The effect of microbial activity on soil water diffusivity

B. U. Choudhury a,b, S. Ferraris c, R. W. Ashton a, D. S. Powlson a & W. R. Whalley a

Introduction

Microbial activity can greatly affect the structure and hydraulic properties of soil (e.g. Or et al., 2007; Colica et al., 2014; Helliwell et al., 2014). One of the explanations for these effects is related to the production of extracellular polymeric substances that alter soil structure at the pore scale (Or et al., 2007). Typically, a smaller hydraulic conductivity is reported and explained by the clogging of pores because of microbial activity. An important stimulus of microbial activity in soil is the carbon released from roots in the form of root exudates (Paterson et al., 2007). Root exudates can have immediate effects on the soil water release characteristics because of their surfactant properties (Read et al., 2003). In the longer term, incubation of soil with root exudates, either natural or synthetic, has been shown to reduce hydraulic conductivity in near-saturated soil (Hallett et al., 2003; Whalley et al., 2004). The study of Colica et al. (2014) showed that induced biological crusts could reduce the rate of evaporation from dry soil. They also found that the hydraulic conductivity of near-saturated soil depended on the molecular weight of carbohydrates added to soil; the hydraulic conductivity was less when higher-molecular-weight carbohydrates were added.

The purpose of this study was to determine the effect of root exudates on soil water release curves and hydraulic conductivity over a wide range of soil water contents. We used a sandy soil, as did Colica et al. (2014), to minimize the effects of complex changes in soil structure that can be induced by microbial activity. The hydraulic properties of relatively dry soil were determined by measuring the rate of evaporation and the data were interpreted with a simple analytical solution to evaporation from bare soil (Black et al., 1969; Parlange et al., 1992). The effects of stimulating microbial activity on soil hydraulic properties have been reported previously, whereas the effects of suppressing microbial activity have received less attention. In our study, we included soil treated with added mercuric chloride to suppress microbial activity. We tested the hypothesis that soil with an active microbial population was less conductive to water. We used our data to investigate the likely effect of microbial activity on water uptake by roots.

Materials and methods

Soil sample preparation

Soil samples from the surface layer (0 to 20 cm) were collected during April 2015 from three ploughed fallow plots of a randomized experiment on Butt Close experimental field, Woburn Experimental
Farm (52° 00' 42" N, 0° 32' 42" W), Rothamsted Research, UK. Each of the plots was in a separate block as described by Shanahan et al. (2015). Butt Close soil is a loamy sand soil (sand: 87.5%, silt: 5.5% and clay: 7.2%), and taxonomically (FAO) this soil is classified as an Arenosol. It has a small organic content (1%), near neutral soil pH (6.63, 1:2 soil:water ratio) and a particle density of 2.65 g cm⁻³ (Whalley et al., 2008).

Three soil samples from each plot were air-dried, ground and sieved through a 2-mm sieve separately and treated as replicates in the laboratory studies. The moisture content of air-dried soil samples was 1% (weight by weight). Soil was packed into stainless cores (3.59 cm long and 3.86 cm in diameter). The bases of the cores were covered with a fine nylon cloth. The cores were filled homogenously with air-dried 2-mm-sieved loamy sand soil to a bulk density of 1.5 g cm⁻³.

We prepared artificial root exudates of low-molecular-weight organic compounds from the mixtures of 15 compounds (Paterson et al., 2007) comprising five carbohydrates (glucose, fructose, sucrose, arabinose and ribose), five amino acids (glycine, valine, glutamine, serine and alanine) and five organic acids (malic, citric, malonic, oxalic and fumaric). A stock solution of 4.166% C concentration (41.66 g l⁻¹) was prepared by dissolving each of these 15 compounds (equal in terms of C content: 1.39 g) in 500 ml of distilled water. From this stock solution, three different working solutions of root exudates were prepared with enough distilled water to maintain the soil at 100% of water-holding capacity while ensuring an enrichment of 1.25, 2.5 and 5.0 g C kg⁻¹ in dry soil packed at a density of 1.5 g cm⁻³. Stainless steel cores were filled with air-dried sieved soil in triplicate and they were saturated with the three solutions for 48 hours at 20°C together with a control (without root exudates). The control was saturated in distilled water. Saturation was achieved by placing the samples on a Haynes apparatus and slowly raising the water table to obtain uniform saturation across each core.

To stop microbial activity, we applied two additional treatments: (i) soil amended with mercuric chloride solution in one root exudates mixture (2.5 g C kg⁻¹ dry soil) and (ii) the soil with distilled water was also amended with mercuric chloride solution. Among the several commonly used soil sterilizing methods in laboratory experiments, mercuric chloride results in effective sterilization with minimal effect on soil chemical and physical properties (Wolf et al., 1973). Importantly for this study, however, mercuric chloride is not a solvent that will evoke and confound our soil evaporation data (see below). Two sterilized treatments with mercuric chloride solution of 0.1% were prepared by dissolving 0.78 g HgCl₂ in 250 cm⁻³ of the previously prepared working solution of root exudates (2.5 g C kg⁻¹ dry soil) and in distilled water. Soil, also packed to a bulk density of 1.5 g cm⁻³, was saturated in 0.1% mercuric solution for 48 hours at 20°C by raising the water table slowly on a Haynes’ apparatus containing the packed soil cores.

Once the soil had been saturated, as described above, the cores were placed on a mesh support over a saturated solution of CaCl₂ in a desiccator. The desiccators were kept at a constant temperature of 20 ± 1°C, to give a relative humidity of 30%. The air in the desiccator was circulated with battery-driven fans.

In total, there were six treatments: control (in distilled water, T₀w), with root exudates at 1.25 g C kg⁻¹ dry soil (T₁₂₅), 2.5 g C kg⁻¹ dry soil (T₂₅) and 5.0 g C kg⁻¹ dry soil (T₅₀), sterilized in distilled water (T₀w + Hg) and finally sterilized root exudates at 2.5 g C kg⁻¹ dry soil (T₂₅ + Hg). The evaporation loss in terms of volumetric water content in the core was measured regularly (hourly) until the water content was constant with time. The cores were removed from the desiccator briefly to measure their mass.

**Soil water release characteristics**

The water release characteristics were measured on duplicate samples. Plastic cylindrical cores of 50 mm in diameter and 25 mm long were filled homogenously to two-thirds height with air-dry 2-mm-sieved loamy sand soil to a packing density of 1.5 g cm⁻³. The exudate treatments were applied to these cores as described above. The saturated soil in the cores was incubated at saturation for 14 days in the dark at room temperature (20 ± 1°C). After 14 days of incubation, all the cores were equilibrated at eight matric potentials varying from −1, −3, −10, −30, −100, −300, −500 and −1500 kPa. To equilibrate samples at higher matric potentials (−1 to −30 kPa) we used a ceramic suction plate for 5–9 days, whereas samples at lower matric potentials (−100 to −1500 kPa) were equilibrated in a pressure chamber (plate apparatus) for 14–36 days, or longer for lower matric potentials of −500 and −1500 kPa. Three replicates were measured for each of the six treatments at each matric potential. At equilibration, the wet soil weight was recorded and water contents were calculated following oven drying at 105°C for 48 hours.

**Estimation of hydraulic diffusivity**

Hydraulic diffusivity is given by dividing hydraulic conductivity by the derivative of the water release curve; its advantage is that its range, or variation, is smaller than that of hydraulic conductivity (Hillel, 1980). We fitted a linearized solution of the desorption process proposed by Black et al. (1969) to our data:

\[
E_i = 20 \frac{t D_{av}}{\pi} \theta_i^{1/2},
\]

where \(E_i\) is the cumulative evaporation (cm) and \(\theta_i\) is the water content at time \(t\), \(D_{av}\) is the weighted mean diffusivity (Black et al., 1969), which was assumed to be constant for a particular soil (Parlange et al., 1992). This equation applies to a semi-infinite column of soil, which is approximated in the early stage of drying when the water content at the base of the core is not yet reduced. We also assume that the water content at the surface had dried instantly to the final water content.
In practice, diffusivity is a function of soil water content, \( D(\theta) \). The weighted mean diffusivity, \( D_{av} \), is related to \( D(\theta) \) as follows:

\[
D_{av} = \frac{1.85}{(\theta_i - \theta)^{1.85}} \int_{\theta_i}^{\theta_s} (\theta_i - \theta)^{-0.85} D(\theta) \, d\theta, \tag{2}
\]

where \( \theta_i \) is the initial water content and \( \theta_s \) is the water content at the soil surface (Black et al., 1969; Parlange et al., 1992). The weighted mean diffusivity can be used to interpret time-series data relating to soil water content (Parlange et al., 1992). Ritchie et al. (2009) used an averaged description of water transport to describe stage 2 evaporation (this is evaporation from unsaturated soil). They called this a ‘functional’ approach instead of a truly ‘mechanistic’ model where, for example, soil water diffusivity depends on water content. Such functional approaches based on constant soil water content (Parlange et al., 1995) are fitting parameters. All of these parameters were estimated by inspection, although the location of the linear region of the curve was indicated by \( M \).

The water release characteristics of soil samples with different treatments were fitted by the Van Genuchten Equation:

\[
\theta_w = \theta_i + \frac{\theta_s - \theta_i}{1 + (\alpha \psi)^{1/n}}, \tag{4}
\]

where \( \theta_w \) is the water content at matric potential \( \psi \), \( \theta_i \) is the residual water content, \( \theta_s \) is the water content at saturation and \( \alpha \), \( n \) and \( m \) are fitting parameters. All of these parameters were estimated with curve fitting and we used the constraint of \( m = 1 - 1/n \) (van Genuchten et al., 1980). For each treatment, separate curves were required. These data were also analysed with analysis of variance.

We used Genstat (VSN Int. Ltd, Hemel Hempstead, UK, or Payne, 2015) to fit all the curves described above to our data and for all statistical analysis.

**Results**

The incubation of soil with artificial root exudates had a small, but significant, effect on the water release characteristics (Figure 1). The water release characteristics in Figure 1 were fitted to the van Genuchten equation (Equation (4)) and the parameter values are listed in Tables 1 and 2. Analysis of variance of these data showed that the main effects of soil treatment and water potential, as well as their interaction, were all significant at \( P < 0.001 \).

The water release data were fitted by the Van Genuchten Equation:

\[
\theta_w = \theta_i + \frac{\theta_s - \theta_i}{1 + (\alpha \psi)^{1/n}}, \tag{4}
\]

where \( \theta_w \) is the water content at matric potential \( \psi \), \( \theta_i \) is the residual water content, \( \theta_s \) is the water content at saturation and \( \alpha \), \( n \) and \( m \) are fitting parameters. All of these parameters were estimated with curve fitting and we used the constraint of \( m = 1 - 1/n \) (van Genuchten et al., 1980). For each treatment, separate curves were required. These data were also analysed with analysis of variance.

We used Genstat (VSN Int. Ltd, Hemel Hempstead, UK, or Payne, 2015) to fit all the curves described above to our data and for all statistical analysis.
Table 1 Parameters of the van Genuchten equation (Equation (4)) for the water release curves plotted in Figure 1

| Treatment        | \( \theta_s \)  | \( \theta_r \)  | \( \alpha \)  | \( n \)  | Percentage of variance accounted for |
|------------------|------------------|------------------|------------------|------------------|-------------------------------------|
| TDW              | 0.508 (0.0047)   | 0.0491 (0.00443) | 1.481 (0.032)    | 3.373 (0.124)    | 99.8 (\( P < 0.001 \))               |
| T1.25            | 0.509 (0.0055)   | 0.0413 (0.00704) | 1.428 (0.039)    | 3.014 (0.135)    | 99.7 (\( P < 0.001 \))               |
| T2.5             | 0.515 (0.0056)   | 0.0428 (0.00759) | 1.407 (0.04)     | 2.988 (0.140)    | 99.7 (\( P < 0.001 \))               |
| T5.0             | 0.541 (0.0057)   | 0.0334 (0.00942) | 1.439 (0.042)    | 2.748 (0.125)    | 99.7 (\( P < 0.001 \))               |
| TDW+Hg           | 0.499 (0.0077)   | 0.0490 (0.00634) | 1.529 (0.005)    | 3.508 (0.202)    | 99.4 (\( P < 0.001 \))               |
| T2.5+Hg          | 0.502 (0.0074)   | 0.0271 (0.0111)  | 1.485 (0.011)    | 2.808 (0.171)    | 99.4 (\( P < 0.001 \))               |

The standard error of the coefficient is shown in brackets. The treatments are as follows: control (in distilled water, TDW), with root exudates at 1.25 g C kg\(^{-1}\) dry soil (T\(_{1.25}\)), 2.5 g C kg\(^{-1}\) dry soil (T\(_{2.5}\)) and 5.0 g C kg\(^{-1}\) dry soil (T\(_{5.0}\)), sterilized in distilled water (TDW+Hg) and finally sterilized root exudates at 2.5 g C kg\(^{-1}\) dry soil (T\(_{2.5}+\)Hg).

Table 2 Results from the analysis of variance of the water release data shown in Figure 1

| Source of variation | d.f. | Sum of squares | Mean square | \( F \) | \( F \) probability |
|---------------------|------|---------------|-------------|--------|---------------------|
| Block stratum       | 2    | 2.38E-06      | 1.19E-06    | 0.41   |                     |
| Block • Sample stratum |  |               |             |        |                     |
| Treatment           | 5    | 1.91E-02      | 3.81E-03    | 1302.7 | <0.001              |
| Matric potential    | 7    | 3.94E+00      | 5.63E-01    | 1.92E+05 | <0.001            |
| Treatment • Matric potential | 35 | 6.45E-03      | 1.84E-04    | 62.94  | 0.001               |
| Residual            | 94   | 2.75E-04      | 2.93E-06    |        |                     |
| Total               | 143  | 3.97E+00      |             |        |                     |

Both the main effect and the interaction were significant at \( P < 0.001 \). d.f., degrees of freedom.

Discussion

Soil porosity

The effects of microbial activity on soil porosity in this research were small. Helliwell et al. (2014), who studied soil that was kept saturated for the duration of the experiment, reported much greater effects of microbial stimulation on soil porosity. They found that microbial stimulation, by the addition of glucose to a soil similar in texture to that used in this study, resulted in an increase in porosity from approximately 38 to 54% (estimated from X-ray imaging). In contrast, the largest porosity we found was for T\(_{5}\), which has a porosity of 54% in comparison with 49% in the treatment designed to limit microbial activity (TDW+Hg). The change in porosity values

---

© 2018 The Authors. *European Journal of Soil Science* published by John Wiley & Sons Ltd on behalf of British Society of Soil Science.
Table 3 Parameter values for Equation (3) when fitted to the drying curves for the different treatments, which are plotted in Figure 1

| Treatment       | \( A^* \) (SE) | \( C \) (SE) | \( B \) (SE) | \( M \) (SE) |
|-----------------|----------------|-------------|-------------|-------------|
| \( T_{DW} \)    | 0.00804 (0.00214) | 0.4418 (0.00804) | -0.5003 (0.014) | 7.19 (0.0588) |
| \( T_{1.25} \)  | 0.01593 (0.00288) | 0.4596 (0.00948) | -0.3776 (0.0135) | 6.58 (0.103) |
| \( T_{2.5} \)   | 0.00823 (0.0033) | 0.4840 (0.0106) | -0.3516 (0.0128) | 6.74 (0.108) |
| \( T_{5} \)     | 0.00126 (0.0046) | 0.5382 (0.0156) | -0.2481 (0.0101) | 7.34 (0.175) |
| \( T_{DW+Hg} \) | 0.01592 (0.00175) | 0.4731 (0.00811) | -0.5447 (0.0171) | 4.94 (0.0798) |
| \( T_{2.5+Hg} \)| 0.02585 (0.00219) | 0.5089 (0.01188) | -0.4119 (0.0140) | 5.01 (0.123) |

Parallel curve fitting accounted for 99.8% of the variance and confirmed that the best fit to the data was obtained with different coefficients for each treatment. Accumulated analysis of variance, following grouped regression, showed that each treatment required separate parameters (Figure 2 also show that the rate of soil drying is much slower in the treatments designed to stimulate microbial activity and faster in those treatments designed to suppress microbial activity. The effects of the treatments on the water release characteristics are statistically significant (Figure 1 and Table 2), although they are small in comparison with those reported by Read et al. (2003) and Ahmed et al. (2014) for the effect of exudates, and by Or et al. (2007) for the effects of extracellular polymeric substances.

**Implications for roots**

Gao et al. (2017) showed that additions of the same synthetic exudates used in this work to the same soil altered the microbial community in both structure and quantity. Our data show that the flow of water through soil is also impeded; Figure 2 and Table 4 show that diffusivity was halved by increased microbial stimulation, which has been widely reported (Or et al., 2007). We also show that the flow of water can be increased by suppressing microbial activity with the addition of mercuric chloride. Our estimated mean diffusivity of the control soil more than doubled from 4.1 to 9.1 cm² day⁻¹ with the addition of mercuric chloride. The key implication is that much of the reported hydraulic data in the literature is affected by the background microbial activity that is present during the measurement process.

Passioura (1991), assuming a mean diffusivity of 2 cm² day⁻¹, concluded that it was macroscopic soil structure (e.g. aggregated or blocky) or the distribution of roots within soil that was most likely to limit water uptake by roots, and not the movement of water through bulk soil. In our study, the least conductive soil obtained by adding the largest amount of exudates (5.0 g C kg⁻¹ dry soil, \( T_{50} \)) had a diffusivity of 2.08 cm² day⁻¹, which was close to half of that estimated for the soil without any added exudates (4.07 cm² day⁻¹). It seems likely that any possible effect of exudates (with respect to water uptake by roots) on the soil we studied must be related to reducing the rate of water sorption from soil. In Figure 4 we have replotted the relation between the time constant for water uptake (i.e. the time taken for the roots to take up half of the available water) and the structural scale derived by Passioura (1991) for \( D = 2 \) cm² day⁻¹ (i.e. \( T_2 \)) alongside the same curve for \( D = 4 \) cm² day⁻¹ (i.e. \( T_{DW} \)). The effect of root
Table 4  Average diffusivities estimated with Equation (1) and the data in Figure 3. These are the mean values for the diffusivities calculated for each individual replicate

| Treatment   | $\log_{10}(D)$ (cm² day⁻¹) | Porosity | Back-transformed diffusivity (cm² day⁻¹) | Water content /cm³100 cm⁻³ |
|-------------|----------------------------|----------|----------------------------------------|----------------------------|
| $T_{DW}$    | 0.61                       | 0.51     | 4.07                                   | 1.3 8.7 3.6               |
| $T_{1.25}$  | 0.67                       | 0.51     | 4.68                                   | 2.1 11.9 6.0              |
| $T_{2.5}$   | 0.55                       | 0.51     | 3.55                                   | 2.1 12.4 6.0              |
| $T_{5.0}$   | 0.32                       | 0.54     | 2.08                                   | 5.7 18.0 10.7             |
| $T_{DW} + \text{HgCl}$ | 0.96                       | 0.50     | 9.12                                   | 1.3 5.4 2.5               |
| $T_{2.5} + \text{HgCl}$ | 0.79                       | 0.50     | 6.17                                   | 2.7 9.2 5.0               |

The least significant difference in $\log_{10}D$ (LSD for $P = 0.05$) is 0.072. The final soil porosity data are also listed (LSD = 0.002 for $P = 0.05$). The minimum (Min), maximum (Max) and mean water contents corresponding to the range of water contents associated with estimated diffusivity are also given. Treatment abbreviations are explained in the text.

Figure 4  The time constant for water uptake (i.e. the time taken for roots to extract half of the available water) plotted against structural scale. These data represent the case for bio-pores (Passioura, 1991). The difference between the two curves represents the range of values of the time constant for water uptake possibly related to the effects of exudates at 5 g kg⁻¹ soil (2 cm² day⁻¹) compared with the control (4 cm² day⁻¹).

In contrast to the more immediate effects of recently applied mucilage in increasing conductance (Ahmed et al., 2014), we found that microbial activity had the effect of reducing conductance. Our data are consistent with those of Colica et al. (2014), who showed that the hydraulic conductivity decreased with increasing additions of high-molecular-weight compounds. At high water potentials, such as those studied by Ahmed et al. (2014), root mucilage can increase the soil water content, and this effect can increase the hydraulic conductance of soil, thereby increasing root water uptake. Simulations show that root mucilage can help plants to sustain transpiration for up to 42 hours as the soil dries (Carminati et al., 2015). In our study, we measured soil drying over a similar period, although our treatments included the growth of microbial communities (Gao et al., 2017) or their suppression (Wolf et al., 2013). It seems that the effects of root-exuded mucilage can be split into short-term effects from the physical effects of surface tension and viscosity (Kroener et al., 2014), and the longer-term effects that arise because exudates stimulate microbial activity. Our data are most relevant to the long-term effects that arise because microbial activity blocks soil pores (e.g. Wolf et al., 2013) or modifies wettability (e.g. Hallett & Young, 1999). The longer-term effects of microbial activity are more commonly associated with the mineralization of nutrients, particularly in the production of nitrate. However, as we have discussed above, the reduction in diffusivity may well play an important role in moderating the use of soil water reserves in arid conditions, or in climates with well-defined wet and dry seasons. Tardieu (2012) has observed that almost any trait may conserve water in the right circumstances.

Conclusions

The addition of synthetic root exudates to a sandy soil reduced the hydraulic diffusivity. Compared with a control soil with no added exudates, the addition of 5 g C kg⁻¹ of soil halved the diffusivity from 4 to 2 cm² day⁻¹. Suppression of microbial activity with the addition of mercuric chloride to soil increased diffusivity more than twofold in comparison with the control, from 4 to 9 cm² day⁻¹. Analysis of root water uptake suggests the effect of the decrease
in diffusivity is comparable to a shift in the soil structural unit, for example moving from a prismatic soil to slab structure.

Acknowledgements

Dr Burhan U. Choudhury was appointed as a Rothamsted International Fellow and in India he is supported by the Indian Council of Agricultural Research. SF was supported by the H2020 project ‘ECOPOTENTIAL: Improving Future Ecosystem Benefits Through Earth Observations’, coordinated by CNR-IGG (http://www.ecopotential-project.eu). The project has received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement No 641762. At Rothamsted Research, WRW and RWA are supported by the BBSRC Designing Future Wheat project and the BBSRC/NERC ASSIST project. DSP is a Lawes Trust Senior Fellow. We thank Rodger White for advice and guidance with respect to the statistical analysis.

References

Ahmed, M.A., Kroener, E., Holz, M., Zarebanadkouki, M. & Carminati, A. 2014. Mucilage exudation facilitates root water uptake in dry soils. Functional Plant Biology, 41, 1129–1137.
Black, T.A., Gardner, W.R. & Thurtell, G.W. 1969. The prediction of evaporation, drainage, and soil water storage for a bare soil. Soil Science Society of America Proceedings, 33, 655–660.
Carminati, A., Kroener, E., Ahmed, M.A., Zarebanadkouki, M., Holz, M. & Ghezzehei, T. 2015. Water for carbon. Vadose Zone Journal. 1–10. https://doi.org/10.2136/vzj2015.04.0060.
Colica, G., Li, H., Rossi, F., Li, D., Liu, Y. & De Philipps, R. 2014. Microbial secreted exopolysaccharides affect the hydrological behaviour of induced biological soil crusts in desert sandy soils. Soil Biology & Biochemistry, 68, 62–70.
Gao, W., Muñoz-Romero, V., Ren, T., Ashton, R.W., Morin, M., Clark, I.M. et al. 2017. Effect of microbial activity on penetrometer resistance and elastic modulus of soil at different temperatures. European Journal of Soil Science, 68, 412–419.
v van Genuchten, M.T. 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Science Society of America Journal, 44, 892–898.
Hallett, P.D. & Young, I.M. 1999. Changes to water repellence of soil aggregates caused by substrate-induced microbial activity. European Journal of Soil Science, 50, 35–40.
Hallett, P.D., Gordon, D.C. & Bengough, A.G. 2003. Plant influence on rhizosphere hydraulic properties/direct measurements using a miniaturized infiltrometer. New Phytologist, 157, 597–603.
Hillel, D. 1980. Fundamentals of Soil Physics. Academic Press, New York.
Kroener, E., Zarebanadkouki, M., Kaestner, A. & Carminati, A. 2014. Nonequilibrium water dynamics in the rhizosphere: how mucilage affects water flows in soil. Water Resources Research, 60, 6479–6495.
Parlange, M.B., Katul, G.G., Cuenca, R.H., Kavvas, M.L., Nielsen, D.R. & Mata, M. 1992. Physical basis for a time series model of soil water content. Water Resources Research, 28, 2437–2446.
Passioura, J.B. 1991. Soil structure and plant growth. Australian Journal of Soil Research, 29, 717–728.
Paterson, E., Gebbing, T., Abel, C., Sim, A. & Telfer, G. 2007. Rhizodeposition shapes rhizosphere microbial community structure in organic soil. New Phytologist, 173, 600–610.
Payne, R.W. 2015. The Guide to GenStat Release 17–Part 2: Statistics. VSN International, Hemel Hempstead.
Or, D., Phutane, S. & Dechesne, A. 2007. Extracellular polymeric substances affecting pore-scale hydrologic conditions for bacterial activity in unsaturated soils. Vadose Zone Journal, 6, 298–305.
Read, D.B., Bengough, A.G., Gregory, P.J., Crawford, J.W., Robinson, D., Scrimgeour, C.M. et al. 2003. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. New Phytologist, 157, 315–326.
Richards, R.A., Rebetzke, G.J., Watt, M., Condon, A.G., Spielmeyer, W. & Dolferus, R. 2010. Breeding for improved water productivity in temperate cereals: phenotyping, quantitative trait loci, markers and the selection environment. Functional Plant Biology, 37, 85–97.
Ritchie, J.T., Porter, C.H., Judge, J.J., Jones, J.W. & Suleiman, A.A. 2009. Extension of an existing model for soil water evaporation and redistribution under high water content conditions. Soil Science Society of America Journal, 73, 792–801.
Shanahan, P., Binley, A., Whalley, W.R. & Watts, C.W. 2015. The use of electromagnetic induction (EMI) to monitor changes in soil moisture profiles beneath different wheat cultivars. Soil Science Society of America Journal, 79, 459–466.
Stephens, K.D., Farenhorst, A. & Fuller, L.G. 2002. Effect of soil sterilization by mercuric chloride on herbicide sorption by soil. Journal of Environmental Science and Health B, 37, 561–571.
Tardieu, F. 2012. Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario. Journal of Experimental Botany, 63, 25–31.
Tuominen, L., Kairesalo, T. & Hartikainen, H. 1994. Comparison of methods for inhibiting bacterial activity in sediment. Applied Environmental Microbiology, 60, 3454–3457.
Wang, C.Y., Wang, F., Wang, T., Yang, X.L., Bian, Y.R., Kengara, F.O. et al. 2011. Effects of autoclaving and mercuric chloride sterilization on PAHs dissipation in a two-liquid-phase soil slurry. Pedosphere, 21, 56–64.
Whalley, W.R., Leeds-Harrison, P.B., Leech, P.K., Riseley, B.A. & Bird, N.R.A. 2004. The hydraulic properties of the soil at root-soil interface. Soil Science, 169, 90–99.
Whalley, W.R., Watts, C.W., Gregory, A.S., Mooney, S.J., Clark, L.J. & Whitmore, A.P. 2008. The effect of soil strength on the yield of wheat. Plant and Soil, 306, 237–247.
Wolf, A.B., Vos, M., de Boer, W. & Kovalchuk, G.A. 2013. Impact of matric potential and pore size distribution on growth dynamics of filamentous and non-filamentous soil bacteria. PLoS One, 8, https://doi.org/10.1371/journal.pone.0083661.
Wolf, D.C., Dao, T.H., Scott, H.D. & Lavy, T.L. 1989. Influence of sterilization methods on selected soil microbiological, physical and chemical properties. Journal of Environmental Quality, 18, 39–44.