$). The maximum root biomass was 14.5 g per pot which was observed in a soil with 386 g kg^{-1} CC. When the CC increased to 426 g kg^{-1}, the root dry matter decreased significantly. Interaction's mean comparison indicated that especially in coarse–textured soils, E^+ plants had greater root biomass than E^- plants but the differences were not significant (P□0.05).

INSERT FIG. 3 HERE

Effect of endophyte infection and soil clay content on soil organic carbon

The ANOVA of the data indicated that the presence of endophyte had significant effect on the rhizosphere SOC ($P<0.01$). The E^+ tall fescue had greater SOC than the E^- plants (Table 2). Also, the CC considerably affected the SOC values ($P<0.01$). In general, increasing CC leads to an increase in the rhizosphere SOC (Table 3). Fig. 4 shows that the interaction of CC and endophyte presence had significant effect on the SOC ($P<0.01$). In all soil types, endophyte presence increased the SOC but in the low CCs (i.e. 161 and 263 g kg^{-1}), the differences between mean SOC values of E^+ and E^- were not significant. The highest SOC was observed in the rhizosphere soil of E^+ tall fescue with 386 g kg^{-1} CC.

INSERT FIG. 4 HERE

Effect of endophyte infection and soil clay content on basal soil respiration

Soil microbial activity (quantified by BSR) was significantly ($P<0.01$) higher in rhizosphere soils of the E^- than E^+ grasses (Table 2). The results (Table 3) suggested that increasing CC could significantly ($P<0.05$) alter the BSR values. The highest and lowest values of BSR were observed in soils with 386 and 161 g kg^{-1} CC, respectively. However, the interactive influence of endophyte infection × CC on BSR was not significant (P□0.05).

Effect of endophyte infection and soil clay content on soluble carbohydrates

The variation trends of HWSC, as an important component of labile SOC, were much similar to the SOC values. Table 2 shows the HWSC concentrations in the rhizosphere soil of E^+ and E^- tall fescue; the effect of endophyte presence on the HWSC was significant ($P<0.01$). The CC affected the HWSC as well (Table 3, $P<0.01$). The mean values of HWSC ranged from 0.59 g kg^{-1} in soil with 161 g kg^{-1} CC to 0.868 g kg^{-1} in soil with 386 g kg^{-1} CC. Increasing CC generally increased the HWSC values. The interactive influence of endophyte infection × CC on HWSC was also significant ($P<0.01$). Similar to SOC, the maximum HWSC was observed in the rhizosphere soil of E^+ tall fescue with 386 g kg^{-1} CC. In all treatments, E^+ tall fescue contained more HWSC in the rhizosphere.

INSERT TABLES 2 & 3 HERE

Effect of endophyte infection and soil clay content on soil water repellency

The ANOVA indicates that the presence of endophyte and increment of CC significantly changed the water repellency of the rhizosphere soil (P<0.01). Fig. 5a shows that endophyte infection increased the RI significantly. However, the increment in CC reduced the RI (Table 4). The highest and lowest values of RI (i.e. 3.91 and 2.38) were observed in the soils with 205 and 426 g kg^{-1} CC, respectively. The RI values (greater than 1.95) indicated that the soils in all treatments are classified as *sub-critically water repellent* based on Tillman *et al.* (1989). The RI was not significantly affected by interaction of CC and endophyte infection. The soil-water contact angle (θ), similar to RI, was significantly affected by endophyte infection and CC. The E^{+} tall fescue rhizosphere soil had greater θ values when compared to E^{-} tall fescue rhizosphere soil (P<0.01, Fig. 5b). Table 4 shows the θ values in the studied soils; in general, greater mean θ values were observed in soils with lower CC (P<0.05).

INSERT FIG. 5 HERE

Effect of endophyte infection and soil clay content on water/ethanol sorptivities

Examples of water and ethanol uptake *vs*. time, as affected by endophyte infection and clay content, are shown in Fig. 6a,b,c,d. The water uptake was slower in E^{+} treatment (Fig. 6a) and in coarse-textured soil (Fig. 6b), whereas ethanol uptake was greater in E^{+} treatment (Fig. 6c) and was not much different among the soils (Fig. 6d). The significant effect of endophyte presence on water (S_{w}) and ethanol (S_{E}) sorptivities is shown in Fig. 7a,b (P<0.05). The E^{+} treatment had greater S_{E} and lower S_{w}. In contrast, E^{-} tall fescue has greater S_{w} and lower S_{E}. The S_{w} and S_{E} as a function of CC are listed in Table 4. For all treatments, the CC did not affect the S_{E} significantly. Unlike the S_{E}, the S_{w} was significantly increased with increment of CC (P<0.01).

INSERT FIGS. 6 & 7 HERE

INSERT TABLE 4 HERE

Relations between soil water repellency and soil properties

Soil physical and chemical properties could affect hydraulic properties and hydrophobicity. Significant relations were not observed between RI values and BSR, HWSC:SOC ratio or

SOC in the studied soils. In all of the graphs, the E^+ and E^- data were shown with different markers to identify the role of each data in overall trend of the relations.

Strong linear and positive relations were established between RI and SOC:CC and HWSC:CC ratios (Fig. 8a,b). Fig. 8c presents the linear and negative relation between RI and CC. Also weak positive correlations were observed between RI and HWSC and sand content (Fig. 8d,e). The results revealed that the θ was significantly related to CC (r^2=0.301, P<0.01), SOC:CC ratio (r^2=0.55, P<0.001) and HWSC:CC ratio (r^2=0.46, P<0.001).

Correlation between water/ethanol sorptivities and soil properties

The results showed that S_E had weak/non-significant correlations with soil properties. A moderate (but still non-significant) correlation was observed between S_E and SOC (r^2 = 0.104, P>0.05). There was no significant correlation between S_w and SOC, HWSC, BSR and HWSC:SOM ratio in the studied soils. A high and positive correlation was observed between S_w and CC (Fig. 9a). The S_w has negatively correlated with SOC:CC and HWSC:CC ratios and sand content (Fig. 9b,c,d).

INSERT FIGS. 8 & 9 HERE

Discussion

Effect of endophyte on root biomass and soil properties

In the absence of stressful conditions, no differences in root biomass were observed due to endophyte infection (Fig. 3a). These results are consistent with the findings of Morse *et al.* (2002) who reported that endophyte infection in Arizona fescue did not affect the root biomass. Khayamim *et al.* (2011) also reported that in sufficient levels of nutrients, biomass of E^+ tall fescue seedlings was insignificantly higher than that of E^- ones.

The SOC storage in E^+ treatment was greater than that of E^- (Table 2). Similarly Franzluebbers & Stuedemann (2005) found that E^+ tall fescue pastures contain larger SOC than E^- ones. Franzluebbers *et al.* (1999) demonstrated that SOC under low E^+ tall fescue was significantly lower than high E^+ one. The most possible mechanisms to promote SOC accumulation in E^+ tall fescue-associated soils include increased root biomass and growth (Franzluebbers, 2006) and enhanced rhizodeposition of roots (Van Hecke *et al.*, 2005).

Moreover, production of secondary metabolites by E^+ tall fescue may alter the soil microbial community structure/functions (Franzluebbers *et al.*, 1999). Inhibited soil microbial activity due to endophyte infection may increase the stability of C-rich soil organic matters (Buyer *et al.*, 2011). The root biomass was not significantly different between the E^+ and E^- plants (Fig. 3a); therefore the increment of SOC in E^+ treatments (Table 2) may be mainly due to changes in soil microbial activity.

The BSR values were approximately 17% higher in E^- compared to E^+ plants (Table 2) supporting the above conclusion. Likewise, Handayani *et al.* (2011) reported that CO_2 evolution was significantly lower in E^+ than in E^- tall fescue. Franzluebbers & Hill (2005) indicated that E^+ tall fescue decreased soil microbial biomass C and C mineralization.

Similar to SOC, E^+ tall fescue had greater HWSC in the rhizosphere (Table 2). Van Hecke *et al.* (2005) have shown that the endophyte infection of tall fescue enhanced the rhizodeposition of organic compounds, particularly carbohydrates. They argued that enhanced photosynthetic rates for E^+ tall fescue could be the reason of increased carbohydrates through rhizodeposition. Malinowski *et al.* (1998) also suggested that higher root exudation of reducing compounds (possibly phenolic compounds) could alter the rhizosphere chemistry for E^+ tall fescue.

Effect of clay content on root biomass and soil properties

In general, increment of CC increased the root dry biomass (Fig. 3b). Franzluebbers *et al.* (1996) suggested that fine-textured soils have a tendency to be more productive than coarse-textured soils because of differences in water holding capacity. Haris *et al.* (2003) suggested that tall fescue grows best on fine- to medium-textured soils. The CC increase to 426 g kg^{-1} decreased the root biomass considerably (Fig. 3b) indicating that high CC might restrict root growth due to greater soil mechanical strength and poor aeration (Ontl *et al.*, 2013). In the course- to medium-textured soils, endophyte presence improved, although not significantly, the root growth (Fig. 3b).

The increment of CC generally increased the SOC of rhizosphere soil (Table 3). Positive linear relations between SOC and CC were reported in temperate and tropical regions (Gami *et al.*, 2009). Jindaluang *et al.* (2013) reported that for similar input of organic matter, fine-textured soils contain more SOC than coarse-textured ones due to physical protection of SOM. Considerable reduction of SOC in the soil with 426 g kg^{-1} CC (Table 3) may be due to suppressed root growth (Fig. 3b) and root exudates (Bottner *et al.*, 1999). Significant interaction between CC and endophyte presence (Fig. 4) revealed that endophyte infection has greater impact on SOC in fine-textured soils due to greater root biomass, physical protection and poor aeration. However, the initial SOC values varied slightly among the soils (Table 1), and may affect the results.

The BSR significantly varied (increased somehow) with an increment in CC (Table 3). This result is not in the line with previous works in which negative relations were reported between BSR and CC. The findings of Franzluebbers (1999) and Jensen *et al.* (1994) have affirmed that the C mineralization rate diminishes with increasing CC. However, the effect of soil texture on BSR due to variability in substrate availability, microbial biomass C and biochemical properties of different soils might not be easily distinguished (Hassink, 1994b). In our study, increased SOC by increment of CC, appears to enhance the BSR (Table 3). Accordingly, Wang *et al.* (2003) reported that in the presence of large available substrate, BSR was not significantly restricted by clay.

We observed differences in HWSC among the studied soils (i.e. increasing trend with CC increment) similar to the SOC trend (Table 3), because a positive correlation was observed between HWSC and SOC (r^2=0.50, P<0.001). Higher clay content by stimulating root growth (Fig. 3a) and increasing SOC (Table 3), could increase the HWSC. Sparling *et al.* (1998) found a strong positive relation between HWSC and SOC.

Effect of endophyte on hydraulic properties of rhizosphere soil

Soil water repellency and hydraulic properties (RI, θ, S_W and S_E) were affected by the endophyte. The RI, S_E and θ were greater and S_W was lower in the rhizosphere of E^+ tall fescue compared to E^- plants (Figs. 5, 7). Differences in the rhizosphere hydraulic properties of E^+ and E^- plants may be due to changes in pore structure (quantified by S_E) and hydrophobic coatings (quantified by S_W) related to the differences in root growth (Fig. 3a) and chemical composition of microbial metabolites and root exudates (Hallett & Young, 1999). Endophyte increases water repellency of rhizosphere soil due to better pore structure and enhancement of SOC pools (Table 2). Soil hydrophobicity can be caused through the low surface tension of organic compounds and non-polar groups (Woche *et al.*, 2005). Peng *et al.* (2003) found that planting restorative vegetation reduced S_W and increased S_E and RI due to greater SOC input. Blanco-Canqui & Lal (2009) have attributed higher hydrophobicity in the no-till soils to the greater SOC and lower CC. However, Urbanek *et al*. (2007) reported that SOC did not affect the soil wettability. Therefore, both quantity and quality of SOM and root exudates are effective on water repellency and physical properties of rhizosphere soil (Wallis & Horne, 1992; Hallett *et al*., 2003).

Soil hydraulic properties are influenced by pore structure (Lipiec *et al*., 2007) which is effectively revealed by the S_E (Hallett & Young, 1999). The rhizosphere soil of E^+ tall fescue had a higher S_E than the E^- plants (Figs. 6c, 7b), suggesting that endophyte can induce changes in soil aggregation and pore structure. The SOM could increase pore space and alter the pore-size distribution, then can increase the S_E. Cosentino *et al*. (2010) found that addition of maize residue to soil increased S_E compared to the reference soil.

The soil–water contact angle (θ) is fundamentally associated with the water repellency. We found higher values of RI and θ in the rhizosphere soil of E^+ tall fescue (Figs. 5a,b). Chenu *et al*. (2000) reported greater θ for the higher SOC in the <2 µm soil fraction. Piccolo and Mbagwu (1999) reported that humic-metal-clay complexes could induce water repellency due to increased θ and surface tension of soil water. Young–Laplace capillary equation was used to show quantitatively the effect of θ on soil water retention and matric suction (h) in different treatments. The h values (at 20 °C) for the water-filled pores with effective diameter of 30 or 100 µm, would be 29.2 or 8.7 cm and 41.3 or 12.4 cm in the rhizosphere of E^+ ($\theta \approx 73$) and E^- ($\theta \approx 65$) tall fescue, respectively. These values are significantly lower than the h values (100 and 30 cm, respectively) for completely wettable soil (i.e. $\theta=0$).

The RI values (Fig. 5, Table 4) represent moderate/sub-critical water repellency according to Lipiec *et al.* (2009), and indicate minimal effects on root water uptake similar to values reported by Hallett *et al.* (2003). At the same time, greater RI in the rhizosphere of E^+ tall fescue (Fig. 5) may stabilize pore structure against fast wetting stresses (Czarnes et al., 2000), providing a better physical environment for root development and water transport.

Effect of clay content on hydraulic properties of rhizosphere soil

The CC had significant effect on RI, θ and S_w but S_E was not affected by soil texture (Table 4). The RI and θ reduced with increasing CC (Table 4) because clayey soils need more hydrophobic materials to become water-repellent (Wallis & Horne, 1992). These results support earlier findings indicating enhanced soil wettability with increasing CC (Chenu *et al*., 2000). Doerr *et al*. (2006) and Wahl (2008) indicated that extreme cases of water repellency were usually observed in sandy soils. Leelamanie *et al*. (2010) reported when the θ of a model soil was 90–100°, addition of kaolinite improved the soil wettability (i.e. $\theta < 90°$).

The S_w increased with an increment in CC (Table 4) due to greater affinity of clay particles for water absoption and higher pore space in finer soils as revealed from BD values in Table 1. Shaver *et al*. (2013) reported a strong linear relation between S_w and porosity. Peng *et al*. (2003) showed that the S_w was increased significantly by CC increment. Lower water repellency in finer soils could be mainly attributed to increased S_w rather than to S_E variation (Table 4). The S_E was not significantly affected by CC (Table 4), indicating that pore structure was not influenced by soil texture. Similarly, De Gryze *et al*. (2006) reported that there was no significant relation between S_E and CC.

Interrelations between water repellency and properties of rhizosphere soil

Data points on the graphs indicated that RI values for E^+ tall fescue were relatively greater than those for E^- tall fescue at similar x values (Fig. 8). The CC and sand content had negative and positive linear relations with RI, respectively. De Gryze *et al*. (2006) reported that there were significant correlations between RI and sand and clay contents. Sandy soils are prone to water repellency due to accumulation of hydrophobic materials on a larger proportion of particles (Woche *et al*., 2005). However, Scott (2000) found a weak correlation between soil texture and water repellency and concluded that soils with any texture can become water-repellent.

Strong positive linear relations were obtained between RI (Fig. 8) or θ (not shown) and SOC:CC ratio indicating that regardless of CC, SOC could enhance the water repellency. Likewise, Aelamanesh *et al*. (2014) reported a positive relation between RI and SOC:CC ratio. Our findings corroborate the findings of Vogelmann *et al*. (2013) who reported a strong positive linear correlation between θ and SOM. However, Doerr & Thomas (2000) argued that greater CC enhanced water repellency due to preservation of hydrophobic substances on the clay surfaces.

Positive relations were derived between RI (Fig. 8) or θ (not shown) and HWSC or HWSC:CC ratio. Although soil carbohydrates are classified as hydrophilic compounds (Capriel, 1997), we observed that hydrophobicity was enhanced by increasing HWSC. Carbohydrates (especially HWSC), as major sources of energy and C for microorganisms, would stimulate soil microbial activity (Ratnayake *et al*., 2013; Uchida *et al*., 2012). Induced microbial activity due to high HWSC can produce water-repellent metabolites and exudates which could affect soil hydraulic properties (Chan, 1992). Hallett & Young (1999) found that addition of nutrient amendments to soil significantly reduced S_W and increased RI of aggregates due to enhanced microbial activity. Positive correlation of RI (Fig. 8) and HWSC:CC ratio confirms that HWSC, irrespective of soil texture, could enhance the water repellency. However, Woche *et al*. (2005) reported that hydrophobicity was associated more with soil texture than to either SOC or pH and severe hydrophobicity occurs primarily in sandy soils.

Significant positive relation was derived between S_w and CC (Fig. 9). Generally a soil with larger pores has smaller sorptivity than a soil with smaller pores (Hallett, 2007). Similarly, De Gryze *et al*. (2006) reported that S_w has a positive significant relation with CC. However, no significant correlation was observed between S_w and CC by Vogelmann *et al*. (2013). A significant negative correlation was observed between S_w and SOC:CC or HWSC:CC ratios (Fig. 9) showing that increasing SOC and HWSC, irrespective of CC, reduced the soil infiltrability. The S_w may be altered through the coating of soil particles with hydrophobic compounds. Our results are confirmed by the findings of Voglemann *et al*. (2013) who obtained a negative correlation between S_w and SOM. Moreover, Czarnes *et al*. (2000) showed that plant-root mucilage analogue (polygalacturonic acid) reduced the S_w and increased the RI. No significant correlation was observed between S_E and soil properties, conforming with the results of Vogelmann *et al*. (2010, 2013). Vogelmann *et al*. (2010) argued that S_E is not affected by the hydrophobicity but it is a function of pore structure. However, De Gryze *et al*. (2006) reported a significant relation between S_E and sand content.

Conclusions

It is concluded that endophyte presence in aboveground parts of plants and soil clay content (CC) greatly affected the rhizosphere soil properties. Enhanced SOC pools were observed in the rhizosphere of E^+ tall fescue especially for the fine-textured soils. Endophyte infection decreased basal soil respiration in the rhizosphere, but it was increased with the CC increment due to more availability of substrate. The HWSC followed the trend of SOC; both endophyte infection and CC increment increased the HWSC because of enhancement in the rhizodeposition of tall fescue roots.

Changes in chemical and biological properties of rhizosphere soil by endophyte infection and increasing CC altered the soil water repellency and hydraulic properties. Water repellency index (RI) and soil-water contact angle (θ) were higher in the E^+ tall fescue associated soils due to increased SOC pools. Lower water sorptivity (due to hydrophobic coatings) and higher ethanol sorptivity (due to altered pore structure) in the rhizosphere soil were responsible for the greater water repellency in the E^+ treatment. Strong and positive relations of RI and θ with SOC:CC, HWSC:CC ratios and negative correlation with CC confirm this conclusion.

Overall, endophyte presence in the shoots of tall fescue could increase the aggregate stability and physical quality of rhizosphere soil due to greater moderate sub-critical water repellency, SOC pools and HWSC as the two important indices of soil quality. Perhaps, slightly greater sub-critical water repellency induced by endophyte infection does not considerably affect root water uptake but could provide favorable impact on soil structural stability and on plant response to water stress in the drought periods. Exploring the interactive impact of endophytic fungi and soil properties on water repellency and hydraulic properties in the field conditions appears to be necessary in further studies.

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Table 1 Physical and chemical properties of the studied soils.

Soil type no.	**Texture class**	**Clay**	**Sand**	**Silt**	**$CaCO_3$**	**SOC**	**EC**	**pH**	**BD**
		------------------------	------------------------	g kg^{-1}	------------------------	------------------------	(dS m^{-1})		**(g cm^{-3})**
1	L	161	352	487	482	5.51	2.7	8.1	1.47
2	SiL	205	217	579	406	6.79	2.5	7.8	1.28
3	L	263	349	388	404	5.86	2.2	7.8	1.35
4	SiCL	324	158	518	453	6.38	2.8	7.7	1.25
5	SiCL	386	105	509	455	6.73	2.5	7.8	1.34
6	SiC	426	119	456	431	6.15	2.4	7.8	1.29
Mean	–	294	217	489	439	6.20	2.5	7.8	1.33
Maximum	–	426	352	579	482	6.79	2.8	8.1	1.47
Minimum	–	161	105	388	404	5.51	2.2	7.7	1.25
Standard deviation	–	103	110	64	31	0.50	0.2	0.1	0.07

Table 2 Means' comparison of soil organic carbon (SOC), hot-water soluble carbohydrates (HWSC) and basal soil respiration (BSR) of the rhizosphere soil of E$^+$ and E$^-$ tall fescues.

Treatment	**SOC**	**HWSC**	**BSR**
	----------- g kg^{-1}	-----------	mg CO_2 kg^{-1} soil
E$^+$	8.40 (±0.48) ^{a}	0.82 (±0.04) ^{a}	141 (±4.7) ^{b}
E$^-$	6.30 (±0.23) ^{b}	0.65 (±0.02) ^{b}	165 (±3.7) ^{a}

Different letters indicate significant differences (LSD, $P<0.05$); Numbers in parenthesis are standard errors.

Table 3 Means' comparison of soil organic carbon (SOC), hot-water soluble carbohydrates (HWSC) and basal soil respiration (BSR) of the tall fescue rhizosphere in the soils with different clay contents.

Clay content	**SOC**	**HWSC**	**BSR**
	g kg^{-1}	g kg^{-1}	mg CO_2 kg^{-1} soil
161	5.60 (±0.21) ^{d}	0.59 (±0.01) ^{d}	140 (±9.5) ^{c}
205	8.21 (±0.68) ^{b}	0.86 (±0.10) ^{a}	160 (±7.8) ^{ab}
263	6.02 (±0.16) ^{d}	0.68 (±0.04) ^{c}	149 (±5.2) ^{bc}
324	7.10 (±0.46) ^{c}	0.66 (±0.03) ^{c}	154 (±4.8) ^{bc}
386	9.66 (±0.79) ^{a}	0.87 (±0.05) ^{a}	174 (±6.9) ^{a}
426	7.41 (±0.82) ^{c}	0.76 (±0.01) ^{b}	142 (±10.8) ^{c}

Different letters indicate significant differences (LSD, $P<0.05$); Numbers in parenthesis are standard errors.

Table 4 Means' comparison of water repellency index (RI), soil-water contact angle (θ), water sorptivity (S_w) and ethanol sorptivity (S_E) of the tall fescue rhizosphere in the soils with different clay contents.

Clay content (g kg^{-1})	RI	θ (°)	S_w (mm s$^{-0.5}$)	S_E (mm s$^{-0.5}$)
161	3.80 (±0.43) ^{a}	73.6 (±2.0) ^{a}	0.513 (±0.010) ^{c}	0.992 (±0.100) ^{a}
205	3.91 (±0.51) ^{a}	73.7 (±2.4) ^{a}	0.527 (±0.045) ^{c}	1.010 (±0.085) ^{a}
263	3.03 (±0.19) ^{b}	70.3 (±1.4) ^{a}	0.559 (±0.058) ^{c}	0.868 (±0.105) ^{a}
324	2.80 (±0.15) ^{b}	68.8 (±1.2) ^{a}	0.736 (±0.055) ^{b}	1.044 (±0.058) ^{a}
386	2.95 (±0.22) ^{b}	69.3 (±2.3) ^{a}	0.703 (±0.076) ^{b}	1.024 (±0.064) ^{a}
426	2.39 (±0.16) ^{b}	58.0 (±7.1) ^{b}	0.880 (±0.034) ^{a}	0.978 (± 0.110) ^{a}

Different letters indicate significant differences (LSD, $P<0.05$); Numbers in parenthesis are standard errors.

Figure legends:

Fig. 1 Microscopic view of endophytic fungi (*Neotyphodium coenophialum*) in the shoot of tall fescue **(a)**, and a picture showing high density of plant roots at the end of experiment **(b)**

Fig. 2 Tension micro-infiltrometer used for measuring soil hydraulic properties

Fig. 3 Means' comparison of root biomass among **(a)** E^+ and E^- tall fescues and **(b)** different soil clay contents. Different letters on the bars indicate significant differences (LSD, $P<0.05$).

Fig. 4 Means' comparison of rhizosphere soil organic carbon (SOC) values as affected by interaction of endophytic symbiosis (E^+ and E^-) and soil clay content. Different letters on the bars indicate significant differences (LSD, $P<0.05$).

Fig. 5 Means' comparison of **(a)** water repellency index (RI) and **(b)** soil-water contact angle (θ) among the E+ and E− tall fescues. Different letters on the bars indicate significant differences (LSD, $P<0.05$).

Fig. 6 Water uptake *vs*. time in **(a)** rhizosphere soil of E^+ and E^- tall fescues and **(b)** two soils with different clay contents, and ethanol uptake *vs*. time in **(c)** the rhizosphere of E^+ and E^- tall fescues and **(d)** two soils with different clay contents.

Fig. 7 Means' comparison of **(a)** water sorptivity (S_w) and **(b)** ethanol sorptivity (S_E) in the rhizosphere of endophyte-infected (E^+) and endophyte-free (E^-) tall fescues. Different letters on the bars indicate significant differences (LSD, $P<0.05$).

Fig. 8 Linear relations between water repellency index (RI) and **(a)** SOC:CC ratio, **(b)** HWSC:CC ratio, **(c)** clay content (CC, g kg^{-1}), **(d)** HWSC concentration (g kg^{-1}) and **(e)** sand content (g kg^{-1}). Symbols ** and * stand for the significance of the relations at $P<0.01$ and $P<0.05$, respectively. The black and white circles represent E^+ and E^- treatments, respectively.

Fig. 9 Linear relations between water sorptivity (S_w) and **(a)** clay content (CC, g kg^{-1}), **(b)** HWSC:CC ratio, **(c)** SOC:CC ratio and **(d)** sand content (g kg^{-1}). Symbol ** shows the significance of the relations at $P<0.01$. The black and white circles represent E^+ and E^- treatments, respectively.

Fig. 1:

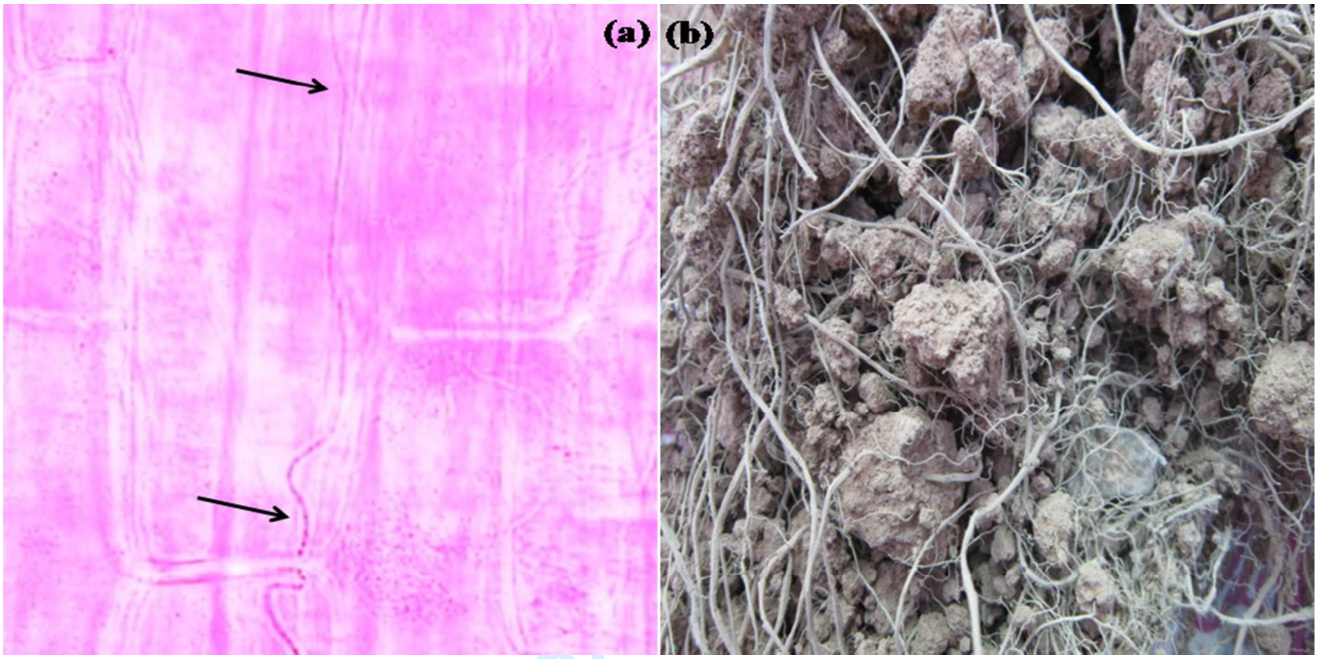


Fig. 2:

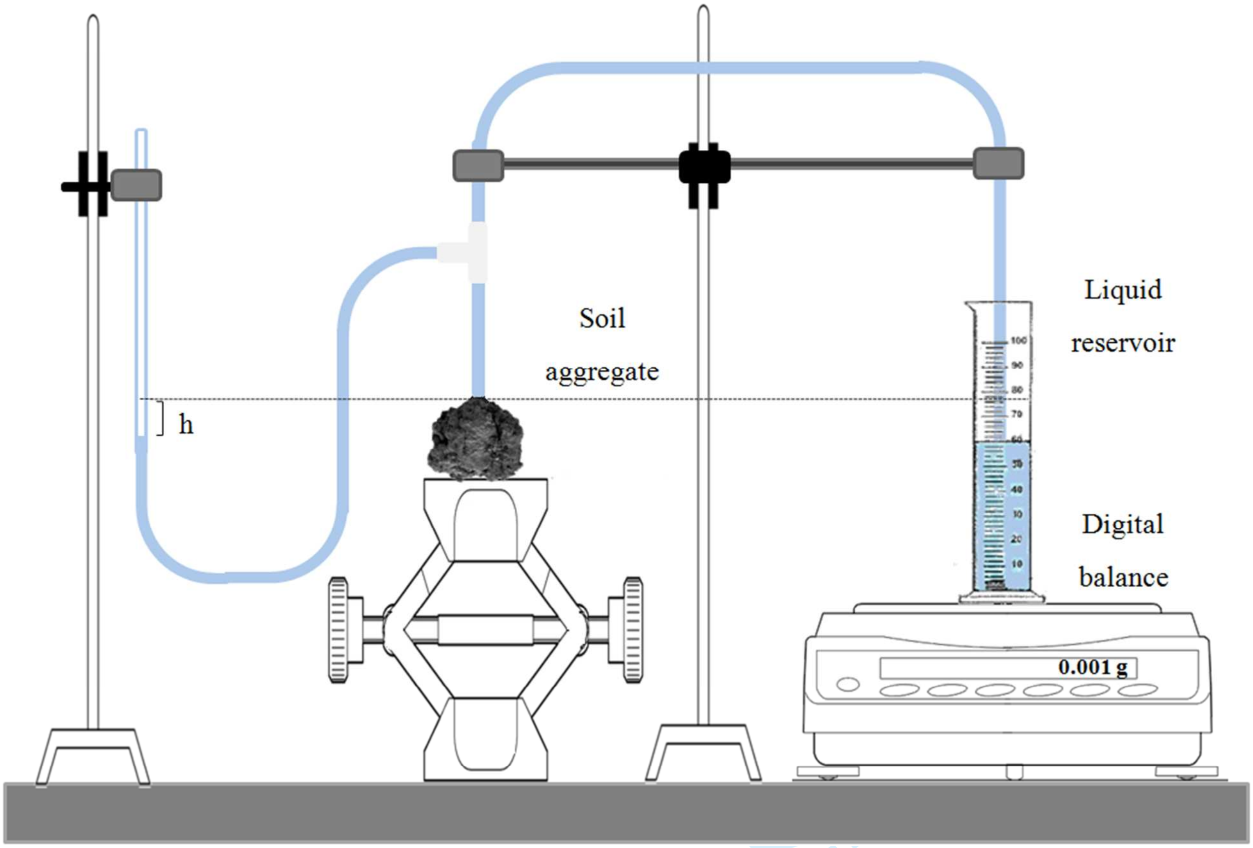


Fig. 3:

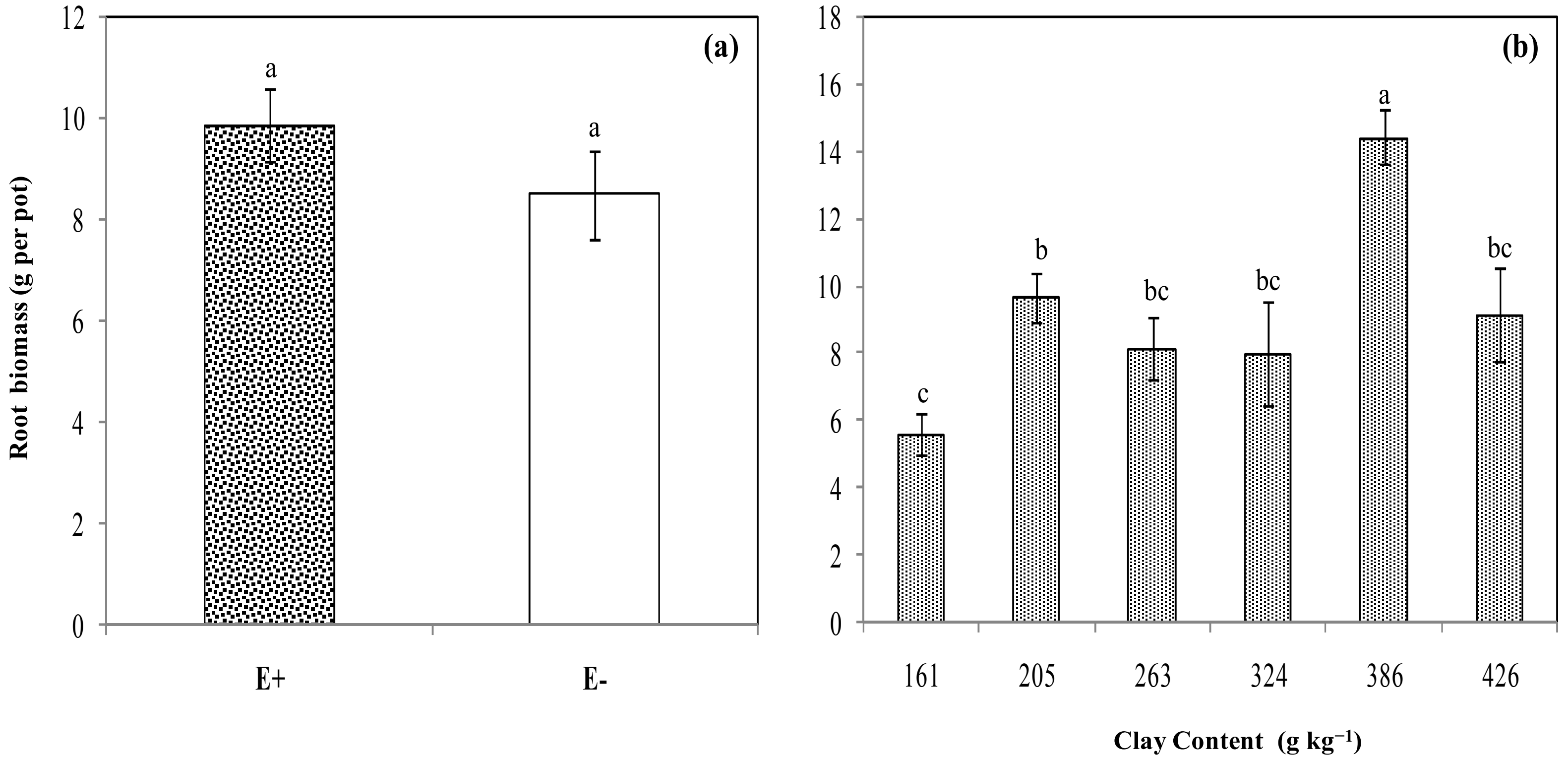

Root biomass (g per pot)
12
10
8
6
4
2
0
(a)
a
a
E+
E-
18
16
14
12
10
8
6
4
2
0
(b)
c
b
bc
bc
a
bc
161
205
263
324
386
426
Clay Content (g kg⁻¹)

Fig. 4:

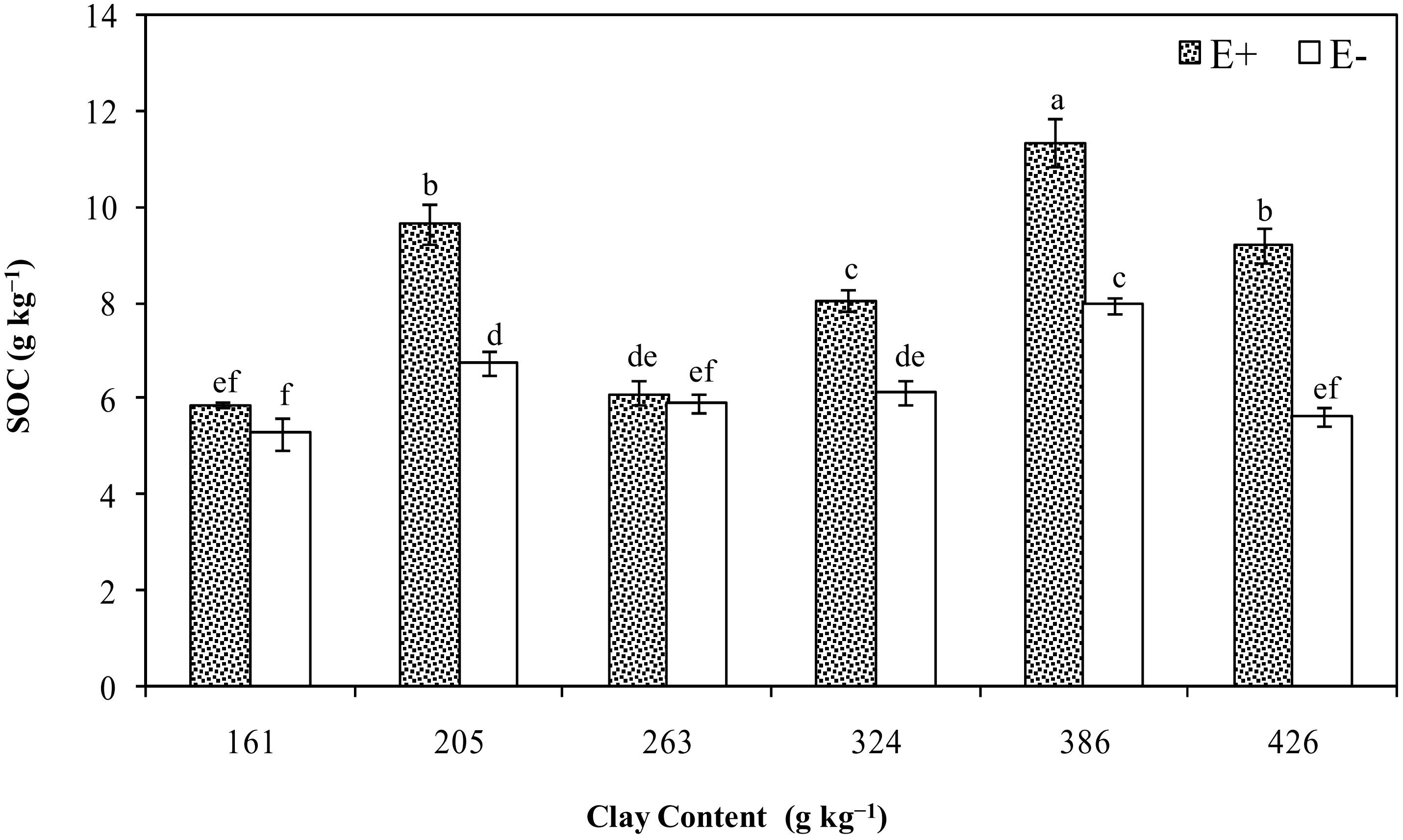

14
12
10
8
6
4
2
0
SOC (g kg^{-1})
▨ E+
☐ E-
ef
f
b
d
de
ef
c
de
a
c
b
ef
161
205
263
324
386
426
Clay Content (g kg^{-1})

Fig. 5:

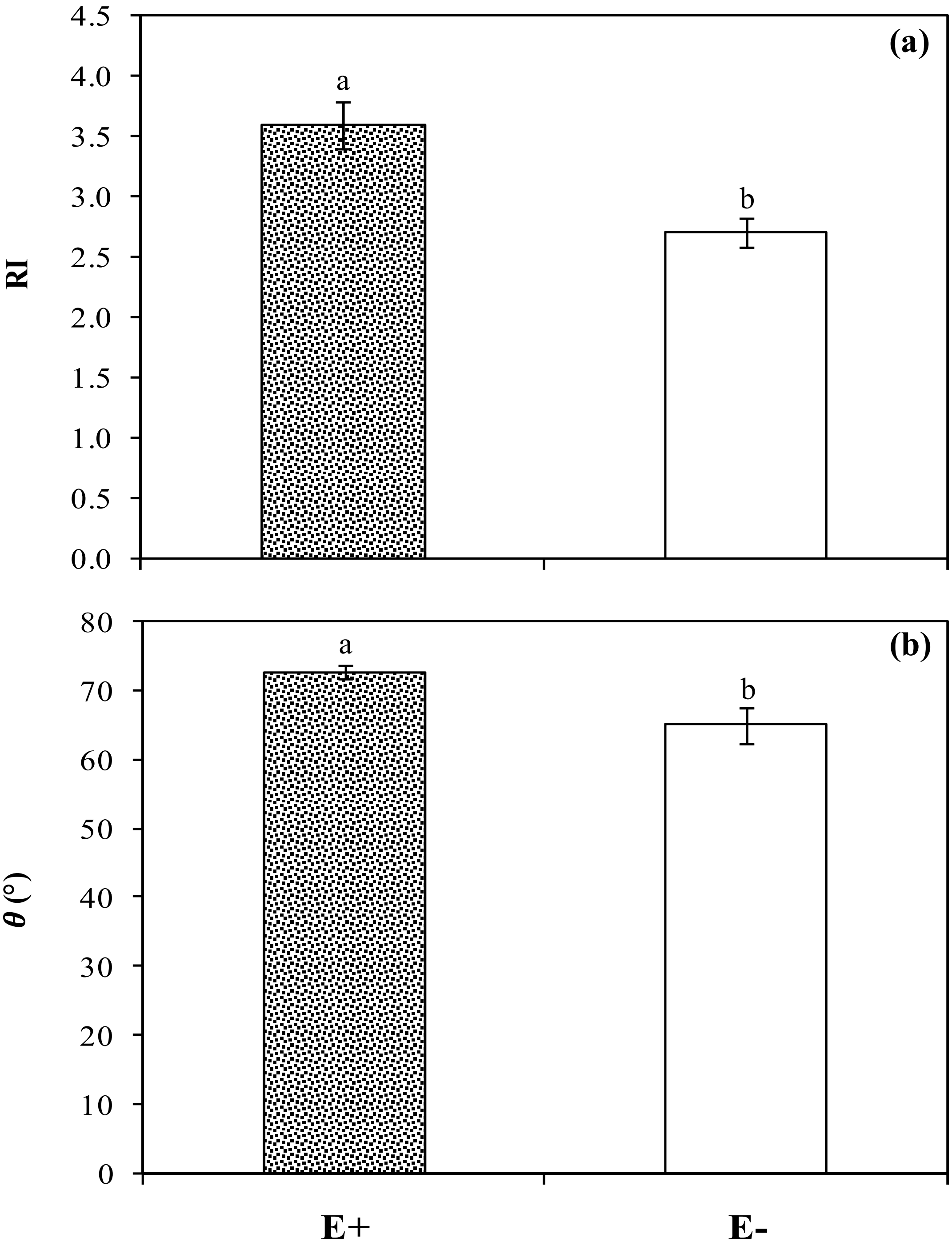


Fig. 6

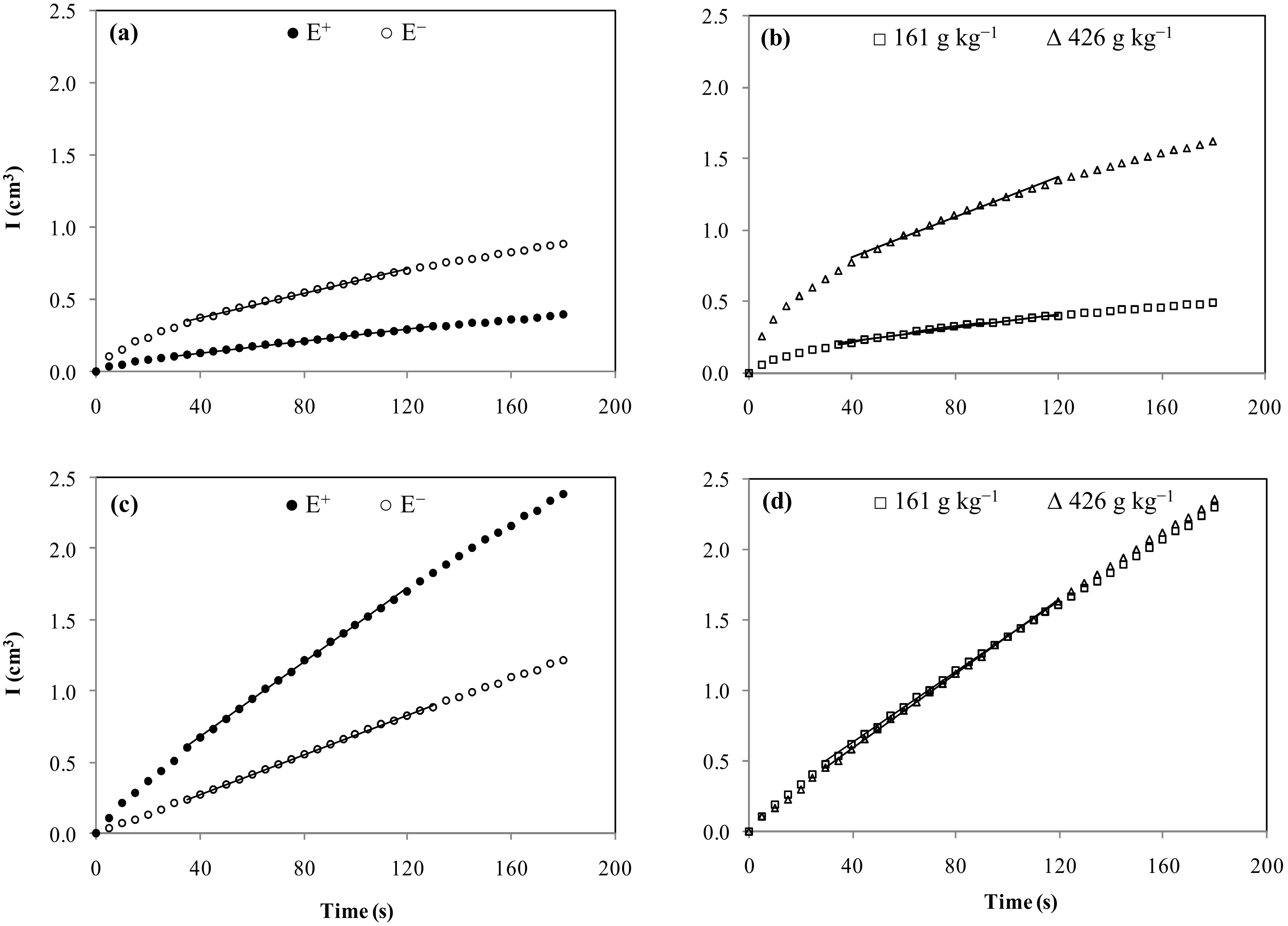

(a)
● E^{+}
○ E^{-}
I (cm^{3})
2.5
2.0
1.5
1.0
0.5
0.0
0
40
80
120
160
200
(b)
□ 161 g kg^{-1}
Δ 426 g kg^{-1}
(c)
● E^{+}
○ E^{-}
(d)
□ 161 g kg^{-1}
Δ 426 g kg^{-1}
Time (s)
Time (s)

Fig. 7

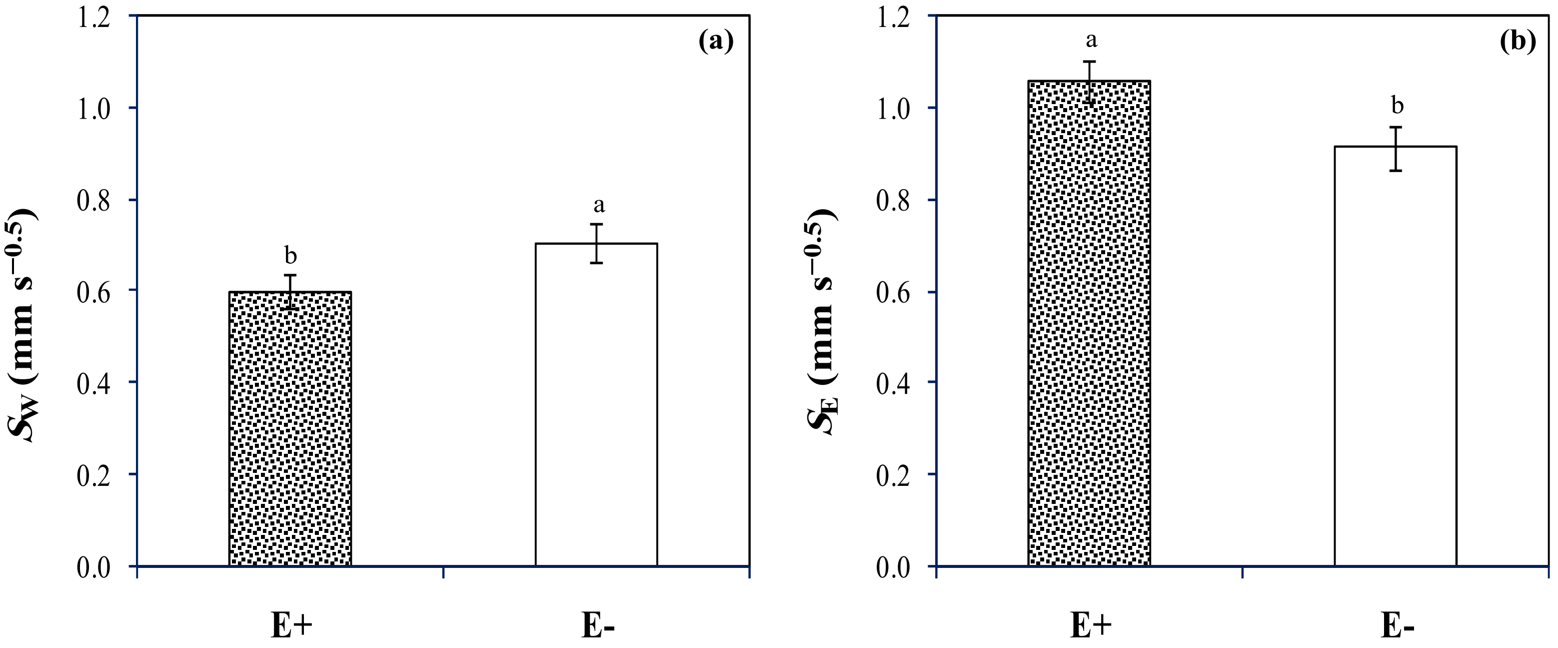


Fig. 8:

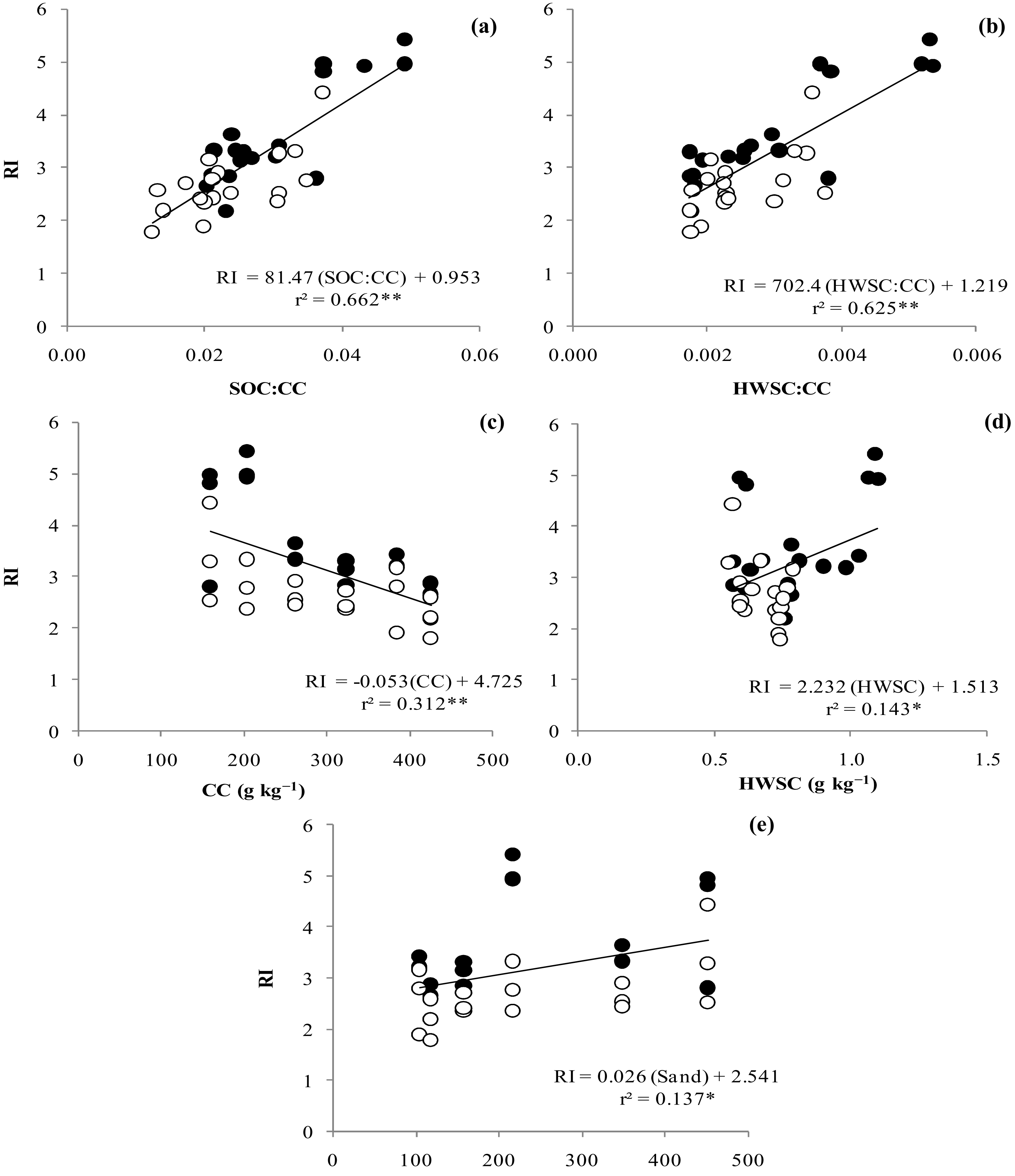
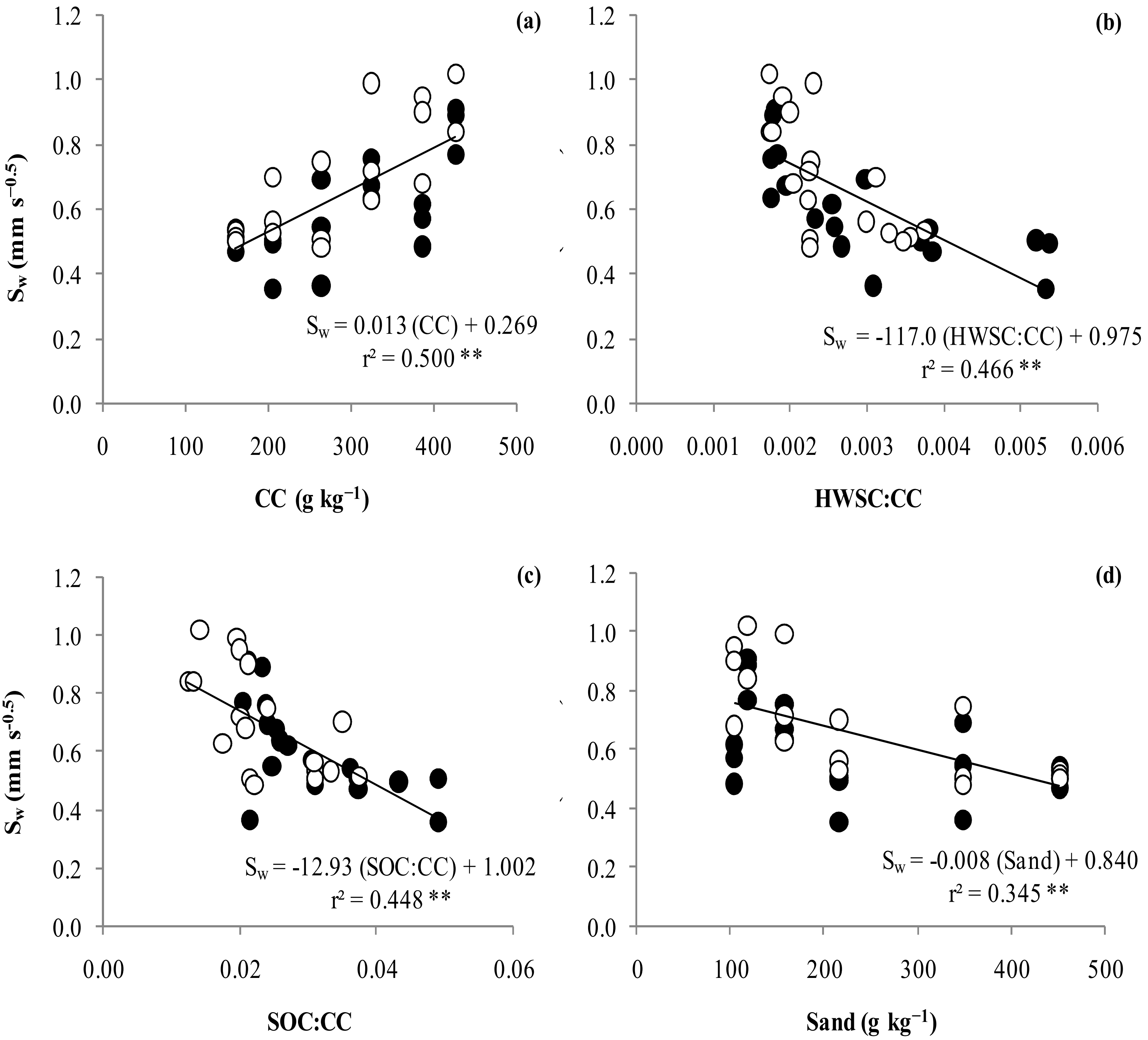

(a)
RI
6
5
4
3
2
1
0
0.00
0.02
0.04
0.06
SOC:CC
RI = 81.47 (SOC:CC) + 0.953
r² = 0.662**
(b)
HWSC:CC
0.000
0.002
0.004
0.006
RI = 702.4 (HWSC:CC) + 1.219
r² = 0.625**
(c)
CC (g kg⁻¹)
0
100
200
300
400
500
RI = -0.053(CC) + 4.725
r² = 0.312**
(d)
HWSC (g kg⁻¹)
0.0
0.5
1.0
1.5
RI = 2.232 (HWSC) + 1.513
r² = 0.143*
(e)
Sand (g kg⁻¹)
RI = 0.026 (Sand) + 2.541
r² = 0.137*

Fig. 9:


(a)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
S_w (mm s$^{-0.5}$)
0
100
200
300
400
500
CC (g kg^{-1})
S_W = 0.013 (CC) + 0.269
r^2 = 0.500 **
(b)
0.000
0.001
0.002
0.003
0.004
0.005
0.006
HWSC:CC
S_W = -117.0 (HWSC:CC) + 0.975
r^2 = 0.466 **
(c)
0.00
0.02
0.04
0.06
SOC:CC
S_W = -12.93 (SOC:CC) + 1.002
r^2 = 0.448 **
(d)
Sand (g kg^{-1})
S_W = -0.008 (Sand) + 0.840
r^2 = 0.345 **