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Soil strength and macropore volume limit root elongation rates in many UK agricultural soils

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• *Background and Aims* Simple indicators of crop and cultivar performance across a range of soil types and management are needed for designing and testing sustainable cropping practices. This paper determined the extent to which soil chemical and physical properties, particularly soil strength and pore-size distribution influences root elongation in a wide range of agricultural top soils, using a seedling-based indicator.
• *Methods* Intact soil cores were sampled from the topsoil of 59 agricultural fields in Scotland, representing a wide geographic spread, range of textures and management practices. Water release characteristics, dry bulk density and needle penetrometer resistance were measured on three cores from each field. Soil samples from the same locations were sieved, analysed for chemical characteristics, and packed to dry bulk density of $1.0 \ \mathrm{g \ cm^{-3}}$ to minimize physical constraints. Root elongation rates were determined for barley seedlings planted in both intact field and packed soil cores at a water content close to field capacity (-20 kPa matric potential).
• *Key Results* Root elongation in field soil was typically less than half of that in packed soils. Penetrometer resistance was typically between 1 and 3 MPa for field soils, indicating the soils were relatively hard, despite their moderately wet condition (compared with <0.2 MPa for packed soil). Root elongation was strongly linked to differences in physical rather than chemical properties. In field soil root elongation was related most closely to the volume of soil pores between 60 µm and 300 µm equivalent diameter, as estimated from water-release characteristics, accounting for 65·7 % of the variation in the elongation rates.
• *Conclusions* Root elongation rate in the majority of field soils was slower than half of the unimpeded (packed) rate. Such major reductions in root elongation rates will decrease rooting volumes and limit crop growth in soils where nutrients and water are scarce.

Key words: Root elongation, abiotic stress, soil chemistry, soil porosity, soil strength, Scotland, macroporosity, dry bulk density, barley, *Hordeum vulgare*, pore diameter.

INTRODUCTION

The calls for innovation in plant science to underpin global increases in food production (Gewin, 2010) have to contend with the ceiling in crop yield that appears to have been reached in some areas of developed, highly productive agriculture, such as the UK (Defra, 2011). One possible reason for this plateau is that despite the level of nutrients applied to agricultural systems there are limitations to the rate at which plants are able to uptake and utilize them. Soil physical conditions can limit the rate at which roots elongate and thus may limit the overall volume of soil that the roots can explore, restricting the rate at which plants access water and nutrients and thereby potentially reducing yield (Whiteley and Dexter, 1982). The effects of physical properties of soils on root growth have been extensively reviewed, notably the effects of drought (Whitmore and Whalley, 2009; Bengough *et al.*, 2011); water logging and oxygen deficiency (Morard and Silvestre, 1996; Setter and Waters, 2003); and compaction and soil strength (Bengough, 2003; Bengough *et al.*, 2006, 2011; Tracy *et al.*, 2011). Crop varietal differences have also been found in their sensitivity to soil physical conditions (e.g.

Masle, 1992). Typically penetrometer resistances >2 MPa, air-filled volume (AFV) of <10 % and a matric potential drier than -1.5 MPa are considered to be significant limits to root elongation, such that root elongation is slowed to less than half of its unimpeded rate (Taylor and Ratliff, 1969; Bengough *et al.*, 2011).

Several artificial systems have been developed to investigate the influence of physical properties on root growth, e.g. reduced oxygen flow in hydroponics (Pitman, 1969), including polyethylene glycol to generate water deficit in hydroponics (Whalley *et al.*, 1998), or utilizing gels (Clark *et al.*, 1999), glass ballotini and gravel mixes to add physical structure (Goss, 1977; Wilson *et al.*, 1977; Goss and Russell, 1980; Bengough *et al.*, 2010; Karley *et al.*, 2011). Alternatively, elongation rates have been recorded in sieved soil packed to specific bulk densities (Taylor and Ratliff, 1969; Eavis, 1972*a*, *b*). However these systems cannot fully mimic the heterogeneity and interacting effects of soil biophysical constraints that occur in field soil.

In field conditions over a growing season, multiple constraints may slow the elongation of roots belonging to a single plant. This is due to both the interdependence of soil

physical properties and the spatial and temporal variation in these properties. For example, in a wet compacted soil the elongation of an individual root may be limited via mechanical impedance and oxygen deficiency, whilst in a compacted dry soil, root elongation may be limited by water deficit and mechanical impedance (Eavis and Payne, 1968; Bengough *et al.*, 2011). Further, the spatial heterogeneity of soil physical properties in the field is often large, with substantial variation in both vertical and horizontal directions, resulting in different roots of the same plant experiencing very different physical limitations. While roots often exploit spatial heterogeneity in pore structure to elongate along pathways of least resistance (Ehlers *et al.*, 1983; McKenzie *et al.*, 2009; White and Kirkegaard, 2010), they may also experience superimposed temporal variation due to fluctuations in the soil water balance (caused by rainfall and evapotranspiration), and tillage and farm-traffic effects (Ehlers *et al.*, 1983; Besson *et al.*, 2010). Heterogeneity therefore can have a major impact on root growth in the field, with soil becoming softer and easier for roots to penetrate after rainfall events, but potentially becoming subject to waterlogging after heavy rain or if the pore space is small.

While the main factors that can impact on root elongation are known, the extent to which these properties are limiting root elongation 'on farm' is less understood. Surveys of the penetrometer resistance of a range of field soils, however, suggest that mechanical impedance often limits root elongation, even when the soil is relatively wet (Bengough *et al.*, 2011). In this paper we hypothesized that there are considerable constraints to root elongation in agricultural top soils under current soil management practices and that these are widespread in the UK. The results are highly topical to current trends towards the adoption of reduced (conservation) tillage systems, where shallower plough pans and large shifts in soil physical structure can occur in relation to the previous practice of inversion tillage to greater depth. We measured root elongation of barley seedlings in soil cores collected from a wide range of agricultural soils equilibrated to -20 kPa matric potential. Samples from the same soils were sieved and repacked to a bulk density of 1.06 g cm^{-3}, and root elongation measured again, to indicate the rate of root elongation in the soil, largely free from soil mechanical impedance and hypoxia. The results from these studies were analysed together with data on the physical and chemical properties of the soils to infer the main factors limiting, and degree of limitation to, root elongation.

MATERIALS AND METHODS

Soil sampling location and soil preparation

Thirty-four farms located in eastern Scotland were identified as representing a wide range of soil types, textures, crop rotation and farm management practices. Soil types included humus-iron podzols, noncalcalcareous gleys, brown earth with gleying, and brown earths. The farms represented a range of organic, integrated [members of LEAF (Linking Environment and Farming) a UK organization that promotes environmentally responsible farming; www.leafuk.org] and intensive management systems (where 'intensive' refers to

commercial farms that adhered to no particular management preference other than current best practice), from across five geographical regions (Inverness-shire, Aberdeenshire, Tayside, Fife and East Lothian). The selection strategy aimed to represent a wide range of agricultural soil types rather than to make comparisons between different farm management practices. Hawes *et al.* (2010) provides further descriptions of the field sites surveyed. On most of the farms two fields under different stages of a crop rotation were sampled, resulting in a total of 59 different fields. Intact soil cores, 56 mm diameter $\times$ 40 mm height, referred to in this paper as 'FIELD', were sampled from the top $0-10$ cm in three separate random locations just following crop harvest in September.

Soils from 20 of these fields were pooled from the three sampling locations in each field, thoroughly mixed and then passed through a 2-mm sieve. A subsample of soil was used to calculate the moisture content of each soil sample using the wet and dry mass (after 24 h at 105 °C). The soil water content was then adjusted to 0.2 g g^{-1}, and the soil was allowed to equilibrate overnight at 4 °C prior to packing the soil into 50-mm-diameter $\times$ 50-mm-height cores at 1.06 g cm^{-3} $\pm$ 0.002 (s.e.). Two packed ('PACKED') soil cores were prepared per field and adjusted to a matric potential of -20 kPa using tension tables. The physical conditions within these soil cores should not significantly limit root elongation, due to the relatively wet matric potential, large air-filled volume, and small penetrometer resistance.

Soil physical properties and chemical analysis

Water-release characteristic, dry bulk density and air-filled volume. FIELD cores, were saturated and placed on silica sand tables (up to -10 kPa) and ceramic suction plates (up to -50 kPa; ELE Ltd, Hemel Hempstead, UK) to adjust the matric potential serially through -0.5, -1, -5, -10, -20 and -50 kPa. The cores were then returned to -20 kPa matric potential for the root-elongation assay described below. The mass of each core was recorded at each stage to determine the volumetric water content (VWC). Soil DBD was calculated from soil dry mass (after drying at 105 °C for 48 h), following the root growth experiments detailed below. Total porosity was calculated from DBD assuming a particle density of 2.65 g cm^{-3}. AFV was calculated by subtracting the VWC from the total porosity.

Penetrometer resistance ($SS_{Instron-20 kPa}$). A needle penetrometer (1 mm diameter, 30 ° cone angle, 4 mm min^{-1} penetration rate, readings; averaged at 1-mm intervals from $5-15$ mm depth range) fitted to a mechanical test frame (Instron model 5544; Instron, MA, USA), with a 50-N load cell accurate to 2 mN at maximum load, was used to measure penetration force and calculate penetrometer resistance (force divided by cone cross-sectional area). All of the FIELD and PACKED cores were measured at a matric potential of -20 kPa (Bengough *et al.*, 1997, 1990; Bengough and Mullins, 1991).

Chemical and texture analysis. The bulk sieved samples used to pack the soil cores were analysed for a range of properties. Soil pH and phosphorus, potassium and magnesium contents were measured by NRM laboratories using British Standard BS 3882: 2007. Carbon and nitrogen concentrations were

measured using an Exeter analytical CE440 elemental analyser (EAI, Coventry, UK). Texture was measured by NRM laboratories using laser diffraction of soils initially dispersed with sodium hexametaphosphate (Malvern Mastersizer 2000; Malvern Instruments Ltd, Malvern, UK).

Root elongation

Barley seeds (*Hordeum vulgare* 'Optic') were soaked for 4 h, washed three times in distilled H_2O and then surface sterilized with 2 % calcium hypochlorite. Seeds were placed between damp filter paper and allowed to germinate at 15 °C for 2 d, prior to being stored at 4 °C for approx. 1 d. Two holes 3 mm wide and 10 mm deep were made in each soil core, 10 mm from the edge at opposite edges of the soil core. The longest seminal root of each of two seedlings was measured prior to inserting all roots from an individual seed into the prepared holes. Seeds were secured in place using a 50-mm-diameter Petri dish as a lid taped to each core. All cores were placed in individual plastic sealable bags to minimize water loss. The FIELD core experiment was performed at a separate time from the PACKED soil experiment. Seeds and soil were incubated at 15 °C for 2 d, after which each seedling was carefully removed from the soil cores and the longest root of each was measured. Soil wet mass (immediately after extraction) and dry mass (after 24 h at 105 °C) were recorded. Gravimetric water content was converted to VWC by multiplying by DBD.

Statistical analysis of soil and root data

Statistical analysis was performed using Genstat 13ed. From the water release data, the equivalent diameter, *d*, of the largest water-filled pore at matric potential, ψ is given by

$$d=300/\psi \qquad (1)$$

(Marshall and Holmes, 1988). For the measured matric potentials -0.5, -1, -5, -10, -20 and -50 kPa, this corresponds to pore diameters of 600, 300, 60, 30, 15 and 6 μm. The volume of pores in a particular diameter range can therefore be estimated from the difference in VWC between the corresponding matric potentials ($Pores_{>300 \ \mu m}$, $Pores_{60-300 \ \mu m}$, $Pores_{30-60 \ \mu m}$, $Pores_{6-30 \ \mu m}$, $Pores_{<6 \ \mu m}$).

Logistic (S-shaped or inverse S-shaped) curves were fitted to both the VWC and AFV against log matric potential data using GENSTAT 13ed – Regression analysis, Standard curves. Indicators are listed as AFV_A, AFV_B, AFV_C, AFV_M or VWC_A, VWC_B, VWC_C and VWC_M where

$$\log \psi = A + \frac{C}{[1 + e^{-B(x-M)}]} \qquad (2)$$

The curve fits were used to estimate the AFV and VWC at -1500 kPa ($AFV_{-1500 \ kPa-est}$ and $VWC_{-1500 \ kPa-est}$), and the VWC at which the AFV would be 10 % ($VWC_{AFV10 \ \%}$). Further the difference in VWC between -20 kPa and the $VWC_{AFV10 \ \%}$ (d_10 %AFV), the $VWC_{-1500 \ kPa-est}$ (PAWvwc) and the field capacity (d_FC) were calculated. All statistical analyses were performed on the mean data for each field. Each

dataset was transformed where required to ensure a normal distribution (see Table 1 for the transformation used for each parameter). Principal component analysis was performed using a correlation matrix methodology. All-subsets regression was used to assess and build models based on the subset of fields that included all chemistry and texture data ($n = 42$). Models were considered significant if the Aiken information coefficient (AIC) value was within 2 of the lowest AIC value for the analysis set and all indicators in the model made a significant contribution to the model. Three subsets of indicators were used: (1) the 14 indicators that described the physical status of the soil at -20 kPa, including pore structure and the water retention curve indicators; (2) 23 'simple' indicators (as marked in Table 1 – indicators that required limited calculations, no line fitting); and (3) all 42 indicators. Since all-subsets regression analysis was limited to 16 indicators for the larger subsets, indicators were randomly assigned to groups of indicators and all-subsets regression was used to assess models. This was repeated ten times. The 16 indicators included in the highest number or highest average proportion of models were assessed in a final analysis.

RESULTS

Root elongation in FIELD and PACKED soils compared

The average root growth of *Hordeum vulgare* ('Optic') seedlings achieved in intact FIELD cores over 48 h was 16.0 ± 0.56 mm, as compared with 48.2 ± 1.1 mm in PACKED cores (Fig. 1). The distribution of the elongation rates between the FIELD core and PACKED core experiments illustrates the significantly slower elongation rate found in the FIELD cores (Fig. 1). The maximum and minimum root elongation achieved in an individual FIELD core set over 48 h was 30·2 mm and 9·8 mm, respectively. Of the FIELD soils tested 94 % had a root growth rate slower than about half of the average root growth achieved for PACKED soils. Further, within the FIELD-cores-only dataset 50 % of the FIELD soils showed a growth rate that was less than half of the maximum growth rate achieved within the FIELD soil-cores experiment. Some of this variation in root elongation was significantly associated with region (REML, $P = 0.035$, $F = 2.84$) but there was no significant association with field management categories and there was no interaction ($P = 0.186$, $F = 1.75$; region × field management, $P = 0.516$, $F = 0.88$). Roots elongated fastest in soil from Aberdeenshire (17.69 ± 0.83 mm), Inverness-shire (16.17 ± 2.89 mm) and Tayside (16.10 ± 0.99 mm). The lowest growth rates were observed in soil from East Lothian (13.56 ± 1.23 mm) and Fife (13.26 ± 1.83 mm).

Figure 2 shows the root elongation in the two experiments against the AFV (-20 kPa; Fig. 2A) and the penetrometer resistance (Fig. 2B). Using all significant data, linear relationships were found between root growth (ln transformed) and both AFV [$P < 0.001$, variance ratio (v.r.) = 876·18, $r^2 = 0.92$; Fig. 2A] and penetrometer resistance ($P < 0.001$, v.r. = 216·31, $r^2 < 0.735$). Figure 2B shows a logarithmic curve fitted to the untransformed root growth penetrometer data ($P < 0.001$, $r^2 = 0.895$). Penetrometer resistance was significantly correlated with the $AFV_{-20 \ kPa}$ ($P < 0.001$,

TABLE 1. *FIELD soil parameter distribution*

Indicator set	Soil parameter	Mean ± s.e.	n	Units	Coefficient of variation	Skewness	Transformation
SS	% C	2·849 ± 0·353		% of dry	84·11	4·52	Complementary log
SS	% N	0·184 ± 0·012	46	mass	44·34	1·455	SQRT
SS	C : N	14·63 ± 0·547		–	25·35	4·582	TriGamma
SS	K	138·7 ± 10·08		mg L^{-1}	48·19	0·923	$\ln(x + 1)$
SS	Mg	136·9 ± 8·896		mg L^{-1}	43·11	0·488	$\ln(x + 1)$
SS	P	41·47 ± 2·525		mg L^{-1}	40·39	1·127	$\ln(x + 1)$
SS	pH	5·684 ± 0·0462	44	log (L mol^{-1})	5·392	0·74	None
SS	% Weight_clay	19·3 ± 1·033		%	35·50	−0·351	None
SS	% Weight_sand	56·41 ± 1·955		%	22·99	0·24	None
SS	% Weight_silt	24·3 ± 1·176		%	32·11	0·554	None
SS, RGE	DBD	1·319 ± 0·0205		g g cm^{-3}	11·97	−0·181	None
SS, RGE	SSInstron$_{-20 \text{ kPa}}$	1·899 ± 0·0789		MPa	31·89	0·43	None
SS	AFV$_{-1 \text{ kPa}}$	0·0332 ± 0·00228		cm^3 cm^{-3}	52·84	1·307	−double log
SS	AFV$_{-5 \text{ kPa}}$	0·127 ± 0·00674		cm^3 cm^{-3}	40·72	0·44	None
SS	AFV$_{-10 \text{ kPa}}$	0·165 ± 0·00755		cm^3 cm^{-3}	35·12	0·337	$\ln(x + 1)$
SS, RGE	AFV$_{-20 \text{ kPa}}$	0·206 ± 0·00766		cm^3 cm^{-3}	28·49	0·374	None
SS	AFV$_{-50 \text{ kPa}}$	0·219 ± 0·0081		cm^3 cm^{-3}	28·44	0·346	None
SS, RGE	VWC$_{sat}$	0·53 ± 0·00652		cm^3 cm^{-3}	9·45	−0·167	None
SS	VWC$_{-1 \text{ kPa}}$	0·496 ± 0·00627		cm^3 cm^{-3}	9·70	−0·161	None
SS	VWC$_{-5 \text{ kPa}}$	0·402 ± 0·00734		cm^3 cm^{-3}	14·03	−0·00546	None
SS	VWC$_{-10 \text{ kPa}}$	0·365 ± 0·00835		cm^3 cm^{-3}	17·60	−0·151	None
SS, RGE	VWC$_{-20 \text{ kPa}}$	0·323 ± 0·00817		cm^3 cm^{-3}	19·41	−0·189	None
SS	WWC$_{-50 \text{ kPa}}$	0·311 ± 0·00825		cm^3 cm^{-3}	20·39	−0·149	None
RGE	Pores$_{>300 \text{ μm}}$	0·0332 ± 0·00228		cm^3 cm^{-3}	52·84	1·307	$\ln(x + 1)$
RGE	Pores$_{60-300 \text{ μm}}$	0·094 ± 0·0057		cm^3 cm^{-3}	46·61	0·504	$\ln(x + 1)$
RGE	Pores$_{30-60 \text{ μm}}$	0·0378 ± 0·00246		cm^3 cm^{-3}	50·04	1·686	$\ln(x + 1)$
RGE	Pores$_{6-30 \text{ μm}}$	0·0537 ± 0·00157	59	cm^3 cm^{-3}	22·50	0·659	None
RGE	Pores$_{<6 \text{ μm}}$	0·311 ± 0·00826		cm^3 cm^{-3}	20·40	−0·149	None
	AFV$_A$	−0·0363 ± 0·00696		cm^3 cm^{-3}	−147·30	−4·164	TAL
	AFV$_B$	3·522 ± 0·118		cm^3 cm^{-3} log kPa^{-1}	25·67	0·643	None
	AFV$_C$	0·264 ± 0·0115		cm^3 cm^{-3}	33·41	1·176	$\ln(x + 1)$
	AFV$_M$	0·662 ± 0·0256		cm^3 cm^{-3}	29·68	−1·569	antilog + 1
	AFV$_{-1500 \text{ kPa-est}}$	0·227 ± 0·00767		cm^3 cm^{-3}	25·92	0·363	None
RGE	VWC$_A$	0·302 ± 0·00777		cm^3 cm^{-3}	19·77	−0·2	None
RGE	VWC$_B$	−3·508 ± 0·118		cm^3 cm^{-3} log kPa^{-1}	−25·82	−0·683	None
RGE	VWC$_C$	0·264 ± 0·0115		cm^3 cm^{-3}	33·55	1·239	−double log (+100)
RGE	VWC$_M$	0·661 ± 0·0257		cm^3 cm^{-3}	29·85	−1·625	−antilog
	VWC$_{-1500 \text{ kPa-est}}$	0·302 ± 0·00778		cm^3 cm^{-3}	19·79	−0·198	None
	VWC$_{AFV10\%}$	0·429 ± 0·00652		cm^3 cm^{-3}	11·65	−0·161	None
	d_10 %$_{AFV}$	0·106 ± 0·00765		cm^3 cm^{-3}	55·28	0·372	None
	d_FC	0·0789 ± 0·00287		cm^3 cm^{-3}	27·95	1·646	−double log (+100)
	PAW$_{vwc}$	0·0211 ± 0·00111		cm^3 cm^{-3}	40·39	0·368	None

The 14 indicators of the 'root growth experiment' set and the indicators used as 'simple set' are shown. Mean, coefficient of variation, skewness and transformation were used for further analysis of complete FIELD core set.

$r^2 = 0.750$). In both cases the predictions made using the FIELD core data underestimates the root growth in the loosely packed cores, compared with the regression curve when all data were included in the line fit. Significant relationships were also found in the FIELD-only data using the same regression analysis, but the percentage of variation was reduced to 61 % and 22 % for air-filled porosity and penetrometer resistance, respectively. VWC explained 63·6 % and DBD explained 53·8 % of the variation in root growth in the combined dataset.

Soil chemical and physical properties in relation to root elongation

PACKED soils. The chemical and physical properties of the PACKED cores are shown in Fig. 3A as a principal components analysis, which allows a large number of variables to be reduced to a smaller number of variables while still
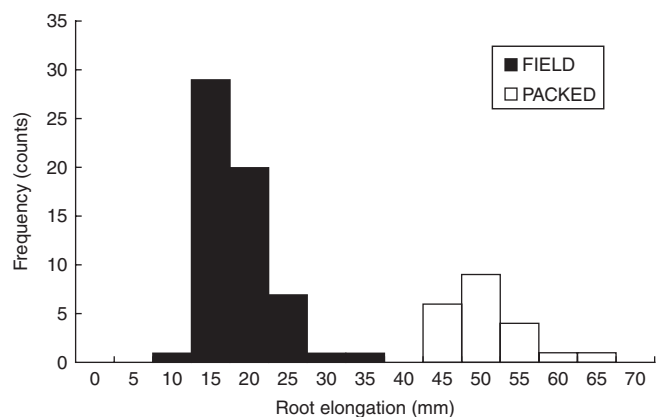

FIG. 1. Relationship between root elongation and soil properties in soil cores, showing distribution of root elongation over 48 h at 15 °C for *Hordeum vulgare* ('Optic') for FIELD and PACKED cores, as indicated.
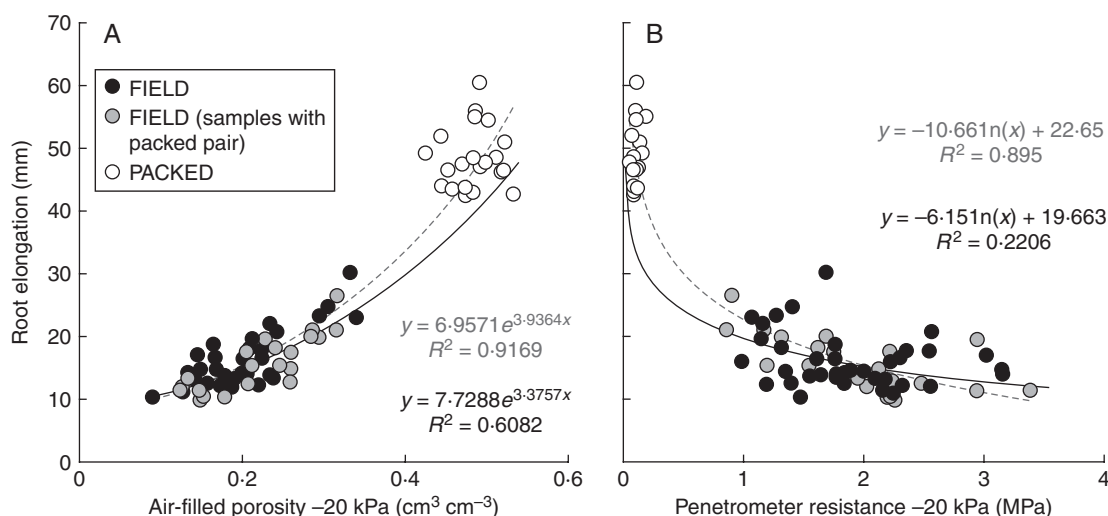
FIG. 2. Root elongation in repacked and field cores. Root growth over 48 h for PACKED and FIELD cores related to (A) air-filled porosity at −20 kPa and (B) penetrometer resistance. Grey dashed line, regression based on all cores; black continuous line, regression based only on FIELD cores (lines forward and backward extended).

capturing the variation in the dataset. Broadly speaking the further along the axis the variables appear on Fig. 3A the larger their contribution to the specific component (Schlens, 2009). Of the variation in the chemical and physical properties, 36 % and 19 %, respectively, were explained by the first two principal components ($PC1_{PACKED}$ and $PC2_{PACKED}$). Soil samples with high values of $PC1_{PACKED}$ tend to have a high percentage of silt (mean 22 ± 1.3 s.e., maximum 32 %) and clay (mean 18 ± 1.6 s.e., maximum 31 %), whereas samples with low $PC1_{PACKED}$ tend to have a high percentage of sand (mean 59 ± 2.7, maximum 84 %). High $PC2_{PACKED}$ values were associated with high pore volume (mean 0.662 ± 0.005 cm^3 cm^{-3}, maximum 0.704), low DBD (minimum 1.04 g cm^{-3}, maximum 1.09 g cm^{-3}) and low C : N ratio (minimum 12.2, maximum 36.2). No significant relationship was found between root growth and either principal component ($P = 0.234$, v.r. $= 1.52$ and $P = 0.789$, v.r. $= 0.07$, $PC1_{PACKED}$ and $PC2_{PACKED}$, respectively; Fig. 3B, $PC1_{PACKED}$). Further, there was no significant relationship between any of the individual soil indicators and the root growth rate ($P > 0.05$) within the PACKED soil. To assess whether any combination of the indicators could explain a significant proportion of the root growth rate in the PACKED soil, all-subsets regression was used. Two models chosen on the basis of the AIC value and the significance of the model indicators (all indicators $P < 0.05$, % clay + ln(K); Fig. 3C) and % sand + ln(K) explained 29 % and 28 % ($P = 0.020$, v.r. $= 4.95$, $P = 0.023$, v.r. $= 4.77$) of the variation in root elongation, respectively.

FIELD soils. Since a large proportion of the variation in root elongation between the two experiments could be explained by differences in soil physical properties, we explored further whether these properties could explain the variation in root growth within the FIELD soils. Forty-two indicators were measured or calculated. Table 1 shows the mean, standard error of mean, coefficient of variance and skewness of these indicators. The soils presented significant variation in many of the individual physical indicators. Initial assessment

showed that at the matric potential (−20 kPa) used for the root elongation assay, the mean AFV was 0.206 ± 0.008 cm^3 cm^{-3}. Moreover, 50 % of cores had an AFV of <28 %, and 1.7 % of the FIELD cores had an AFV of <10 %, suggesting that between 50 % and 1.7 % of the FIELD soil cores potentially presented an oxygen-limited environment. Further, 26 out of the 59 fields, had a penetrometer resistance above 2 MPa (average 1.899 ± 0.079 MPa at −20 kPa) suggesting that 44 % of the fields contained soil that would cause substantial impedance to root growth due to the strength of the soil, even though the soil was relatively wet. As matric potential was maintained at −20 kPa, water availability would not be expected to be limiting during the root growth experiments.

Regression analyses of each individual soil parameter and root growth are summarized in Fig. 4. The highest percentage of variation in root elongation was accounted for by: (1) air-filled volumes ($AFV_{-5 kPa}$ 65.7 %, $AFV_{-10 kPa}$, 59.6 %, $AFV_{-20 kPa}$ 60.3 %, $AFV_{-50 kPa}$ 60.7 %); (2) 60–300 μm pore volume ($Pores_{60-300 μm}$ 61.1 %); (3) AFV estimated at −1500 kPa (using the AFV against matric potential curve fit values – $AFV_{-1500 kPa\_est}$ 60.7 %); and (4) the volume of water required to reduce the AFV to 10 % (d_10 %AFV 60.2 %). Figure 4 illustrates where, based on the effect from the regression analysis, the average values for soil obtained from the five regions would predict a positive or negative effect on root growth [low root growth predicted (red) and high root growth predicted (green)]. In tabular form Fig. 4 illustrates that in some soil, e.g. from Inverness-shire, some indicators (e.g DBD and SS_{PR}) indicate a constraint on root growth, whereas other indicators such as the $AFV_{-20 kPa}$ indicate a strong positive effect on root growth. The highest ranking four individual parameter relations based on an all-subsets comparison are illustrated in Fig. 5A ($AFV_{-5 kPa}$, $AFV_{-20 kPa}$, $AFV_{-50 kPa}$ and $Pores_{60-300 μm}$).

A significant but relatively low correlation between the soil strength and the root growth was found in the FIELD cores
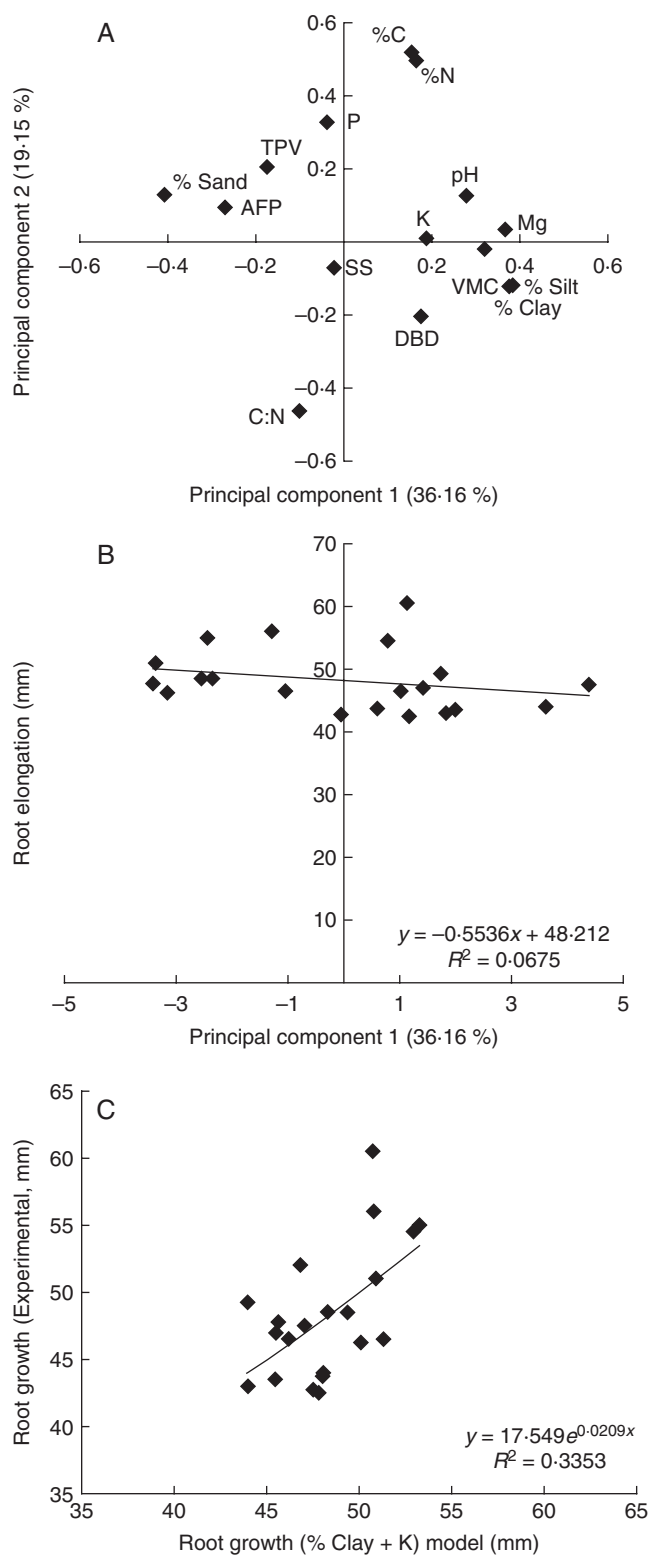
FIG. 3. Relationship between root elongation over 48 h for *Hordeum vulgare* ('Optic') and soil properties in repacked soil cores, showing (A) latent roots of principal component analysis of soil physical and chemical indicators; (B) regression analysis of root elongation against component 1 (scores) of the principal components analysis ($P = 0.234$); and (C) predictions of root elongation from the highest-ranked all-subsets regression model.

($P < 0.001$, v.r. $= 12.55$), this relationship was not significant for penetration resistance when the effect of AFV$_{-20 kPa}$ or the effect of pores (60–300 µm) was taken into account, despite many of the cores recording a penetrometer resistance above 2 MPa (FIELD cores). Figure 5(B, C) illustrates the relationships between penetrometer resistance and AFV$_{-20 kPa}$ or volume of pores with diameter 60–300 µm (Pores$_{60-300µm}$) and root elongation (bubble size). It can be seen that even at relatively low penetrometer resistance (<1.5 MPa) there is a significant variation in the root elongation rate. We then looked at the moderating effect of pores (60–300 µm) and air-filled porosity (AFP) on root elongation after the effect of soil strength had been taken into account. Figure 5D shows each plotted against the residual of the regression analysis of soil strength against root elongation ($P < 0.001$, $r^2 = 0.401$, AFP$_{-20 kPa}$), illustrating that those roots with a higher than expected root growth tend to have larger values of Pores$_{60-300 µm}$ or higher AFP$_{-20 kPa.}$

The subset of data that included all the texture and chemical indicators was used to compare multiple parameter models of indicators using all-subsets regression. Models were compared based on their Adjusted R^2 value, the AIC value and the level of significance of each of the individual indicators in the model. Initially an all-subsets regression was performed using a subset of 14 indicators thought to most likely describe the physical indicators to which the roots would be exposed during the root growth experiment (AFV$_{-20 kPa}$, VWC$_{sat}$, DBD, VWC$_{-20 kPa}$, soil strength, Pores$_{>300 µm}$, Pores$_{60-300 µm}$, Pores$_{30-60µm}$, Pores$_{6-30µm}$, Pores$_{<6 µm}$, VWC$_A$, VWC$_B$, VWC$_C$ and VWC$_M$). The highest ranking model is shown in Table 2 (73.6 %, v.r. $= 33.31$, $P < 0.001$; DBD, $P < 0.001$; VWC$_{-20 kPa}$, $P < 0.001$; Pores$_{60-300 µm}$, $P < 0.001$; VWC$_B$, $P = 0.003$; VWC$_M$, $P = 0.003$) Other high-ranking models with AIC values within two of the illustrated models included AFV$_{-20 kPa}$, Pores$_{<6 µm}$, VWC$_{sat}$ and VWC$_A$. All high-ranking models included the parameter Pores$_{60-300 µm}$. Two other groups of indicators were assessed, 23 'simple' indicators (see Table 1) or all 42 indicators. The highest ranking models are shown in Table 2, accounting for >70.0 % of the variation in the root elongation in the subset of data and 69.4 % when applied to the data from all 59 fields.

Variation in soil physical and chemical properties

Principle component analysis was used to summarize the variation and condense the number of variables in soil physical and chemical parameter data (Fig. 6), a subset of 42 fields was used for this analysis. The first and second principal components accounted for 47.21 % and 22.11 % of the variation in the soil physical data. Soils with a more negative principal component 1 (PCA1) value tended to have greater VWC whereas those with a more positive PCA1 values tend to be associated with larger than average AFV at each of the matric potentials tested, irrespective of the DBD (Fig. 6A, loadings; B, scores). More negative principal component 2 (PCA2) values were associated with high DBD as opposed to more positive values which were associated with high VWC at saturation and −1 kPa matric potential. Principal component analysis of the chemical data are shown in Fig. 6

	Regression analysis: relationship between parameter values and root growth				Average parameter values for regional groups									
	Relationship to root growth	v.r.	t (42–57)	P	% of root growth variation	Fife		Edinburgh		Tayside		Inverness		Aberdeen	
RG_Growth						13·26	±0·97	13·56	±0·92	16·1	±1·03	16·17	±1·34	17·69	±0·95
AFV_{-5kPa}	P	112·1	10·59	<0·001	65·7	0·09	±0·02	0·1	±0·02	0·14	±0·01	0·11	±0·01	0·14	±0·01
$Pores_{60-300\mu m}$	P	92·13	9·6	<0·001	61·1	0·07	±0·02	0·06	±0·01	0·11	±0·01	0·09	±0	0·1	±0·01
AFV_{-50kPa}	P	90·73	9·53	<0·001	60·7	0·18	±0·03	0·17	±0·02	0·24	±0·01	0·25	±0·03	0·23	±0·01
$AFV_{-1500kPa-est}$	P	90·51	9·51	<0·001	60·7	0·19	±0·02	0·18	±0·02	0·24	±0·01	0·26	±0·03	0·24	±0·01
AFV_{-20kPa}	P	89·03	9·44	<0·001	60·3	0·17	±0·02	0·17	±0·02	0·22	±0·01	0·23	±0·03	0·22	±0·01
d_10% AFV	P	88·83	9·42	<0·001	60·2	0·07	±0·02	0·07	±0·02	0·12	±0·01	0·13	±0·03	0·12	±0·01
AFV_{-10kPa}	P	86·4	9·3	<0·001	59·6	0·13	±0·02	0·13	±0·02	0·18	±0·01	0·18	±0·02	0·18	±0·01
VWC_C	P	55·93	7·48	<0·001	48·6	0·2	±0·02	0·21	±0·03	0·28	±0·02	0·27	±0·02	0·29	±0·02
AFV_C	P	52·05	7·21	<0·001	46·8	0·2	±0·02	0·21	±0·03	0·28	±0·02	0·27	±0·02	0·29	±0·02
AFV_{-1kPa}	P	14·04	3·75	<0·001	18·4	0·02	±0	0·04	±0·01	0·03	±0·01	0·02	±0	0·04	±0
$Pores_{>300\mu m}$	P	13·88	3·73	<0·001	18·2	0·02	±0	0·04	±0·01	0·03	±0·01	0·02	±0	0·04	±0
VWCS	P	11·23	3·35	0·001	15	0·49	±0·02	0·48	±0·01	0·53	±0·01	0·49	±0·02	0·56	±0·01
$VWC_{AFV10\%}$	P	11·22	3·35	0·001	15	0·39	±0·02	0·38	±0·01	0·43	±0·01	0·39	±0·02	0·46	±0·01
$Pores_{6-30\mu m}$	P	5·43	2·33	0·023	7·1	0·05	±0	0·04	±0	0·06	±0	0·07	±0·01	0·05	±0
%Weight_Sand	P	4·35	2·09	0·043	7·2	52·8	±4·66	50·82	±2·57	56·88	±2·55	71·5	±5·5	61	±6·65
VWC_{-1kPa}	P	4·24	2·06	0·044	5·3	0·47	±0·02	0·44	±0·01	0·5	±0·01	0·47	±0·03	0·53	±0·01
P	ns	2·37	1·54	0·131	3·1	33·48	±4·05	37·42	±5·98	44·87	±3·57	58	±22·6	40·76	±5·35
%N	ns	1·82	1·35	0·184	1·8	0·18	±0·03	0·15	±0·02	0·19	±0·02	0·13	±0	0·22	±0·03
d_FC	ns	1·6	1·26	0·212	1	0·09	±0·01	0·07	±0	0·08	±0	0·12	±0·03	0·08	±0
AFV_B	ns	1·42	1·19	0·238	0·7	3·97	±0·37	3·31	±0·22	3·71	±0·19	4·25	±0·76	3·33	±0·21
%C	ns	0·94	0·97	0·337	Res > Res	2·54	±0·37	2·04	±0·26	3·32	±0·99	1·89	±0·11	3·25	±0·42
$Pores_{30-60\mu m}$	ns	0·79	0·89	0·377	Res > Res	0·04	±0·01	0·03	±0	0·04	±0	0·07	±0·02	0·03	±0
$PAW_{VWC-est}$	ns	0·03	0·19	0·853	Res > Res	0·02	±0	0·02	±0	0·02	±0	0·03	±0	0·02	±0
C:N	ns	0·05	−0·23	0·816	Res > Res	13·78	±0·29	13·66	±0·38	15·32	±1·61	14·05	±0·29	15·08	±0·45
%Weight_Silt	ns	0·41	−0·64	0·526	Res > Res	25·2	±2·75	24·82	±1·78	24·18	±1·61	17·5	±1·5	24·89	±4·25
pH	ns	0·85	−0·92	0·362	Res > Res	5·72	±0·07	5·81	±0·13	5·66	±0·07	5·45	±0·05	5·61	±0·07
VWC_B	ns	1·39	−1·18	0·244	0·7	−3·94	±0·38	−3·31	±0·23	−3·68	±0·19	−4·27	±0·74	−3·32	±0·21
PD	ns	3·1	−1·76	0·084	3·5	2·92	±0·04	2·63	±0·01	2·97	±0·05	2·91	±0·08	2·74	±0·04
Mg	N	4·73	−2·17	0·035	8	183·6	±28·46	141·36	±13·47	154·94	±14·89	102·5	±18·5	79	±6·84
K	N	5·71	−2·39	0·021	9·9	125·2	±18·24	150·64	±16·42	163·18	±18·46	120·5	±42·5	89·56	±18·47
AFV_A	N	8·61	−2·93	0·005	11·6	−0·01	±0	−0·03	±0·01	−0·03	±0·01	−0·01	±0·01	−0·05	±0·01
VWC_{-10kPa}	N	10·1	−3·18	0·002	13·6	0·36	±0·02	0·35	±0·02	0·35	±0·01	0·31	±0·01	0·39	±0·02
VWC_{-5kPa}	N	10·16	−3·19	0·002	13·6	0·4	±0·02	0·38	±0·02	0·39	±0·01	0·38	±0·03	0·42	±0·01
VWC_{-20kPa}	N	11·39	−3·38	0·001	15·2	0·32	±0·02	0·31	±0·02	0·31	±0·02	0·26	±0	0·35	±0·02
%Weight_Clay	N	11·78	−3·43	0·001	20	22	±2·1	24·36	±1·66	18·94	±1·17	11	±4	14·11	±2·69
$SS_{Instron-20kPa}$	N	12·55	−3·54	<0·001	16·6	1·78	±0·18	2·07	±0·22	2·01	±0·18	2·17	±0·05	1·74	±0·09
$VWC_{-1500kPa-est}$	N	13·06	−3·61	<0·001	17·2	0·3	±0·02	0·3	±0·02	0·28	±0·01	0·24	±0	0·32	±0·01
VWC_A	N	13·09	−3·62	<0·001	17·2	0·3	±0·02	0·3	±0·02	0·28	±0·01	0·24	±0	0·32	±0·01
VWC_M	N	14·21	−3·77	<0·001	18·5	0·82	±0·04	0·68	±0·07	0·68	±0·03	0·81	±0·08	0·59	±0·04
$Pores_{<6\mu m}$	N	14·35	−3·79	<0·001	18·7	0·31	±0·02	0·31	±0·02	0·29	±0·01	0·24	±0·01	0·33	±0·02
VWC_{-50kPa}	N	14·44	−3·8	<0·001	18·8	0·31	±0·02	0·31	±0·02	0·29	±0·01	0·24	±0·01	0·33	±0·02
AFV_M	N	16·21	−4·03	<0·001	20·8	0·82	±0·04	0·68	±0·07	0·68	±0·03	0·81	±0·08	0·6	±0·04
DBD	N	18·17	−4·26	<0·001	22·8	1·49	±0·06	1·37	±0·03	1·4	±0·03	1·47	±0·03	1·19	±0·03

F<small>IG</small>. 4. Linear regression of each soil parameter against root elongation in intact (FIELD) cores (mean ± s.e. of each indicator based on regional groupings). P indicates a significant positive correlation with root elongation, N indicates a significant negative correlation with root elongation; ns indicates no significant relationship; v.r. = variance ratio. Res > Res indicates residual variance exceeds variance of response variate. Also shown are mean soil physical indicators for Regions. Colour coding: green, parameter value indicates enhanced root elongation; red; parameter value indicates reduced root elongation. Shading indicates the strength of the response.
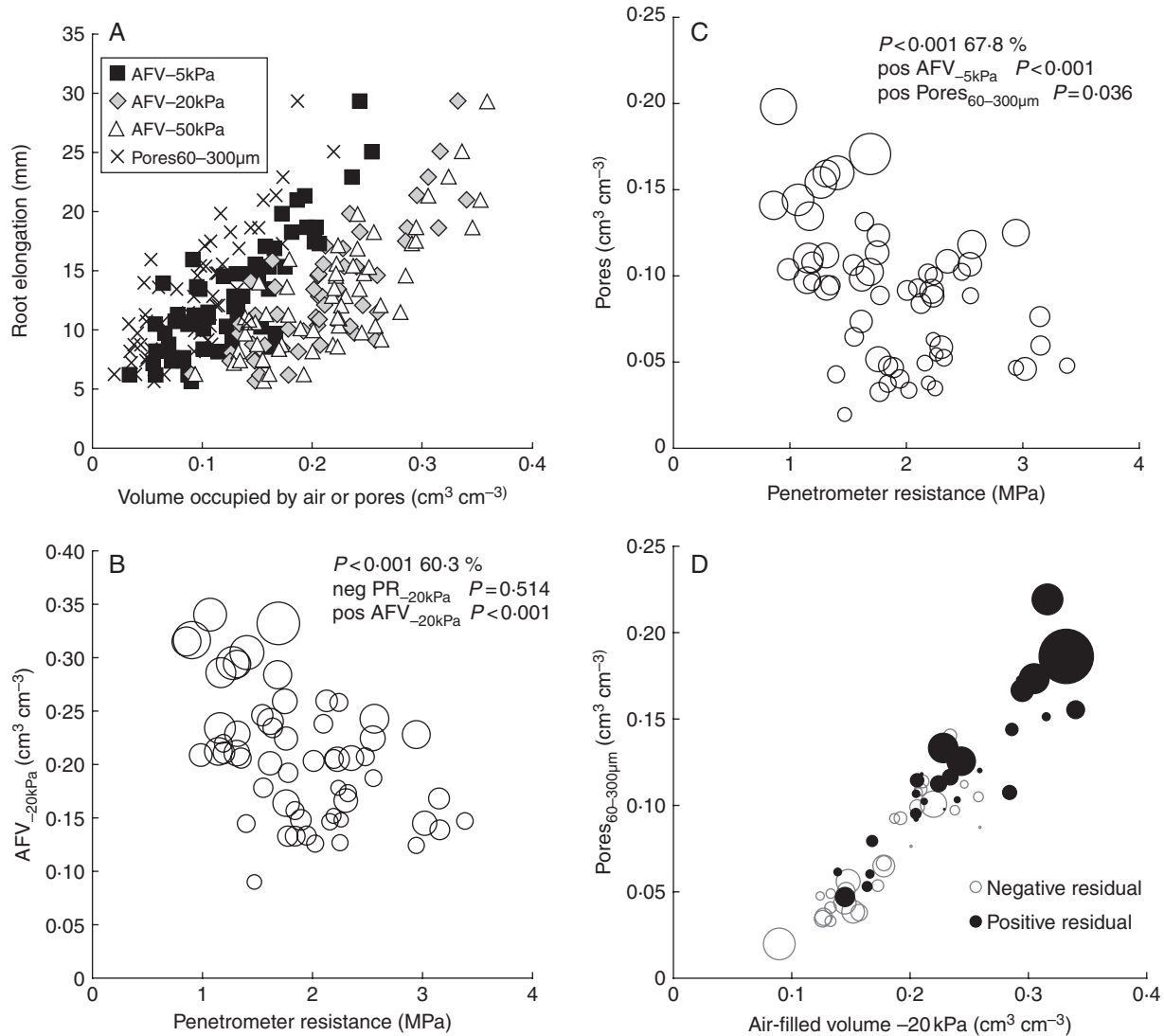
FIG. 5. Regression analysis of root elongation against soil physical indicators: (A) highest ranking individual parameter models; (B, C) dual parameter models in which the size of the circles is proportional to root elongation [B, penetrometer resistance against $AFV_{-20\,kPa}$; C, penetrometer resistance against volume of pores with diameter $60–300\ \mu m$ ($Pores_{60–300\ \mu m}$)]; (D) relationship between root growth after soil strength has been accounted for, and volume of pores with diameter $60–300\ \mu m$ ($Pores_{60–300\ \mu m}$) and $AFV_{-20\,kPa}$ (circles: size equals residual of the regression of root growth against penetrometer resistance; closed, positive residuals; open, negative residuals).

(E, loadings; D, scores). $PC1_{chem}$ (36·05 %) separated soils mainly on C and N variation, whereas $PC2_{chem}$ (26·23 %) separated mainly on the nutrient concentration.

Regression analysis of root elongation against the principal components of the physical properties of the soil cores produced significant correlations (Fig. 6C). The first principal component of the soil physical indicators accounted for 60·8 % of the variation in root elongation (PCA1, $P < 0.001$, v.r. = 64·52, Fig. 6C; PCA2, n.s. 1·4 %, $P = 0.218$, v.r. = 1·57, data not shown). PCA1 and PCA2 combined to account for 62·9 % of the variation ($P < 0.001$, v.r. = 24·18). Neither of the two principal components based on the chemistry of the soils significantly predicted the root elongation rate ($PC1_{chem}$, n.s. 1·3 %, $P = 0.220$, v.r. = 1·55, data not shown; $PC2_{chem}$, n.s. 6·6 %, $P = 0.056$, v.r. = 0·056; Fig. 6F). However $PC1_{chem}$ and $PC2_{chem}$ combined to accounted

for 20·6 % of the variation in root elongation ($P = 0.008$, v.r. = 4·54)

DISCUSSION

It is recognized that an essential element in agricultural systems necessary to maintain and potentially increase crop yields is the ability of crop roots to extend and extract vital nutrients and water throughout the soil profile (Cooper *et al.*, 1987; Stalham and Allen, 2001; Gewin, 2010). Future crop varieties, able to perform well under a range of adverse conditions, may require a larger or differently arranged root system, and be more physiologically efficient for both nutrient and water utilization (Ceccarelli, 1996; Palta *et al.*, 2011). Any soil property that inhibits a plant from elongating and proliferating its roots into the most efficient spatial arrangement to

TABLE 2. *Models generated by all-subsets regression using three different subsets of indicators: values are the probability (P) for each of the parameters from a multiple regression including all parameters with P values against the root elongation rates (a value of 0 means the P value is <0.001)*

	% of root elongation accounted for	DBD	Pores 60–300 μm	Pores <6 μm	AFV_ 10 kPa	AFV_ 20 kPa	AFV_B	AFV_M	VWC_S	VWC_ 1 kPa	VWC_ 5 kPa	VWC_ 10kPa	VWC_ 20 kPa	VWC_ 50 kPa	VWC_A	VWC_B	VWC_M	PAW_vwc-est
Root	73·6	0	0	–									0		–	0	0	–
elongation	73·6	0	0	0		–							–		0	0	0	–
experiment	73·5	0	0	–		0							–		0	0	0	–
	73·2	0	0	–		0·01							–		–	0	0	–
Basic 23	72·9	0·02			0				0	0	0	0	0·05	0·01				
indicators*	72·4	0·03			0·01	0·01			0	–	0·001	0·01	0	0·01				
All	74	0·001	–					0	0	0	0				0·001	0·001	–	–
indicators	73·7	0·001	0					0	0	–	0·001				0·001	0·001	–	–
	73·7	0	–					–		0·001	0				0·001	0·001	0	–
	73·5	0·001	0				0·001	0		–	–				0·001	0·001	–	–
	73·6	0·001	–				0·001	–		–	0				–	–	0	–
	73·2	0	0					–		0	0				0·001	–	0	–
	74·8	0	–					–			0				–	–	–	0·001
	73·2	0·001	0				0·001	0		–	0·001				–	–	–	–

Values within the table in *italics* show that the indicator is having a positive effect in the model, whilst values in **bold** show that it is having a negative effect. Italics and bold in the column headings shows the effect of the indicator in the single regression model. For information on indicators included in the root-elongation experiment group see Materials and Methods and Table 1.
* The basic 23 indicator group is listed in Table 1.

extract water and nutrients from the soil may have a profound detrimental effect on plant productivity. The simplified, *ex situ* soil test used here was sensitive enough to demonstrate significant variation in root elongation and associate it with soil physical properties indicative of the state of the field.

Effect of soil strength and soil porosity on root elongation

The average root elongation rate in the FIELD soils was only one-third of that in the PACKED soils, indicating that the physical structure of the soil was a major limit to root extension in the field soils. The relatively fast root elongation rates in the PACKED soils, with relatively little variation, suggests that soil physical conditions in the FIELD soils represented a far greater limitation to seedling root elongation than chemical and biological factors. Given that the matric potential of the soil when tested was relatively wet (-20 kPa), it is likely that soil physical limitations may be even greater than this *in situ* for much of the growing season, since penetration resistance increases as soil dries (Taylor and Ratliff, 1969; Bengough *et al.*, 2011). While biological factors were not measured in the FIELD cores, aspects of the variation in biological factors in the sieved soil samples will be discussed in separate publications.

Root elongation was correlated with both the volume of large pores (60–300 μm), and with penetrometer resistance. The strong correlation between the root elongation rate and the volume of large pores (air-filled at -20 kPa matric potential) could have two explanations: (1) that roots are taking advantage of the low-resistance channels presented by the larger soil pores to avoid mechanical impedance due to the strength of the bulk soil; or (2) that root elongation is directly limited by hypoxia (or some combination of hypoxia and soil strength) if the rate of oxygen diffusion to the root surface is too slow. Initially we shall consider the evidence for the first of these explanations (a primarily soil structure–strength effect), and then possible evidence for the second (hypoxia).

Root elongation, soil strength and macroporosity. The relationship between root elongation rate and penetrometer resistance across the PACKED and FIELD soils is reasonably consistent with published data for peanut, cotton (Taylor and Ratliff, 1969) and maize roots (Mirreh and Ketcheso, 1973; Veen and Boone, 1990) although Fig. 2 suggests a relatively reduced rate of decline in elongation rate between 1- and 3-MPa penetrometer resistance than is apparent in other data. This shallower decline may be associated with the presence of continuous pores within the field soils that permit root growth to continue even in soils where the bulk matrix (as measured by penetrometer resistance) is relatively hard. Roots can exploit cracks and pores within the soil that have relatively little effect on the resistance to a penetrometer that is confined to move in a straight line (McKenzie *et al.*, 2009). Indeed, the spatial variation in penetrometer resistance is greater for field soils than packed cores (Perfect *et al.*, 1990). For instance, the field penetrometer resistance that limits oat root growth was found to be 4·6–5·1 MPa in untilled soil layers, as compared with 3·6 MPa for tilled topsoils (Ehlers *et al.*, 1983) due to roots exploiting a network of continuous biopores in the untilled soil. Such pore networks enable
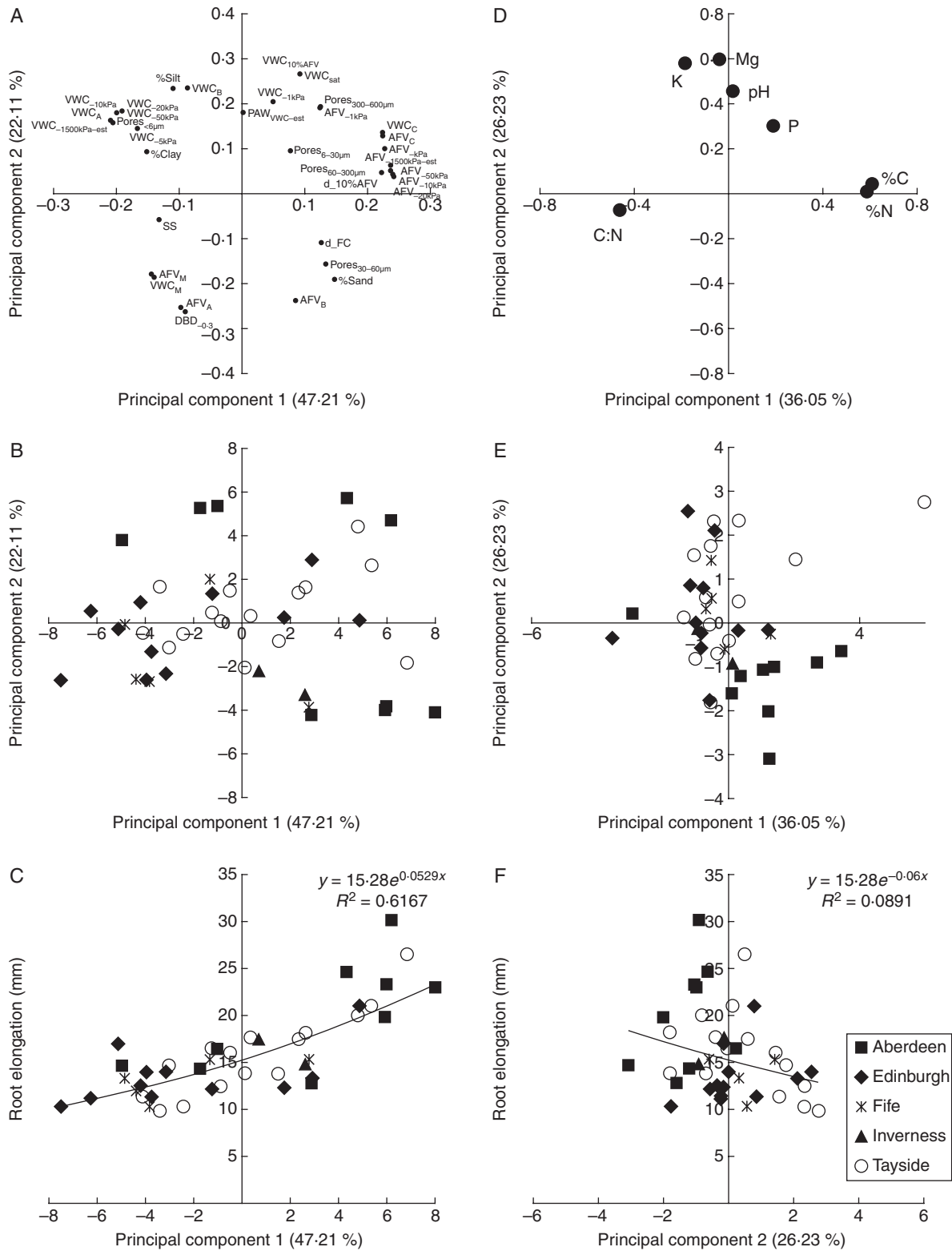
FIG. 6. Principal component analysis of soil physical and chemical indicators of intact field cores from 42 agricultural fields: (A–C) physical; (D–F) chemical; (A, D) loadings of the PCA; (B, E) scores of the PCA for individual fields coded by the field region groups; (C, F) regression analysis of root elongation of *Hordeum vulgare* ('Optic'), in cores against component 1 from physical and component 2 from chemical PCA, respectively.

roots to penetrate to depth in very hard Australian sub-soils, where wheat root growth is confined almost entirely to biopores (White and Kirkegaard, 2010).

Further, a significant correlation has been found between soil strength and root-penetration resistance in field soil cores, but with greater variation between root- and probe-penetration resistances in intact soil cores than in packed soil cores (Bengough and Mullins, 1991): in one such instance, root-penetration resistance was only one-quarter of that expected from the penetrometer measurement, due to the presence of a crack. In the current experiment, only one penetrometer resistance measurement was made per soil core (<15 mm distance, with surface 0–4·5 mm readings omitted) – additional penetrometer measurements, to greater depths and at multiple spatial locations, may have further improved correlations with root elongation by better characterizing the soil strength.

Root elongation and hypoxia. It is important to consider whether hypoxia could be limiting root elongation rates in many of these soils, giving rise to the slower elongation rates measured. Previous approaches to consider aeration as a limit to root growth have often taken a figure of <10 % air-filled porosity to indicate possible hypoxia (Grable and Siemer, 1968; Letey, 1985; daSilva *et al.*, 1994). Oxygen limitation has, however, been suggested to limit pea root elongation at up to 28 % AFV in sand (Eavis, 1972*b*; Warnaars and Eavis, 1972), although peas are relatively sensitive to waterlogging stress. Within the FIELD cores, after the effect of soil strength had been taken into account, only soil cores with values of AFV <26 % were found to have negative residuals, suggesting a possible extra impact of oxygen deficiency in these cores (though 54 % of cores had air-filled porosities <26 %). However, there were still many examples where root elongation was still faster than would be expected (positive residuals) down to 13·9 % AFV. The data are therefore inconclusive on the importance of hypoxia, although the balance of the literature would suggest that for barley roots growing near the surface of soil cores with air-filled porosities >10 %, hypoxia would not normally be the primary constraint to root elongation.

Seedling root elongation as an assay

The method of *ex situ* root extension described in this paper offers a potential indicator of the biophysical condition of agricultural soil. Root extension varied between soils over a 4-fold range, and was primarily correlated with soil physical conditions. By incorporating a control treatment with sieved repacked soil, it is possible to isolate soil physical effects from biological and chemical factors that survive the sieving process.

While being successful in these tests, the assay should be used with consideration. To describe fully the potential variation in root elongation rate under field conditions, measurements for the full range of representative matric potentials will always be required, since physical limitations such as hypoxia in wetter soil or mechanical impedance and water stress in drier soil are likely to play an even more important limiting role in the field. Another factor that needs to be accounted for is the quantity of nutrients already present in the plants when the assay begins. Early seminal root development in barley under non-inhibiting conditions is supported by the initial energy and nutrients stored in the grain, and this may reduce sensitivity to nutrient limitations in the soil tested.

More generally, the assay should be valuable in comparing the genetic variation in root elongation responses to soil physical limitations. The seminal root of barley ('Optic') was chosen for this study because it is one of the most commonly grown malting varieties in northern UK. This cultivar has a mean diameter of seminal root of 0·605 ± 0·03 mm when grown in the gel system base (Bengough *et al.*, 2004). Its diameter is typical of other varieties, e.g. when compared with 23 other cultivars and mutants it appeared in position 10 within the range of lines tested (T. A. Valentine *et al.*, unpubl. res.). Variation in root diameter may impact on a roots ability to push through hard soil (Materechera *et al.*, 1992) or change the range of pores that are accessible for root elongation (i.e. narrower seminal roots or lateral roots may have access to smaller diameter pores). There is also evidence from McKenzie *et al.* (2009) that some varieties are better able to penetrate and proliferate into subsoil when pore options are limited. Therefore an understanding of the range of responses to soil physical properties among varieties and species may identify bespoke phenotypes for particular soil physical constraints.

Although the aim of the paper was not primarily to compare regions and farming preferences, regions differed significantly in terms of the indicator. Moreover, root elongation and the soil physical conditions ranged widely among fields within a region or within a farm management system. We know the method of cultivation can have major effects on soil structure and can affect crop establishment (Atkinson *et al.*, 2009*a*, *b*). The extent to which such differences between fields are related to agronomic factors such as crop sequence, inputs and tillage will be examined in a further paper.

In summary, there is significant evidence that root elongation is being severely inhibited in many of the agricultural soils tested. Different regions and fields are constraining root elongation as a result of soil strength and oxygen deficiency. In some fields, however these constraints are being partially mitigated by the availability of macropores that are accessible to the roots and enabling root elongation. Soil physical constraints are likely to be more severe deeper in the soil profile due to presence of compacted subsoils. Thus, there is much scope to improve root penetration of soil by identifying cultivars and root traits better suited to these conditions, in partnership with improvements in the management of soil.

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