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Root Responses to Alterations in Macroporosity and Penetrability in a Silt Loam Soil

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Changes in soil physical conditions can have an impact on plant root growth. However, the underlying functional responses of root growth to variations in soil physical properties still remain poorly understood. We assessed the responses of barley (*Hordeum vulgare* L.) roots to a typical range of soil physical properties created by applying different degrees of loosening or compaction to subsurface soil layers. A replicated field experiment was established on a Templeton silt loam soil (Dystric Ustochrept) in Canterbury, New Zealand. Following removal of the top 15 cm of soil, five mechanical treatments were applied: loosened by cultivation, three degrees of compaction using a roller (one pass, eight passes, and eight passes with vibration), and an untreated control. Subsequently, the top 15 cm of soil was repositioned. The impact of these treatments on soil physical properties in the subsurface soil layer (15–30 cm) produced a discernible gradient that was well characterized by shifts in pore-size distribution, in particular macroporosity (radii > 30 μm). Macroporosity values were well represented throughout the range from 0.035 up to 0.20 m^3 m^{-3} (n = 50), and these values were negatively correlated with both penetration resistance and bulk density measurements ($r \leq -0.80$; $P < 0.001$). We found clear responses of root growth to this established gradient. As macroporosity decreased, root diameter increased by 42% ($r = -0.63$), while root length density decreased by 65% ($r = +0.66$). However, these divergent responses of root diameter and length density to changes in macroporosity were not linear over the whole range but exhibited specific response thresholds. The thresholds of macroporosity, where root responses inflected and became particularly pronounced, were <0.077 m^3 m^{-3} for root diameter and >0.12 m^3 m^{-3} for root length density, suggesting that macroporosity values above 0.13 m^3 m^{-3} can facilitate root growth. Although these belowground responses were clearly evident, we detected no effects of these varying conditions on aboveground plant productivity. Moreover, the results also indicate that moderate-to-high soil water contents during the early stages of plant development allow annual roots to overcome potentially restricting soil physical conditions.

Abbreviations: HSD, honest significant distance.

Changes in soil physical conditions can influence plant root growth (Unger and Kaspar, 1994; Batey, 2009). Soil provides physical voids into which roots can elongate (Chen and Weil, 2010) and, hence, access water and nutrients within soil profiles (Taylor and Brar, 1991). Flow and exchange of water and gases needed for root growth also take place through the network of soil pores (Lipiec and Hatano, 2003). Alterations in soil physical properties can occur by mechanical compression, loosening, or rearrangement of soil particles. Recurring management practices such as tillage or naturally occurring processes such as wetting–drying cycles can lead to changes in soil physical properties (Grimes et

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al., 1975; Greenwood and Cameron, 1990Greenwood and Cameron, 1990). Although existing literature indicates that root growth can be affected by alterations in the soil physical properties (Logsdon et al., 1987; Smucker and Erickson, 1989; Oussible et al., 1992), the specific responses of root diameter and root length density to variations in soil physical properties still remain understudied. Characterizing these responses is critical to better understanding and predicting the adaptation and constraints of plant root growth to variations in edaphic-climatic conditions and land management systems.

Soil physical properties frequently linked to root growth include bulk density (Ahmad et al., 2009), penetration resistance (Logsdon et al., 1987), and macroporosity (Smucker and Erickson, 1989; Schwen et al., 2011). Although bulk density is the most commonly used indicator of soil physical condition, it is of limited value for predicting or interpreting root growth responses because it lacks a direct functional relationship with plant growth (Kaufmann et al., 2010). As discussed by Logsdon and Karlen (2004), bulk density depends on a broad array of other soil attributes such as organic matter content, aggregation, texture, and parent material as well as weather conditions, whereas root growth may respond differently to these attributes. Other soil physical properties such as penetration resistance (Logsdon et al., 1987), macroporosity, pore size distribution, and pore connectivity (Carter, 1988; Valentine et al., 2012; Schjønning et al., 2013) may be more useful predictors of root growth responses to variations in soil physical conditions. Each of these soil properties has particular advantages and disadvantages as indicators of root growth. For example, penetration resistance provides an instantaneous field quantification of the soil strength that growing roots experience in a given point in time; however, penetration resistance measurements are profoundly influenced by changes in soil water content (da Silva et al., 1994; Busscher and Bauer, 2003), and hence, comparisons amongst different sampling times or across soils with differing water content typically become confounded. In contrast, quantification of pore size distribution and macroporosity can directly characterize differences in soil physical conditions in great detail and with minimal dependency on spatiotemporal variations of soil water content although it can be time consuming and costly to complete.

To date, limited data are available for explicitly describing the root growth responses to differences in soil physical condition, in particular when focusing on subsurface soil layers under field conditions. Wolfe et al. (1995) suggested a reduction in the root growth of maize plants in soils exhibiting increased penetration resistance. Coelho et al. (2000) also indicated that penetration resistance is inversely associated with root length density based on an assessment of subsurface soil layers under varying soil physical conditions. Other earlier studies also found inverse relationships between penetration resistance and root length density (Grimes et al., 1975; Oussible et al., 1992; Busscher and Bauer, 2003). Similarly, results of aboveground plant productivity by Carter (1988) suggested that a relatively high soil macroporosity is required to facilitate an optimum root growth of annual plants. Since the existing literature on this subject remains limited and fragmented, additional research is required to verify the validity and to expand the applicability of these postulated soil–root relationships as a function of common variations in soil physical conditions.

The objective of this study was to examine the response of barley root growth parameters (e.g., root diameter and root length density) to variations in soil physical properties including macroporosity, penetration resistance, bulk density, and water retention. Our aim was to explore hypothetical relationships between these soil physical properties and root growth, and also to identify any particular response thresholds along a range of typical physical conditions in a silt loam soil. The majority of the earlier studies addressing root responses to variations in soil physical conditions have assessed only the early stages of root growth using surface soils in packed columns under controlled environments. To advance the knowledge in this subject, our study examined root responses to differences in soil physical properties under in situ field conditions, with a particular focus on the peak of root growth (~corresponding to the anthesis growth stage).

MATERIALS AND METHODS

Experiment Site

The study site was located at the experimental farm of the New Zealand Institute for Plant and Food Research Ltd. near Lincoln, New Zealand (43°38′ S lat; 172°30′ E long), on an Immature Pallic Templeton silt loam soil series (Dystric Ustochrept) over gravel. Particle size analysis (0- to 30-cm soil depth) using the sedimentation method (Gee and Bauder, 1986) resulted in sand and clay contents of 0.230 and 0.250 kg kg^{-1}, respectively. Soil organic C content was 25 g kg^{-1} (0- to 30-cm depth) as determined by the dry combustion method (Nelson and Sommers, 1996).

Rainfall, air temperature, and solar radiation data for the study period (Fig. 1a) were recorded by a weather station within 2 km of the experimental site. The long-term mean annual precipitation and mean air temperature at this location are 634 mm and 11.4°C, respectively (1960–2009 data).

To establish a gradient of soil physical properties and observe their potential effects on plant root growth, we applied five mechanical treatments. For all five treatments (including the control), the top 15 cm of soil was first removed using a mechanical excavator operated from outside each experimental plot. The experimental treatments were then applied to the underlying soil. An untreated control treatment was included. Another treatment was a mechanical cultivation using two tillage passes with a chisel plow implement including grubber and crumbler functions (Maxi-till, Rata Industries, Inc., Timaru, New Zealand) applied to loosen the 15- to 25-cm soil layer. This loosening treatment had the aim of reducing any possibly preexisting impediment to root penetration in the subsurface soil layer. The other three treatments used a roller–compactor (transverse length: 5.6 m, total equipment mass: 10.3 Mg, drum mass: 5.85 Mg, drum width: 2.13 m, drum diameter: 1.6 m) to establish three degrees of compaction in the subsurface soil layer (i.e., one roller pass, eight roller passes, and eight roller passes with vibration). The roller–compactor applied a static, vertical pressure of approximately 49.5 kPa, assuming that 10% of the surface of the drum was in physical contact with the subsurface soil for a contact area of 1.07 m^2. Subsequently, the topsoil material (15 cm) was returned to each of the corresponding plots. The experiment design was a Latin square with five replicates, and dimensions of the experimental plots were 20 by 3 m.

Treatments were applied in the spring between 21 and 23 Oct. 2009. The volumetric soil water content at the time of treatment establishment was estimated to be 0.23 and 0.27 $m^3\ m^{-3}$ for the 0- to 20- and 20- to 40-cm depth increments, respectively. These values were derived from modeling daily water balance based on soil water retention parameters (Table 1), field measurements (Fig. 1), and accounting for the incidence of rainfall and drainage events as well as evaporative losses. The mechanical treatments were established under these soil water contents (83–92% of field capacity) to allow the trafficking of the heavy machinery while avoiding any unintended soil damage across the experimental site (e.g., deep wheel tracks).

On 5 Nov. 2009, all experimental plots were surface cultivated to a depth of 8 cm, fertilized at rates of 31, 198, 24, and 19 kg ha^{-1} of N, P_2O_5, K_2O, and S, respectively, and mechanically sown to barley at 170 kg seed ha^{-1}. Urea was surface-applied at 100 kg N ha^{-1} on 11 Dec. 2009. Fertilizer applications were aimed to ensure sufficient nutrient availability for barley growth. Irrigation was evenly applied across all experimental plots using a linear boom. The amounts of added water and timing of irrigation events was scheduled using weekly measured volumetric soil water contents (Fig. 1b) with the aim of maintaining a soil water deficit lower than 60 mm. Irrigation ceased when barley reached anthesis growth stage (11 Jan. 2010). Irrigation amounts and application dates are presented in Fig. 1a. For the planting-to-anthesis period (68 d), cumulative irrigation and rainfall were 110 and 66 mm, respectively.

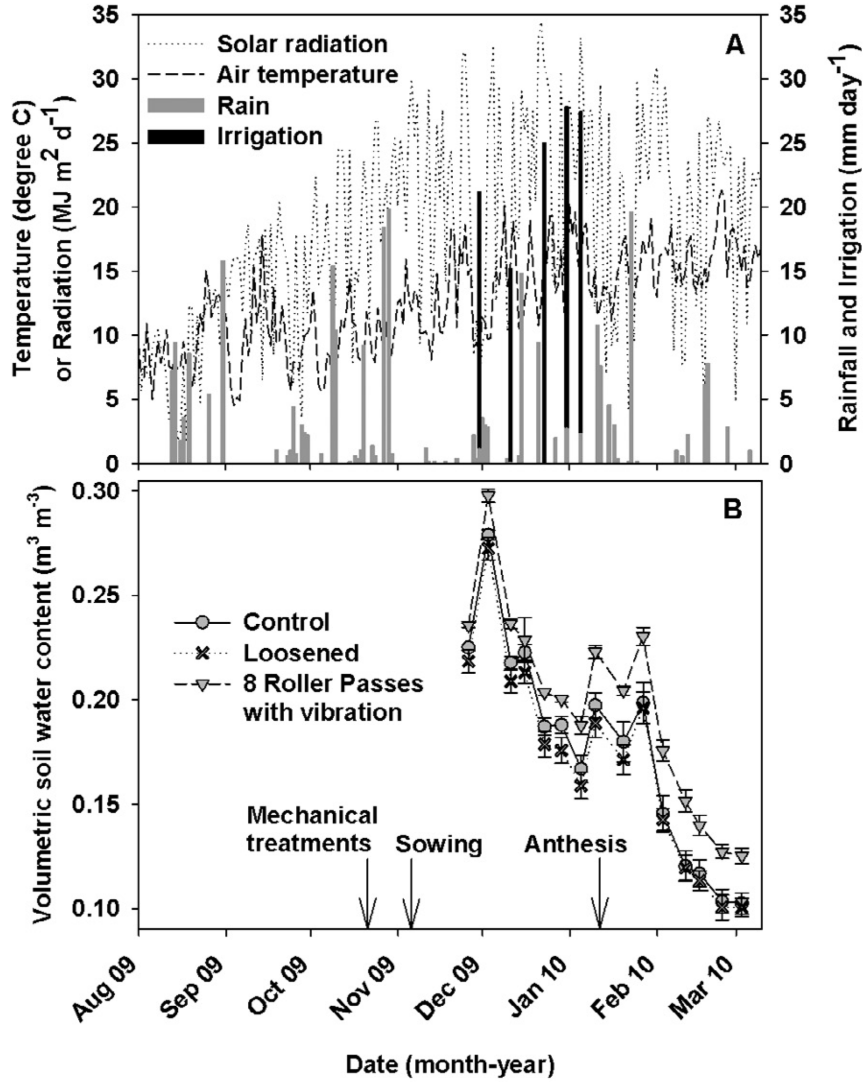

Fig. 1. (A) Solar radiation, air temperature, rainfall, and irrigation water, and (B) soil water content for the 0- to 40-cm depth increment during the experimental period as a function of three selected subsurface mechanical treatments. Shown values are (A) daily means for air temperature and solar radiation and daily cumulative for rainfall plus irrigation water, and (B) treatment means of weekly soil water content measurements within the barley growing season, with standard errors as error bars (*n* = 5). Times of establishment of mechanical treatments as well as barley sowing and anthesis are indicated.

Measurements

Barley root growth parameters (i.e., root length, diameter, surface area, and mass) were determined by collecting six soil cores (4.99-cm i.d.) in each experimental plot. Within every plot, two soil cores were collected in the barley rows, two in the middle position between two rows, and two at one-fourth position between two rows. These soil cores were composited for each separated plot. Subsequently, roots were separated by rinsing and sieving, and these root samples were scanned and digitized using LC4800 and WinRHIZO 2005, respectively (Regent Instruments, Inc., QC, Canada). Root mass was determined by oven-drying and weighing the root samples. Field sample collections for root analyses were conducted on three dates (7 and 22 Dec. 2009, and 11 Jan. 2010). Because a primary focus of this study was on root responses at the peak of root growth (~plant anthesis stage), root analyses for the samples taken on 11 Jan. 2010 were conducted for all four soil depth increments (0–15, 15–22.5, 22.5–30, and 30–50 cm). Conversely, for the samples taken on both 7 and 22 Dec. 2009, root analyses were conducted only on the 22.5- to 30-cm depth increment. We also quantified aboveground biomass weekly throughout the growing season from 0.2-m^2 quadrats as well as from harvested grain and

Table 1. Soil physical properties and water retention characteristics in the 18- to 20.5-cm depth increment as affected by subsurface mechanical treatments (e.g., loosened by tillage or compaction by roller passes applied at the 15-cm depth). Soil cores were collected from barley fields during January 2010.

Variable or parameter	Treatment					Overall mean	$P > F$†
	Control	Loosened	One roller pass	Eight roller passes	Eight roller passes with vibration		
Bulk density, Mg m^{-3}	1.22 b‡	1.19 b	1.22 b	1.27 a	1.29 a	1.24	***
Total porosity§, m^3 m^{-3}	0.539 a	0.553 a	0.539 a	0.522 ab	0.512 b	0.533	**
θ saturation¶, m^3 m^{-3}	0.502 ab	0.519 a	0.505 ab	0.503 ab	0.471 b	0.500	**
θ field capacity, m^3 m^{-3}	0.292 b	0.289 b	0.290 b	0.309 ab	0.313 a	0.299	***
θ at −1500 kPa, m^3 m^{-3}	0.193 ab	0.174 b	0.202 a	0.205 a	0.205 a	0.196	***
θ available#, m^3 m^{-3}	0.097 b	0.116 a	0.089 b	0.099 b	0.106 ab	0.101	***
Macroporosity††, m^3 m^{-3}	0.155 a	0.170 a	0.158 a	0.135 ab	0.112 b	0.146	***
Mesoporosity, m^3 m^{-3}	0.106 ab	0.124 a	0.108 ab	0.114 ab	0.101 b	0.111	*
Microporosity, m^3 m^{-3}	0.240 ab	0.226 b	0.241 ab	0.248 a	0.256 a	0.242	***
Van Genuchten–Mualem model							
α, cm^{-1}	0.90	0.86	0.85	0.82	0.85	0.86	NS‡‡
n	1.50	1.48	1.51	1.50	1.43	1.48	NS

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† $P > F$, probabilities beyond F values for treatment effects within each soil depth increment and soil parameter after ANOVA models.

‡ Within rows, means followed by the same letter are not significantly different according to Tukey's HSD test ($\alpha = 0.05$).

§ Estimations were based on bulk density values and assuming a soil particle density of 2.65 g cm^{-3}.

¶ θ, volumetric soil water content. θ field capacity and θ at −1500 kPa were defined as volumetric soil water contents at −10 and −1500 kPa water potentials at equilibrium, respectively.

θ available was calculated as the subtraction between volumetric water contents at −10 and −1500 kPa water potentials at equilibrium.

†† Macroporosity, mesoporosity, and microporosity were defined as volume of pores with radii within >30, 30–4.5, and <4.5 μm, respectively. The 30- and 4.5-μm boundaries of pore radii were estimated to correspond to −5 and −33 kPa water potentials at equilibrium (Eq. [1]), respectively.

‡‡ NS, nonsignificant.

aboveground biomass at maturity from 0.7-m^2 quadrats on 2 and 3 Mar. 2010.

Soil strength was measured using a cone penetrometer (1.28-cm cone diameter, 30° cone angle; Field Scout SC-900, Spectrum Technologies, Inc., Plainfield, IL). We took penetration resistance readings at five locations within each experimental plot, with single point readings at 2.5-cm intervals from the soil surface to a depth of 40 cm (i.e., 16 intervals at each given measurement location). These penetration resistance measurements were taken at the beginning of the barley growing season on 7 Dec. 2009 and after harvest on 28 Apr. 2010. Volumetric soil water content was measured for the 0- to 20-cm depth by time domain reflectometry and for the 20- to 140-cm depth by the neutron probe method. Additionally, undisturbed soil cores (5.1-cm i.d, 2.5-cm height) were collected in each experimental plot at 5- to 7.5- ($n = 2$), 18- to 20.5- ($n = 4$), 25- to 27.5- ($n = 4$), and 35- to 37.5- ($n = 2$) cm depth increments during January 2010 to quantify soil bulk density and to assess the pore size distribution. The pore size distribution was determined using water retention measurements that followed water saturation of the undisturbed soil cores on tension tables with supplied suctions of −0.5, −1, −2, −5, and −10 kPa, and on pressure plate extractors (Soil Moisture Equip. Co., Santa Barbara, CA) at −33-, −100-, −500-, and −1500-kPa water potentials (Dane and Topp, 2002).

To quantify in situ soil water content at field capacity, we undertook repeated measurements ($n = 6$) of volumetric water content for the 0- to 20- and 20- to 40-cm depth increments over an 8-d period following a series of successive irrigation events that were applied after crop harvest with the purpose of increasing soil water content above field capacity. A total of 231 mm of water was applied during the 22 d before initiating this series of repeated soil water content measurements on 20 Apr. 2010. To minimize soil evaporation and rainwater infiltration while these field capacity measurements were conducted, the soil surface was covered with plastic film (1 m^2; Dane and Topp, 2002).

Data Calculations and Analysis

The in situ repeated measurements of volumetric water content conducted in late April 2010 were used to determine field capacity for the 0- to 20-cm soil layer. The same data were also used to calculate the fractional amounts of soil water drained every day during the period from saturation to field capacity. These estimated drainage rates were presented in a 24-h time step.

Soil total porosity was estimated using measured bulk density values, assuming a soil particle density of 2.65 g cm^{-3} and expressed on a fractional basis (m^3 m^{-3}).

Available water was calculated as the difference between volumetric soil water contents (θ) at −10- and −1500-kPa water potentials.

Using water retention measurements from undisturbed soil cores, soil pore radii were estimated from the applied water potentials (i.e., −0.5, −1, −2, −5, −10, −33, −100, −500, and −1500 kPa) after Vomocil (1965) as

$$\text{Pore radius} = \frac{2 \times \text{surface tension of water} \times \cos(\text{contact angle})}{\text{density of water} \times g \times |\text{applied water potential}|} \quad [1]$$

where the surface tension of water was 0.0728 N m^{-1} (at 20°C), the contact angle between the water–air interface and the solid phase was assumed to be 0°, water density was assumed to be 1 g cm^{-3} (at 20°C), and the *g* constant is 9.81 m s^{-2}. In this study, macroporosity, mesoporosity, and microporosity were defined as the fractional volume of pores with radii >30, 30 to 4.5, and <4.5 μm, respectively. The 30- and 4.5-μm boundaries of pore radii were estimated to correspond to −5 and −33 kPa water potentials at equilibrium (Eq. [1]), respectively.

The van Genuchten–Mualem model (van Genuchten, 1980) was fitted to the measured soil water retention data as follows:

$$\frac{(\theta_{measured} - \theta_{at-1500\ kPa})}{(\theta_{saturation} - \theta_{at-1500\ kPa})} = \frac{1}{(1 + |\propto \times applied\ water\ potential|^{n})^{(1-1/n)}} \quad [2]$$

where θ saturation was the saturated volumetric water content (m^3 m^{-3}), and *n* and a (cm^{-1}) were the empirical curve-shape parameters. The resulting fitted models had coefficients of determination (r^2) equal to or greater than 0.97. The parameters derived using Eq. [2] integrated information of water retention for the full range of water potentials measured in this study (i.e., −0.5 to −1500 kPa), allowing for overall comparisons across treatments.

Root length density and root mass density were calculated by dividing root length and root mass by the core volume (six soil cores per plot). Specific root length was calculated as root length divided by root mass. Ratio of shoot to root mass was estimated using above ground plant biomass and root mass density data.

Values of aboveground biomass and harvested grain yield at plant maturity were used to estimate dry matter partitioning and harvest indices (Hernandez-Ramirez et al., 2011).

All variables were statistically assessed for influential points, homogeneity of variance, and normality by Cook's distance, Bartlett, and Shapiro–Wilk tests, respectively. In cases where homogeneity of variance and normality assumptions were not fulfilled, data transformations were applied using the Box–Cox method. We examined the relationships amongst variables by Pearson product moment correlations (*r*). In accordance with the Latin square design, additive ANOVA models were run to assess treatment effects (fixed factors) and including both row and column as random factors. Subsequently, Tukey's honest significant distance (HSD) tests were performed for multiple treatment mean comparisons. These statistical analyses were performed using Minitab 14 (Minitab Inc., State College, PA). Because root data as a function of soil physical properties graphically exhibited clustering and shifting tendencies, we fitted piecewise regression models. This regressive method consists of fitting two linear segments over adjacent data intervals. This analysis allowed for examination of the diverging relationships between variables in two neighboring data regions as well as identification of threshold boundaries or breakpoints between these data clusters. Piecewise regressions were performed using SigmaPlot ver. 11.0 (Systat Software Inc., San Jose, CA). All significance statistics were processed at $\alpha = 0.05$.

RESULTS

Induced Gradient of Soil Physical Properties

In general, the most pronounced changes in soil physical conditions as a function of the established mechanical treatments were observed within the 18- to 32.5-cm soil layer (Tables 1 and 2, Fig. 2). This is directly beneath the 15-cm depth where loosening with tillage passes or compression with roller passes were applied before sowing of the barley crop. There were no significant differences among treatments in the surface (~0- to 15-cm depth) and deep (35- to 37.5-cm depth) layers for any of the measured soil physical properties.

Soil penetration resistance results were clearly influenced by the applied subsurface mechanical treatments (Fig. 2). For the penetration resistance measurements made at the beginning of the growing season (7 Dec. 2009) in the 22.5- to 27.5-cm depth increment, the loosened treatment soil averaged 2.09 ± 0.36 MPa whereas the heaviest compaction treatment (eight roller passes with vibration) resulted in a significantly higher soil strength (2.90 ± 0.22 MPa) (Fig. 2a; $P < 0.05$). Likewise, based on penetration resistance measurements on 28 Apr. 2010 (after barley harvest), the heaviest compaction treatment resulted in a 49% increase in penetration resistance relative to the control (2.22 ± 0.14 and 1.49 ± 0.11 MPa, respectively, for the 22.5- to 32.5-cm depth increment) (Fig. 2b; $P < 0.01$). These penetration resistance results showed that the range of soil impedance conditions established across the experimental treatments persisted throughout the entire growing season. Additionally, field measurements of soil water contents indicated that these penetration resistance readings were conducted at times (7 Dec. 2009 and 28 Apr. 2010) when water contents were close to field capacity (Fig. 2c and 2d, Tables 1 and 2). Soil water content measurements were particularly consistent for the 0- to 20-cm soil layer with no differences across treatment means ($P > 0.05$), while certain variations in soil water contents were detected amongst the treatments for the 20- to 40-cm soil layer ($P < 0.05$), but the magnitude of these treatment differences was lower than 0.05 m^3 m^{-3} (Fig. 2c and 2d).

Soil bulk density and total porosity also differed in accordance with the applied treatments. The bulk density of the heaviest compacted soil (eight roller passes with vibration) was 8% higher than that of the loosened soil (Tables 1 and 2; $P < 0.001$).

Measurements of water content at field capacity using both undisturbed soil cores on tension tables [18- to 20.5-cm depth (Table 1), and 25- to 27.5-cm depth (Table 2)] and in situ methods [~following saturation and drainage phases; 20- to 40-cm depth (Fig. 2d and 3)] showed that water retention at field capacity was significantly higher in the heaviest compaction treatment than in either the control or the loosened treatments ($P <$ 0.01). Similarly, the water content at −1500 kPa was also higher in heaviest compaction treatment than in the loosened treatment at the 18- to 20.5-cm depth (Table 1). These increases in water retention were in direct association with greater soil bulk density. Despite these treatment effects on water retention at field capacity and −1500 kPa, there were no significant differences in

Table 2. Soil physical properties and water retention characteristics at various depth increments as affected by two selected subsurface mechanical treatments (i.e., loosened by tillage or compaction by multiple roller passes applied at the 15-cm depth). Soil cores were collected from barley fields during January 2010.

Variable or parameter	Treatment: Loosened	Treatment: Eight roller passes with vibration	Overall mean	$P > F$†
	5- to 7.5-cm depth			
Bulk density, Mg m^{-3}	1.14	1.13	1.14	NS‡
Total porosity§, m^3 m^{-3}	0.570	0.575	0.573	NS
θ saturation¶, m^3 m^{-3}	0.542	0.544	0.543	NS
θ field capacity, m^3 m^{-3}	0.278	0.280	0.279	NS
θ at -1500 kPa, m^3 m^{-3}	0.165	0.167	0.166	NS
θ available#, m^3 m^{-3}	0.113	0.114	0.114	NS
Macroporosity††, m^3 m^{-3}	0.195	0.193	0.194	NS
Mesoporosity, m^3 m^{-3}	0.135	0.130	0.133	NS
Microporosity, m^3 m^{-3}	0.212	0.221	0.217	NS
Van Genuchten–Mualem model				
n	1.65	1.69	1.67	NS
α, cm^{-1}	0.74	0.64	0.69	NS
	25- to 27.5-cm depth			
Bulk density, Mg m^{-3}	1.36	1.47	1.42	***
Total porosity, m^3 m^{-3}	0.487	0.447	0.467	***
θ saturation, m^3 m^{-3}	0.438	0.406	0.422	*
θ field capacity, m^3 m^{-3}	0.292	0.325	0.309	***
θ at −1500 kPa, m^3 m^{-3}	0.212	0.203	0.208	NS
θ available, m^3 m^{-3}	0.080	0.122	0.101	NS
Macroporosity††, m^3 m^{-3}	0.101	0.046	0.074	***
Mesoporosity, m^3 m^{-3}	0.072	0.084	0.078	NS
Microporosity, m^3 m^{-3}	0.265	0.276	0.271	NS
Van Genuchten–Mualem model				
n	1.40	1.61	1.51	NS
α, cm^{-1}	0.68	0.28	0.48	NS
	35- to 37.5-cm depth			
Bulk density, Mg m^{-3}	1.55	1.59	1.57	NS
Total porosity, m^3 m^{-3}	0.413	0.401	0.407	NS
θ saturation, m^3 m^{-3}	0.375	0.367	0.371	NS
θ field capacity, m^3 m^{-3}	0.262	0.269	0.266	NS
θ at −1500 kPa, m^3 m^{-3}	0.194	0.182	0.188	NS
θ available, m^3 m^{-3}	0.068	0.087	0.078	NS
Macroporosity††, m^3 m^{-3}	0.077	0.064	0.071	NS
Mesoporosity, m^3 m^{-3}	0.074	0.076	0.075	NS
Microporosity, m^3 m^{-3}	0.224	0.227	0.226	NS
Van Genuchten–Mualem model				
n	1.40	1.56	1.48	NS
α, cm^{-1}	0.62	0.32	0.47	NS

* Significant at the 0.05 probability level.

*** Significant at the 0.001 probability level.

† $P > F$, probabilities beyond F values for treatment effects within each soil depth increment and soil parameter after ANOVA models.

‡ NS, nonsignificant.

§ Estimations for total porosity were based on bulk density values and assumed a soil particle density of 2.65 g cm^{-3}.

¶ θ, saturation, θ field capacity, and θ at -1500 kPa were defined as volumetric soil water contents at zero, −10, and −1500 kPa water potentials at equilibrium, respectively.

\# θ available was calculated as the subtraction between volumetric water contents at −10 and −1500 kPa water potentials at equilibrium.

†† Macroporosity, mesoporosity, and microporosity were defined as volume of pores with radii within >30, 30–4.5, and <4.5 μm, respectively. The 30- and 4.5-μm boundaries of pore radii were estimated to correspond to −5 and −33 kPa water potentials at equilibrium (Eq. [1]), respectively.

the available water when comparing the heaviest compacted soil to either the control or the loosened soil (Table 1). However, more available water was found in the loosened soil than in the control ($P < 0.05$); this effect apparently arose because the water content at −1500 kPa tended to be lower in the loosened soil than in the control (Table 1).

Similar to other measured soil physical properties, pore size fractions were affected by the mechanical treatments (Table 1; macroporosity, mesoporosity, and microporosity were defined as fractional volume of pores with radii within >30, 30–4.5, and <4.5 μm, respectively). Soil pore size distribution was significantly different when comparing the loosened treatment with the heaviest compaction treatment. For the 18- to 20.5-cm depth increment, both macroporosity and mesoporosity were substantially greater (by 34 and 19%, respectively) while microporosity was 13% lower in the loosened soil than in the heaviest compacted soil. The more profound differences in pore size distribution across the treatments were observed in the 75- to 300-μm radius class, where, compared to the control, the loosened soil was 26% higher and the heaviest compacted soil was 28% lower pore volumes ($P < 0.01$; Fig. 4). In addition, for the >300 μm radius class, the heaviest compacted soil exhibited 30% lower pore volume than in the loosened soil ($P = 0.04$).

In the soil layers immediately below where loosened or compaction treatments were applied (18- to 20.5- and 25- to 27.5-cm depth increments), there were strong negative correlations between macroporosity and both penetration resistance and bulk density ($r = -0.80$ and -0.94, respectively, $P < 0.001$; Fig. 5). More importantly, soil macroporosity was well represented with values ranging from as low as 0.035 up to 0.20 m^3 m^{-3}, which comprises a typical range of macroporosity for arable soils. Likewise, wide ranges of penetration resistance and bulk density across experimental units also evidenced the presence of a gradient of soil physical conditions in this study (Fig. 5). The coefficients of variation for the individual observations were 42% for macroporosity, 33% for penetration resistance, and 8% for bulk density.

The in situ measurements of water content used to determine field capacity for the 0- to 20-cm soil depth increment (Fig. 3b) also allowed us to estimate the fraction of soil water that apparently moved downward every day during the free drainage phase between soil saturation and field capacity. We found that these estimated water drainage rates substantially differed across the 3 d when successive decreases in water content were observed (Fig. 3b). Specifically, these fractional daily drainage rates decreased from 0.30 to 0.04 d^{-1} from the first to the third day of apparent drainage. However, these estimations did not significantly differ amongst the mechanical treatments.

After fitting the van Genuchten–Mualem model to the water retention data (Tables 1 and 2), we observed no significant effects of the treatments on the empirical model parameters (n and α), indicating that the overall shape of these fitted curves was rather similar. This finding can be attributed to the fact that although we detected differences across treatments for certain pore classes (e.g., 75- to 300-μm radius class as mentioned above, Fig. 4), the van Genuchten–Mualem model integrated information for the full range of assessed water potentials in this study (i.e., −0.5 to −1500 kPa), and hence, the effect of mechanical treatments on the overall patterns of water retention becomes indiscernible at this scale using this model.

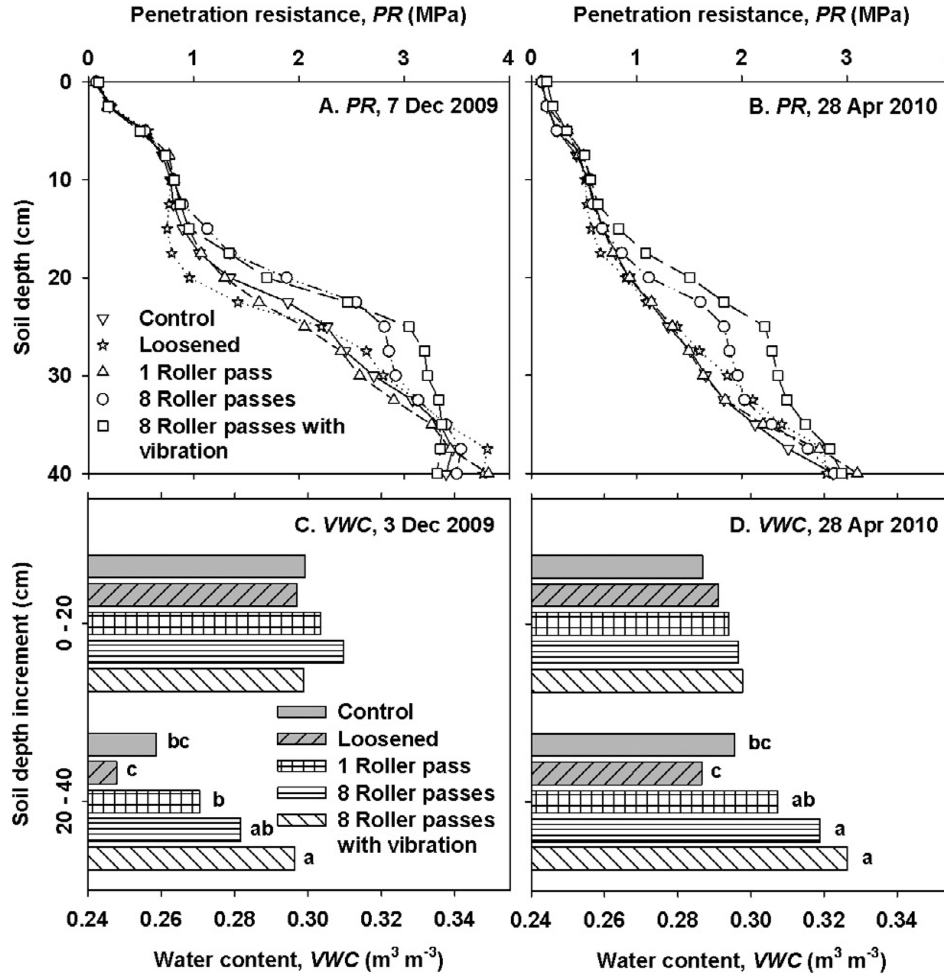

Fig. 2. (A) and (B) Soil penetration resistance (PR) and (C) and (D) volumetric water content (VWC) within the 0- to 40-cm surface layer (A) and (C) at the beginning of the barley growing season and (B) and (D) after harvest as a function of subsurface mechanical treatments (e.g., loosened by tillage or compaction by roller passes applied at the 15-cm depth). Standard errors are not shown for clarity. Within the panels (C) and (D), the VWC horizontal bars labelled with the same letter are not significantly different according to Tukey's honest significant distance test ($\alpha = 0.05$).

Root Growth Responses to Established Mechanical Treatments

The mechanical treatments resulted in significant effects on certain growth parameters of barley roots. The diameter of roots was significantly greater (up to 30%) in the heaviest compaction treatment than in the loosened and control treatments ($P < 0.01$; Table 3). This pattern was evident for the 22.5- to 30- and 30- to 50-cm depth increments as well as for the weighted averages of the whole profiles. In contrast to the results for root diameter, root length density did not differ significantly amongst the mechanical treatments at these two depth increments. However, for the shallower 15- to 22.5-cm depth increment sampled on 11 Jan. 2010 (anthesis stage), root length density was twice as high as in the loosened soil as in the heaviest compacted soil (Table 3). Regarding results of root mass and root surface area densities, no significant differences across treatments were detected although it can be noted that both root mass and root surface area data tended to exhibit similar patterns as root length density (e.g., for the 15- to 22.5-cm depth on 11 Jan. 2010, Table 3). In close agreement with root length density data, specific root length was approximately one-third reduced in the heaviest compacted soil than in the loosened soil (145 vs. 220 m g^{-1} for the 22.5- to 30-cm depth increment on 11 Jan. 2010; Table 3). Nearly all the significant treatment effects on root growth were localized in the same soil depths where most alterations in soil physical properties were observed. In general, the loosened treatment produced evidence of enhanced root growth (i.e., larger root length density, larger specific root length, and smaller root diameter), whereas the heaviest compaction treatment comparatively restricted root growth (i.e., lower root length density, lower specific root length, and greater root diameter). The effects of the other three mechanical treatments fell between these two boundaries.

Our analyses revealed pronounced changes in both root diameter and root length density as a function of varying soil physical properties for the depth increments where mechanical treatments were established (Fig. 6). Based on assembled data from the 15- to 22.5- and 22.5- to 30-cm depth increments on 11 Jan. 2010 (anthesis stage), root diameter increased with increases in both bulk density and penetration resistance, and decreased with increasing macroporosity ($r = 0.73$, 0.75, and −0.72, respectively; $P < 0.001$). In contrast, root length density decreased with increases in both bulk density and penetration resistance, and increased with increasing macroporosity ($r = -0.66$, −0.63, and 0.65, respectively; $P < 0.001$). Furthermore, root diameter was inversely correlated to root length density ($r = -0.36$; $P = 0.02$). Consistent with this result, root diameter was also inversely associated with for specific

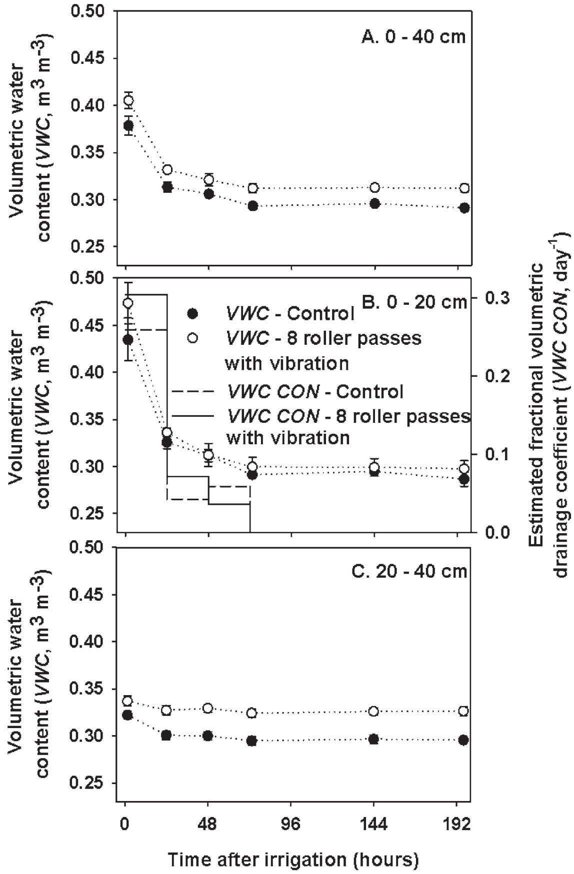

Fig. 3. Soil water content with time at several depth increments [(A) 0–40 cm, (B) 0–20 cm, and (C) 20–40 cm] and (B) apparent daily drainage rates for the 0- to 20-cm depth increment of two selected subsurface mechanical treatments. Fractional daily drainage rates were estimated as the absolute values of step decrements between consecutive times of soil water content measurements and, subsequently, adjusted to 24-h periods. Measurements were taken as soils were draining following a series of eight successive irrigations (231 mm water applied within the 22 d before the beginning of soil water content measurements). Volumetric soil water content measurements were initiated on 20 Apr. 2010 under fallow conditions. Error bars are standard errors (n = 5).

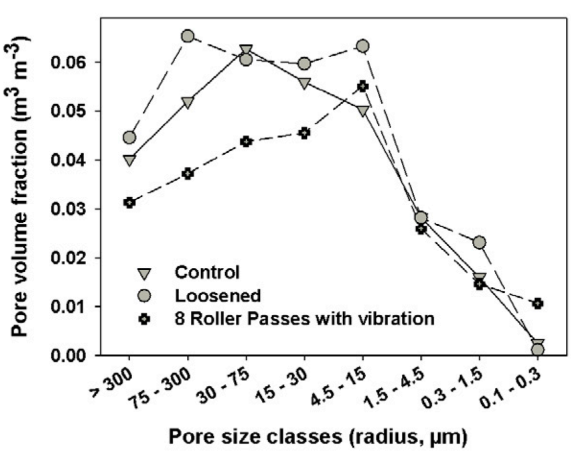

Fig. 4. Pore size distributions for the 18- to 20.5-cm soil layer in three selected subsurface mechanical treatments (e.g., loosened by tillage or compaction by roller passes applied at 15-cm depth) in barley fields. Soil cores were collected during January 2010. Standard errors are not shown for clarity.

root length ($r = -0.54$; $P < 0.001$). Coefficients of variation based on individual observations were 53% for root length density, 43% for root mass density, 38% for root surface area, 27% for specific root length, and 12% for root diameter. Additional analysis focusing on a specific data subset for the 22.5- to 30-cm depth increment further support these observed overall patterns of increasing root diameter with simultaneous increased penetration resistance and decreased macroporosity (Fig. 7).

Aboveground biomass and grain yield of barley did not differ significantly across the treatments ($P > 0.05$; data not shown). Overall averages for aboveground biomass and grain yield were 15.8 ± 0.1 and 8.69 ± 0.07 Mg dry matter ha^{-1}, respectively. No treatment differences were observed for dry matter partitioning into grain with an overall fractional harvest index of 0.55 ± 0.01. Based on the aboveground biomass results and the root mass density data for the 0- to 50-cm soil depth aggregated layer (Table 3), our estimations of the ratio of shoot to root mass revealed that this plant parameter was 33% higher for the heaviest compaction treatment than for the loosened treatment ($P = 0.04$). The ratios of shoot to root mass were 16.3 for heaviest compaction, 12.3 for loosened, and 14.9 for the control treatments (dimensionless data). This indicates that barley plants growing in the loosened treatment allocated relatively more biomass belowground compared to the plants in the heaviest compaction treatment. Nonetheless, these two treatments were not statistically different from the control with respect to this parameter.

DISCUSSION

Effects of Macroporosity and Penetrability on Root Diameter and Length Density

This field study created a wide range of soil physical conditions in the subsurface soil that was well-characterized by gradual shifts in soil macroporosity, penetration resistance, and bulk

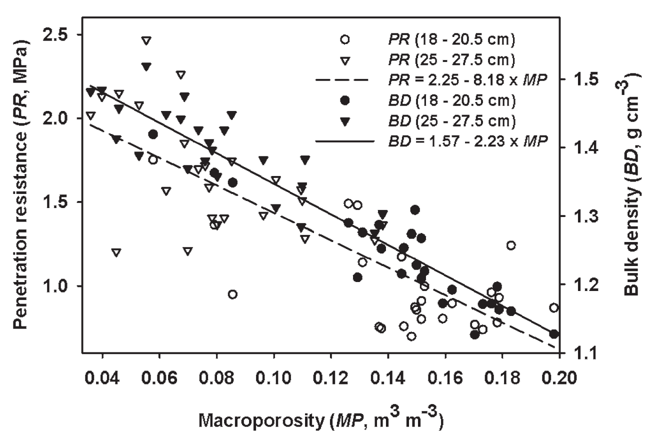

Fig. 5. Interrelationships amongst selected soil physical properties in barley fields. Soil cores for determination of macroporosity and bulk density were collected during January 2010, and penetration resistance measurements were taken on 28 Apr. 2010 when water contents were at field capacity. Each point represents an experimental unit. Data compilation (n = 50) from two contiguous soil depth increments (i.e., 18–20.5 and 25–27.5 cm). Fitted linear regression models and corresponding equations are presented. All regression coefficients and intercepts were statistically different from zero (α = 0.05).

Table 3. Root growth parameters at four soil depth increments and on three different sampling dates in barley fields as affected by subsurface mechanical treatments (e.g., loosened by tillage or compaction by roller passes applied at 15 cm depth). Note that only the 22.5 to 30 cm depth increment was analysed for the sampling dates 7 and 22 Dec. 2009. Sowing and anthesis dates were on 5 Nov. 2009 and approximately 11 Jan. 2010, respectively. Specific root length is a length-to-mass ratio of a root sample.

Treatment or statistic	Root diameter	Root length density	Root surface area density	Specific root length	Root mass density
	mm root	cm root cm^{-3} soil	mm^2 root cm^{-3} soil	m root g^{-1} root	g root m^{-3} soil
			22.5- to 30-cm depth (7 Dec. 2009)		
Control	0.364 b†	0.75	8.37	209.6	49
Loosened	0.368 b	0.91	10.53	196.2	50
One roller pass	0.380 ab	0.84	9.95	194.5	40
Eight roller passes	0.420 a	0.76	10.07	206.6	54
Eight roller passes with vibration	0.413 a	0.68	8.70	187.5	41
Overall mean	0.389	0.79	9.52	198.9	47
P > *F*‡	**	NS§	NS	NS	NS
			22.5- to 30-cm depth (22 Dec. 2009)		
Control	0.334 a	1.03	10.68	172.0	60
Loosened	0.333 b	0.85	8.87	159.3	56
One roller pass	0.343 ab	2.11	6.07	129.6	80
Eight roller passes	0.388 ab	0.83	10.09	151.8	56
Eight roller passes with vibration	0.415 a	0.83	10.89	142.2	58
Overall mean	0.363	1.13	9.32	151.0	62
P > *F*	**	NS	NS	NS	NS
			0- to 15-cm depth (11 Jan. 2010—anthesis stage)		
Control	0.241	5.86	44.39	219.4	267
Loosened	0.237	7.10	52.84	214.3	330
Eight roller passes with vibration	0.239	5.28	38.87	207.2	248
Overall mean	0.239	6.08	45.37	213.6	282
P > *F*	NS	NS	NS	NS	NS
			15- to 22.5-cm depth (11 Jan. 2010)		
Control	0.251	1.77 ab	13.95	205.8	86
Loosened	0.246	2.61 a	20.20	272.5	102
Eight roller passes with vibration	0.269	1.44 b	12.19	192.7	75
Overall mean	0.255	1.94	15.45	223.7	88
P > *F*	NS	*	NS	NS	NS
			22.5- to 30-cm depth (11 Jan. 2010)		
Control	0.267 b	1.09	9.09	208.4 a	52
Loosened	0.259 b	0.95	7.72	219.9 a	44
One roller pass	0.266 b	1.07	8.92	200.3 ab	54
Eight roller passes	0.287 b	0.79	7.23	170.7 bc	47
Eight roller passes with vibration	0.343 a	0.90	9.76	145.0 c	62
Overall mean	0.284	0.96	8.54	188.9	52
P > *F*	***	NS	NS	***	NS
			30- to 50-cm depth (11 Jan. 2010)		
Control	0.235 b	0.26	1.96	216.8	12
Loosened	0.245 b	0.39	3.03	213.5	18
Eight roller passes with vibration	0.291 a	0.30	2.69	194.0	15
Overall mean	0.257	0.32	2.56	208.1	15
P > *F*	*	NS	NS	NS	NS
			Whole profile (0– 50 cm depth, 11 Jan. 2010)¶		
Control	0.244 b	2.29	17.56	214.7	106
Loosened	0.245 b	2.82	21.26	223.6	128
Eight roller passes with vibration	0.280 a	2.05	16.03	190.4	101
Overall mean	0.256	2.39	18.28	209.6	112
P > *F*	***	NS	NS	NS	NS

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Within columns, means followed by the same letter are not significantly different according to Tukey's honest significant distance test (α = 0.05).

‡ *P* > *F*, probabilities beyond *F* values for treatment effects within each soil depth increment and root parameter after ANOVA models.

§ NS, nonsignificant.

¶ The whole profile aggregated values were estimated as weighted averages accounting for differences in thickness amongst depth increments (0–15, 15–22.5, 22.5–30, and 30–50 cm).

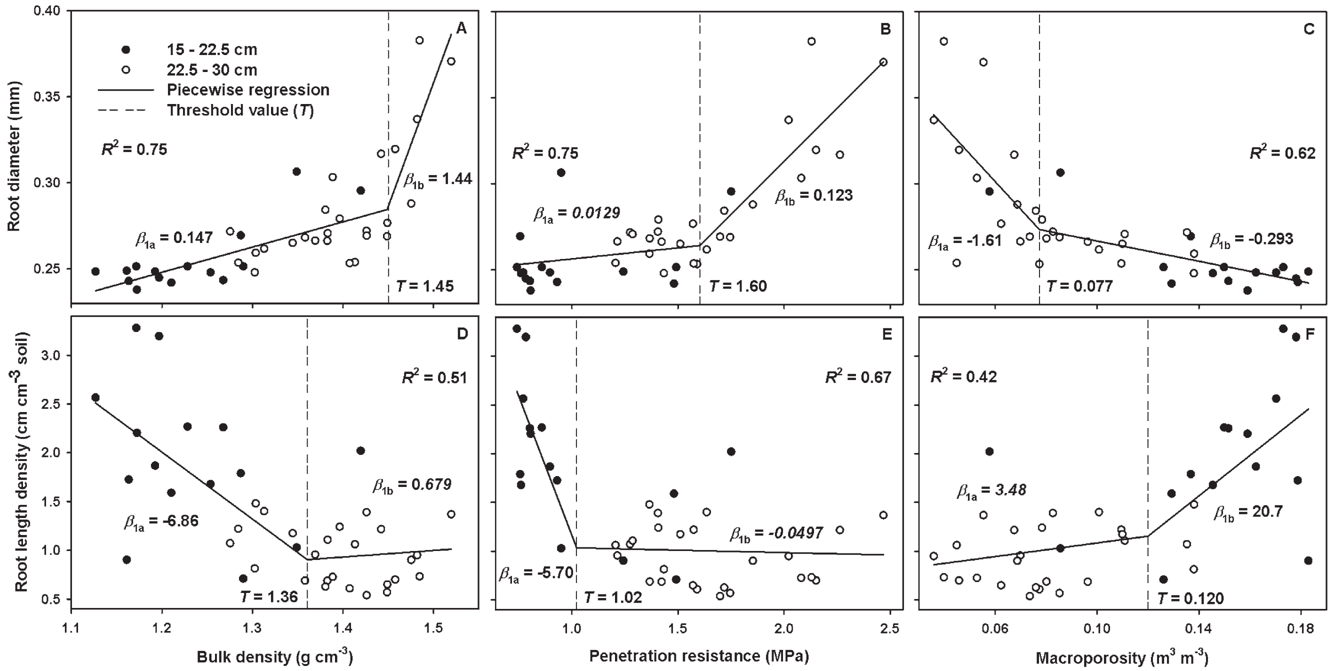

Fig. 6. (A), (B), and (C) Root diameter and (D), (E), and (F) root length density as functions of soil bulk density, penetration resistance, and macroporosity in barley fields. Samples for root growth analyses were collected on 11 Jan. 2010 at approximately anthesis stage of barley. Soil cores for determination of bulk density and macroporosity were also collected during January 2010, and penetration resistance measurements were taken on 28 Apr. 2010 when water contents were at field capacity level. Each data point represents an experimental unit (*n* = 40). Data from two contiguous soil depth increments (i.e., 15–22.5 and 22.5–30 cm) were pooled for these analyses. Fitted piecewise regression models with two linear segments or intervals (a) and (b) are shown; breakpoints or threshold boundary values (*T*), regression coefficients (β_{1a} and β_{1b}), and coefficient of determinations (R^2) are presented in each panel. Italicized regression coefficient values are not statistically different from zero (α = 0.05), while nonitalicized regression coefficients are significant (P < 0.05).

density (Fig. 5). Thus, this experimental setting, using a series of loosening or compaction treatments, enabled the systematic evaluation of the corresponding responses of root growth during a barley growing season in a fine-textured soil. Root diameter and root length density responded to the variations in macroporosity, penetration resistance, and bulk density that were created by the treatments (Fig. 6). These divergent responses of root diameter and root length density were well-described by the piecewise regression analyses, where two fitted linear segments were interconnected at a particular "breakpoint" for each soil property (Fig. 6 and 7). These "breakpoints" can be interpreted as critical thresholds, beyond which more rapid changes in root growth parameters were observed in response to variations in soil physical conditions.

Barley root growth showed discernible responses to variations in soil macroporosity (>30 μm radii) when pooling the data for two soil depths below where the mechanical treatments were applied (i.e., 15–22.5 and 22.5–30 cm). Our analyses revealed that root length density increased sharply only where macroporosity exceeded a threshold value of 0.120 m^3 m^{-3} (*T*, Fig. 6f). Conversely, root diameter was inversely related to macroporosity for the entire range of values, but, more importantly, the rate of change in root diameter (regression coefficient, β_1) was amplified five times where macroporosity was less than 0.077 m^3 m^{-3} (*T*, Fig. 6c). To our knowledge, these asymmetric, differential responses of root growth parameters to changes in soil macroporosity have not been explicitly described before at this degree of detail. Yet, our results are consistent with general inferences from the previous reports. For example, Carter (1988) suggested that soil macroporosity values greater than 0.14 m^3 m^{-3} are needed to sustain optimum aboveground growth of annual plants. Similarly, Smucker and Erickson (1989) postulated that annual root growth can be detrimentally affected by soil air-filled porosities below 0.15 m^3 m^{-3}. Likewise, our post hoc analysis of data by Oussible et al. (1992) for subsurface soil layers under wheat (*Triticum aestivum* L.) fields indicates that a 40% decrease in root length can be linked to 60% reduction in air-filled porosity. Such intense reductions in macropore volume due to compaction of subsurface soils have been observed to persist after multiple decades following the application of mechanical compaction in fine-textured soils (Schjønning et al., 2013)

Because the volume of soil pores larger than the average root diameter was much lower under the heaviest compacted soil than in the loosened soil, it is likely that restrictions to O_2 diffusion and root elongation were important detrimental factors for reducing root growth under increasing soil compaction. The average diameter of roots at barley anthesis in the control treatment at the 22.5- to 30-cm depth was 0.267 mm (Table 3); equal or larger soil pores than 135 μm radius would facilitate readily unrestricted root growth throughout the soil profile. In this study, relative to the loosened soil, the heaviest compacted soil (eight roller passes with vibration) reduced by 38% the volume of >75 μm-radius pores [i.e., 75- to 300- and >300-μm radius (Fig. 4)]. As previously postulated by Chen and Weil (2010) and Valentine et al. (2012), our observed changes in pore size distribution relative to typical thickness of barley root may have constrained root growth in soils dominated by pores much smaller than roots. Moreover, the predominance of relatively small soil pores reduces the potential for O_2 to diffuse towards roots because of lower pore connectivity as well as greater pore tortuosity and water content (Lipiec and Hatano, 2003; Valentine et al., 2012). Within this context, rhizospheric hypoxia leads to slower root metabolism (Glinski and Lipiec, 1990), which can reduce root growth.

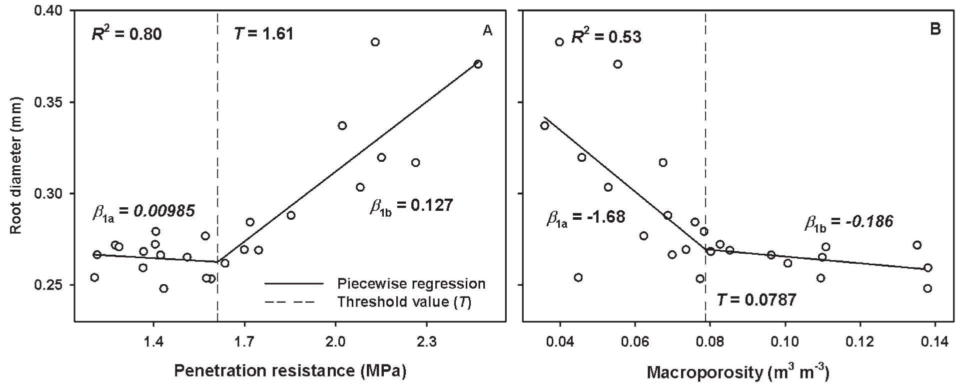

Fig. 7. Root diameter as a function of soil (A) penetration resistance and (B) macroporosity in barley fields. Samples for root growth analyses were collected on 11 Jan. 2010 at approximately anthesis stage of barley. Soil cores for determination of macroporosity were also collected during January 2010, and penetration resistance measurements were taken on 28 Apr. 2010 when water contents were at field capacity level. Each data point represents an experimental unit (n = 25). Data subset corresponds to the 22.5- to 30-cm soil depth increment. Fitted piecewise regression models with two linear segments or intervals (A) and (B) are shown; breakpoints or threshold boundary values (T), regression coefficients (β_{1a} and β_{1b}), and coefficient of determinations (R^2) are presented in each panel. Italicized regression coefficient values are not statistically different from zero (α = 0.05) while nonitalicized regression coefficients are significant (P < 0.05).

Previous research has examined the dependency of root growth of annual plants on changes in soil physical properties. Focusing on the effects of penetration resistance, Taylor and Gardner (1963) reported sharp reductions in root growth for cotton (*Gossypium hirsutum* L.) seedlings in sandy soils under high soil strengths. Similarly, Logsdon et al. (1987) observed simultaneous decreases in root length and increases in root diameter of corn (*Zea mays* L.) seedlings as functions of increased mechanical impedance in a fine-textured soil. As reviewed by Clark et al. (2003), increases in root diameter seems to be the key plant response for enabling effective root growth through soil layers with high penetration resistance. They speculated that ethylene accumulation in the rhizosphere mediates this adaptive mechanism of roots to increasing soil mechanical impedance. Based on experimental work in silt loam soils, da Silva et al. (1994) proposed a penetration resistance threshold of 2 MPa above which root growth becomes severely limited. In general agreement with Clark et al. (2003) and da Silva et al. (1994), our results indicates the that there is a critical threshold for penetration resistance beyond which root diameter (i.e., 1.60 MPa; Fig. 6b) becomes markedly increased and where root length density (1.02 MPa; Fig. 6e) is significantly reduced. Inverse relationships between penetration resistance and root length density have been previously reported for a variety of plant species and soils, including cotton in coarse-textured soils (Busscher and Bauer, 2003), wheat in fine-textured soils (Oussible et al., 1992), and irrigated corn in loamy soils (Grimes et al., 1975). However, the majority of the existing studies on these effects have been conducted in surface soil layers, assessing early root growth, or using soil columns in greenhouse or growth chamber settings; our study further supports and extends the validity of these functional biophysical relationships by evaluating the subsurface layers of in situ soil profiles as well as the root growth at plant anthesis stage, which is typically the peak of root growth in annual plants.

Temporal Patterns of Soil Water Affected Root Growth

In this study, the abundant supply of water in the period between sowing and anthesis (176 mm from rainfall and irrigation during 68 d; Fig. 1a) may have facilitated the growth of barley roots across the entire range of established soil physical conditions although, as noted above, there was an evident tradeoff between root diameter and root length density as a function of changes in soil physical properties (Fig. 6 and 7). In addition to the considerable water input during vegetative growth, soil water content was also high at the beginning of the growing season (Fig. 1b) because the preceding winter and early spring periods had replenished soil water storage to levels near field capacity (Fig. 1a). These observations indicate that information about soil water content patterns is important to interpretation and prediction of root growth as a function of varying soil physical properties (da Silva et al., 1994). Additionally, it is likely that relatively drier soil conditions would exacerbate the effects of compaction on root growth (Lipiec and Hatano, 2003), in addition to any direct detrimental effects resulting from plant water stress (Ahmad et al., 2009). Moreover, other reports also show that significant soil impedance to root elongation could still take place even under reasonably moist soil conditions (approximately −20 kPa) (Bengough et al., 2011; Valentine et al., 2012).

As well as the adaptive physiological responses of annual roots to lower macroporosity and greater penetration resistance observed in this study, other soil factors may have facilitated roots to find and follow pathways of relative less resistance, particularly in subsurface soil layers dominated by small pores. These additional soil factors, that could enable root growth by ameliorating physical constraints, may include wet–dry cycles that rearrange soil particles during shrinking and swelling of soils allowing the formation of void spaces (Lipiec and Hatano, 2003; Konopka et al., 2008), the creation of biopores due to faunal activity (e.g., earthworms and beetles) (Unger and Kaspar, 1994; Hamza and Anderson, 2005), and spatial heterogeneity providing a random, wide distribution of pore sizes occasionally including the presence of large pores even within soil profiles primarily dominated by small pores (Coelho et al., 2000; Konopka et al., 2008).

CONCLUSION

This study provides strong evidence that roots respond to changes in soil physical properties created by different degrees of soil loosening or compaction under field conditions. Whereas root length density increased and root diameter decreased with increases in soil macroporosity over a normal range of values, there was also clear evidence that a critical threshold of macroporosity existed for each of these root growth parameters where the root growth responses do inflect and become much stronger. Similar threshold responses of root growth were observed along gradients of penetration resistance and soil bulk density. Although the root responses along these gradients were evident and in several cases substantial, they did not result in differences in aboveground crop production. Results also indicate that high soil water content during the vegetative growth of barley can reduce any severe physical constraints to root growth and function. Future research should be aimed at evaluating the adaptive responses of roots of other plant species to varying soil physical conditions, and testing the nature of these biological responses across a broader range of soil water regimes.

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