Root length densities of UK wheat and oilseed rape crops with implications for water capture and yield

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Abstract

Root length density (RLD) was measured to 1 m depth for 17 commercial crops of winter wheat (Triticum aestivum) and 40 crops of winter oilseed rape [Brassica napus; oilseed rape (OSR)] grown in the UK between 2004 and 2013. Taking the critical RLD (cRLD) for water capture as 1 cm cm⁻³, RLDs appeared inadequate for full water capture on average below a depth of 0.32 m for winter wheat and below 0.45 m for OSR. These depths compare unfavourably (for wheat) with average depths of ‘full capture’ of 0.86 m and 0.48 m, respectively, determined for three wheat crops and one OSR crop studied in the 1970s and 1980s, and treated as references here. A simple model of water uptake and yield indicated that these shortfalls in wheat and OSR rooting compared with the reference data might be associated with shortfalls of up to 3.5 t ha⁻¹ and 1.2 t ha⁻¹, respectively, in grain yields under water-limited conditions, as increasingly occur through climate change. Coupled with decreased summer rainfall, poor rooting of modern arable crops could explain much of the yield stagnation that has been observed on UK farms since the 1990s. Methods of monitoring and improving rooting under commercial conditions are reviewed and discussed.

Key words: Drought, oilseed rape, roots, root length density, wheat, yield stagnation.

Introduction

It has been estimated that crop yields should be increasing by 2.4% per year to meet demand by 2050 (Ray et al., 2013). Estimates of current increases in yield are well below this figure, for example global wheat (Triticum aestivum) yields are increasing at 0.9% per year (Ray et al., 2013). In the UK, on-farm wheat yields have been static since 1996, despite a 0.05 t ha⁻¹ increase per year in the potential of new varieties (Clarke et al., 2012). Knight et al. (2012) reported that oilseed rape (OSR; Brassica napus) yields on UK farms fell by 0.04 t ha⁻¹ per year between 1984 and 1994, but that yields have been increasing by 0.075 t ha⁻¹ per year since 2004. This recent improvement is in part attributable to improved uptake of new OSR varieties by growers on-farm (Knight et al., 2012). Analyses in several countries have been unable to account fully for cereal yield stagnation (Brisson et al., 2010; Petersen et al., 2010), but have commonly suggested that the combination of changing climates and deteriorating soil conditions may be the primary cause.

Plant roots are crucial for water and nutrient uptake and as such influence yield. Several studies have correlated rooting depth with water extraction and root activity (Gregory et al., 1978a). In the UK, the maximum rooting depth of winter
cereals, often reported to be ~2 m, is generally achieved by anthesis (Böhm, 1978; Gregory et al., 1978b; Gales, 1983; Lucas et al., 2000). Root length density (RLD) of field-grown wheat crops has been reported to range between 5.6 cm cm$^{-3}$ and 10 cm cm$^{-3}$ in the top 20 cm of soil and between 0.4 cm cm$^{-3}$ and 1.5 cm cm$^{-3}$ in the 80–100 cm soil horizon when measured at or after anthesis (Gregory et al., 1978b; Barraclough et al., 1989, 1991). More recently, Pillinger et al. (2005) reported RLDs of 7 cm cm$^{-3}$ in the topsoil and 0.2 in the 80–100 cm soil horizon. Hoad et al. (2004) found that RLDs in the plough layer ranged between 3 cm cm$^{-3}$ and 6 cm cm$^{-3}$, but were <1 cm cm$^{-3}$ below 0.4 m depth. In Australia, Atta et al. (2013) found RLDs of 15 wheat genotypes to range between 0.6 cm cm$^{-3}$ and 2 cm cm$^{-3}$ in the top 15 cm of soil. There are limited data available on rooting in OSR. Barraclough et al. (1989) reported OSR reaching depths of at least 1.8 m and found average RLDs of ~8 cm cm$^{-3}$ in the top 20 cm of soil with 0.35 cm cm$^{-3}$ at 60–180 cm. RLD is an important plant trait that changes with water availability; when water is not limiting, RLD can increase in the topsoil, but during long dry periods it can increase deeper in the soil profile (Blum, 2005).

Crop yields in the UK currently tend to be light limited (Foulkes et al., 2001; Beed et al., 2007), but, as yield potentials are improved, for example through prolonging growth or increasing growth rate, crop water demand is likely to increase. As a consequence, water supply and/or capture will probably limit an increasing proportion of crops in the UK unless water capture and/or conversion to dry matter can also be improved. Analysis of factors affecting wheat yields in UK variety trials (Knight et al., 2012) suggested that spring or summer droughts have had an impact on wheat performance; however, it is not clear to what extent inadequate rooting contributes to this.

Climate change is increasing seasonality and intensity of rainfall in the UK; there is more frequent winter flooding and the south and south-west regions have experienced more frequent droughts and water stress (Jenkins et al., 2008). Many climate change models predict further reductions in summer rainfall and increased soil moisture deficits for many UK cropping regions (Knox et al., 2010; Dodd et al., 2011). It has been estimated that 30% of the UK wheat area is planted on drought-prone land, resulting in a 10% loss of potential production annually (Foulkes et al., 2001, 2007). It is expected that these kinds of losses will increase due both to an increase in crop demand for water as yields increase and to the effects of climate change.

Measurement difficulties have been a major factor contributing to the relatively small amount of data available on crop roots, methods generally being time consuming and destructive. Early and detailed work carried out by Weaver in the 1920s involved careful excavation of the soil around the roots and of drawing the root system (Weaver, 2006). Excavation techniques were adapted further by Schuurman and Goedewaagen (1964), Goederam (1969), and Bloomberg (1974), and various further in-field methods are available (Smit et al., 2000) including counting roots in soil pits (Hoad et al., 2004); using radioisotopes, in which a detectable isotope is placed at a particular soil depth and the plant shoots monitored for isotope uptake (Hall et al., 1953; Bassett et al., 1970; Ellis and Barnes, 1973); and mini-rhizotrons (Johnson et al., 2001; Metcalfe et al., 2007). However, with some mechanization (Wasson et al., 2012), soil coring coupled with root assessment after separation by washing is probably regarded as the most reliable measure of root systems in the field, even though this technique remains labour intensive.

Of the root parameters that are commonly measured (Atkinson, 2000), RLD (cm cm$^{-3}$) by depth is the most helpful in estimating water uptake because models of water uptake by roots (e.g., de Willigen, 2000; Feddes and Raats, 2004; Javou et al., 2013; Benchmann et al., 2014) are generally based on relationships with RLD (Tinker and Nye, 2000). Crop water uptake can be reasonably approximated using crop water demand, RLD, the maximum amount of extractable water from the soil, elapsed time, and a resource capture coefficient (Passioura, 1983; Monteith, 1986; King et al., 2003). These models generally show that RLDs >1 cm cm$^{-3}$ are associated with only small increases in the total amount of water taken up, even in periods of high moisture demand (King et al., 2003).

This paper reports a collation of in-field RLD data from wheat and OSR crops grown across the UK between 2004 and 2013, and considers the impact of rooting on water capture and crop yield under water-limiting conditions. Whilst these data were initially collected for other purposes (i.e., as controls in tests of agro-chemical or genetic effects), they are used here to exemplify rooting of recent commercial crops of wheat and OSR in the UK, and to explore the hypothesis that inadequate rooting (due to a combination of poor soil conditions, agronomic management, and lack of focused selection in breeding schemes) may be contributing to current yield stagnation in the UK.

**Materials and methods**

**Data collation**

RLD data from experiments across the UK were collated to provide information on the extent of rooting in commercial fields (Tables 1 and 2). For winter wheat, the data were from 17 experiments carried out between 2007 and 2013, and for winter OSR the data were from 40 experiments carried out between 2004 and 2013. All wheat crops followed a break crop of either winter OSR or winter beans, and all OSR crops followed either winter wheat or winter barley. The root data were derived from replicated plots of the control treatments from various public and commercially funded studies under commercial farming conditions; conditions in these plots thus represent normal practice on each farm.

**Root assessments**

The RLD data were obtained from soil coring (to 1 m depth), root washing, and scanning. The number of soil cores per plot varied by experiment, but was usually four or six depending on whether the core diameter was 2.6 cm or 1.9 cm, respectively. Half of the cores were sampled in the rows or next to a plant, and half were taken between the rows, or equidistant between plants. In all of the OSR experiments and the majority of the winter wheat experiments, the soil cores were subdivided into 20 cm soil horizons. In five winter wheat experiments, cores were divided into 25 cm horizons; here, empirical fitted relationships (usually polynomial) between RLD...
Table 1. Site details, growing conditions, sampling details, measured root lengths to 1 m depth (with values in parentheses estimated by extrapolation where some horizons were not sampled), and estimated proportion of total root to 0.5 m depth and depth with RLD >1 cm cm⁻³ (inferred by applying Gale and Grigal’s 1987 model to cumulative distribution of roots with cm depth) for 17 winter wheat experiments

| No. | Harvest year | Farm postcode | Soil type | Variety | Sowing date | Stage of sampling | Sample depths (cm) | Total root length (km m⁻²) with estimates for 0–100 cm if not all depths sampled | Roots at 0.5 m | Depth (cm) with >1 cm cm⁻³ |
|-----|--------------|---------------|-----------|---------|-------------|------------------|-------------------|---------------------------------------------------------------------------------|---------------|-------------------------|
| 1   | 2007         | CB23 4NN      | C         | LYS RiSa DH lines | 03/10/2006 | Post-harvest | 40–60            | 3.4 (9.8)                                                                       | 74%           | 36                      |
| 2   | 2007         | CB23 4NN      | C         | HYT RiSa DH lines | 03/10/2006 | Post-harvest | 40–60            | 3.5 (10.1)                                                                       | 73%           | 37                      |
| 6   | 2011         | HR1 3PG       | ZCL       | Duxford   | 16/10/2010 | GS75          | 0–75             | 6.8 (9.1)                                                                       | 64%           | 25                      |
| 3   | 2012         | PE34 4HZ      | ZCL       | Alchemy   | 12/10/2011 | Anthesis      | 0–100            | 18.2                                                                       | 74%           | 59                      |
| 4   | 2012         | PE34 4HZ      | ZCL       | Oakley    | 12/10/2011 | Anthesis      | 0–100            | 15.7                                                                       | 76%           | 53                      |
| 5   | 2012         | PE34 4HZ      | ZCL       | Viscount  | 12/10/2011 | Anthesis      | 0–100            | 17.9                                                                       | 71%           | 60                      |
| 7   | 2012         | CB23 4NN      | C         | Gallant   | 21/09/2011 | GS39          | 0–60             | 9.0 (11.1)                                                                       | 73%           | 41                      |
| 8   | 2012         | YO17 8BP      | SL        | Duxford   | 24/10/2011 | GS39          | 0–100            | 15.3                                                                       | 78%           | 51                      |
| 9   | 2012         | HR1 3PG       | SCL       | Gallant   | 30/09/2011 | GS75          | 0–100            | 6.7                                                                        | 88%           | 26                      |
| 10  | 2012         | YO17 8BP      | SCL       | Beluga    | 05/10/2011 | Post-harvest | 0–100            | 2.9                                                                        | 72%           | 0                       |
| 11  | 2012         | YO17 8BP      | SCL       | JB Diego  | 05/10/2011 | Post-harvest | 0–100            | 4.3                                                                        | 75%           | 7                       |
| 12  | 2013         | YO17 8BP      | SCL       | Beluga    | 09/10/2012 | Post-harvest | 0–100            | 8.2                                                                        | 80%           | 30                      |
| 13  | 2013         | YO17 8BP      | SCL       | JB Diego  | 09/10/2012 | Post-harvest | 0–100            | 5.3                                                                        | 82%           | 17                      |
| 14  | 2013         | CB23 4NN      | C         | Target    | 03/10/2012 | GS65          | 0–100            | 8.5                                                                        | 76%           | 31                      |
| 15  | 2013         | YO17 8BP      | SL        | Viscount  | 19/10/2012 | GS65          | 0–100            | 4.6                                                                        | 78%           | 10                      |
| 16  | 2013         | PE34 4HZ      | SL        | Oakley    | 30/09/2012 | GS65          | 0–100            | 6.3                                                                        | 71%           | 18                      |
| 17  | 2013         | PE34 4HZ      | SCL       | Invicta   | 07/10/2012 | GS75          | 0–100            | 12.8 (9.8)                                                                   | 63%           | 47                      |

C, clay; SCL, sandy clay loam; ZCL, silty clay loam; SL, sandy loam.

The germplasm at sites 1 and 2 were low-yielding short (LYS) or high-yielding tall (HYT) lines selected from a doubled haploid population from Rialto and Savannah.

and depth were used to infer an RLD estimate for each 20 cm horizon. The samples for the OSR experiments were taken between June (seed development) and harvest; the wheat samples were taken between late stem extension (GS39) and harvest. The cores were frozen until the day before processing in order to reduce degradation (Barraclough and Leigh, 1984; Kätterer et al., 1993). They were then thawed at room temperature before washing. For the long storage periods used here, freezing was the best storage option (Do Rosário et al., 2000).

The roots were extracted from the soil cores using a root washing system (Delta-T devices Ltd, Burwill, Cambridge, UK.) and collected on a 550 μm wire mesh filter. Root length was assessed using a WinRHIZO STD 4800 scanner and software (Regent Instruments Inc, Sainte Foy, Qc, Canada).

This method is considered sufficiently similar to those used in the previous assessments of UK rooting in the 1970s and 1980s for the values of RLD to be comparable (Table 3). The differences between methods were primarily in the number and diameter of the soil cores, and the method of determining root length. The previous studies used larger diameter soil cores compared with those used here, and (usually) a greater number of cores. More recent studies have used smaller cores and fewer cores per treatment, for example Svoboda and Haberle (2006) used 3.5 cm diameter cores and six replicates, Kirkegaard et al. (2007) used 4.2 cm diameter cores and three replicates, and Atta et al. (2013) used 4.4 cm diameter cores and one replicate. The experiments in this study used a flatbed scanner with WinRHIZO™ software to determine root lengths, whereas the older publications used the classical line intersect method of either Newman (1966) or Tennant (1975). In all of these methods, root length is estimated from the number of intersections of roots with a superimposed grid. The WinRHIZO™ software measures the roots continuously, and overlaps are accounted for using a correction method (Arsenault et al., 1995), and it uses the statistical method of Tennant (1975).

Total measured root lengths (km m⁻²) were calculated and reported. Normally these were from the surface to 1 m depth; where the sampled depths were less than this, reported values are accompanied by extrapolated estimates of total root length to 1 m depth. The extrapolations assumed that the average proportion of total root length in each horizon within the complete data sets (13 for wheat and 19 for OSR) applied at each site with incomplete data. Then for all data sets (including those with extrapolated values), the average value for the whole profile of a parameter β was determined using Gale and Grigal’s model (1987), as follows

$$\beta = (1 – Y)^{1/d}$$

where Y is the cumulative proportion of total roots from the shallowest level sampled to the reported level and d is depth (cm). Using the average β for each data set, estimates were made of the proportion of all measured roots in the 0–50 cm horizon, and the depth to which RLD exceeded 1 cm cm⁻³.

The water capture model

A wheat resource capture model developed by King et al. (2003) was used to estimate the proportion of available water which could be extracted by root systems with the minimum, median and
maximum RLDs measured (or estimated) for all 17 wheat and 40 OSR crops. Here, 
\[ \Phi = 1 - e^{-kL_v} \]

where \( \Phi \) is the fraction of water which is potentially available; \( L_v \) is the RLD, and \( k \) is a resource capture coefficient. A coefficient of resource capture (\( k \)) of 2 was assumed, describing the relationship between RLD and capture of soil water. This value of \( k \) implied that water capture became near complete as RLD approached \( \sim 1 \text{ cm} \text{ cm}^{-1} \) as was assumed by Barraclough (1984) and shown by Gregory and Brown (1989); thus 1 cm \( \text{ cm}^{-1} \) was dubbed the critical RLD (cRLD). Three soil types were chosen; silt loam, clay loam, and loamy medium sand to represent soil types of high, medium, or low available water capacity (AWC), respectively. AWC is taken to be the total amount of water available for crop uptake when the soil is at field capacity. AWCs for these soil types were sourced from MAFF (1988) based on a 0.3 m topsoil depth with good structural conditions, plus 0.7 m subsoil depth with average structural conditions, giving AWCs of 223 mm for silt loam, 166 mm for clay loam, and 102 mm for loamy medium sand. The water taken up by each crop was calculated by estimating \( \Phi \) from RLD and multiplying \( \Phi \) by the AWC.

Model scenarios

Water-limited growth was estimated, to predict the effect of rooting on yield. It was assumed that: the soil was at field capacity at the start of stem extension on 15 March for OSR and 1 April for wheat; that the crop grew actively until 1 July for OSR and 15 July for wheat; there was 50 mm rain per month; standard transpiration efficiency was 5 g dry matter (DM) \( \text{ m}^{-2} \text{ month}^{-1} \) for wheat and 4.61 g DM \( \text{ m}^{-2} \text{ month}^{-1} \) for OSR (to account for production of lipid-rich seed; Defra, 2005); maximum rooting depth was 1 m; the crop had produced 2 t ha\(^{-1}\) biomass before stem extension; and the harvest index (HI) was 0.3 for OSR and 0.5 for wheat.

A separate higher yielding scenario was considered, again assuming water limitation, but in which the maximum rooting depth was increased to 1.8 m. For this, the minimum, median and maximum RLDs to 1 m were extrapolated to a depth of 1.8 m using scaling factors, so that the roots in any horizon had the same ratio to total roots above that depth as reported by Gregory et al. (1978a, b) for winter wheat, and by Barraclough (1989) for OSR. These extrapolated RLDs were used to calculate water uptake, hence yield, with subsoil AWCs being extended to 1.8 m depth.

Results

Winter wheat rooting

The total length of root measured varied greatly between the 17 wheat experiments carried out between 2007 and 2013 (Tables 1 and 4); mean root length was 9.8 km m\(^{-2}\) but ranged between 2.9 km m\(^{-2}\) and 18.2 km m\(^{-2}\). Relative root distribution between horizons varied less; the lowest estimated percentage of roots in the top 0.5 m was 63%, while the greatest was 87%. The collated RLDs of field winter wheat crops from 17 experiments are shown in Fig. 1. The topsoil contained most roots and thence RLD decreased down the soil profile. The average RLD in the top horizon was 1.94 cm cm\(^{-3}\) (range 0.57–3.39), and 1.18 cm cm\(^{-3}\) in the second (20–40 cm) horizon. The rate of decrease in RLD in the lower three horizons was less than that between the top two: average RLDs were 0.74, 0.52, and 0.46 cm cm\(^{-3}\). The RLD maxima were similar to the cRLD but the minimum RLDs were low, with 0.57 cm cm\(^{-3}\) in the topsoil and 0.13 cm cm\(^{-3}\) and 0.16 cm cm\(^{-3}\) in the lower two soil horizons. Figure 1 also shows the average RLD from reference publications (Gregory et al., 1978b; Barraclough et al., 1989, 1991); this average in the upper horizon was four times greater at 7.8 cm cm\(^{-3}\) than the average in this study. The reference RLDs were greater than maximum RLDs in these experiments in all top three horizons; reference RLDs in lower horizons were similar to the maximum RLDs measured here.

A cRLD of 1 cm cm\(^{-3}\) indicates that the average winter wheat field crop had inadequate roots to extract the available water below 40 cm soil depth (Fig. 1). Minimum RLDs at 0.57 cm cm\(^{-3}\) were less than the cRLD, even in the topsoil. The maximum RLDs were 3.39 cm cm\(^{-3}\) in the topsoil and 1.02 cm cm\(^{-3}\) in the deepest horizon, indicating that some crops probably had sufficient roots for full water capture at all points in the full 1 m soil profile. The depths to which the roots at each site exceeded 1 cm cm\(^{-3}\), estimated using Gale and Grigal’s model (1987), are given in Table 1. There was wide variation, depths ranging between 0 and >1 m, with the average depth being 32 cm. There was little obvious association between these depths and recorded growing conditions. However, there were no usable assessments that would allow safe comparison of soil conditions.

Modelled water-limited wheat yield

By assuming 1 m was the maximum rooting depth, the predicted yield with median RLD for wheat on a medium AWC soil type was 10.1 t ha\(^{-1}\) (Table 5). Predicted yields ranged from 7.5 t ha\(^{-1}\) with the minimum RLDs on a low AWC soil type to 12.5 t ha\(^{-1}\) with the maximum RLDs on a high AWC soil. Increasing the maximum rooting depth to 1.8 m (extrapolating the RLDs below the maximum measured depth) did not increase the predicted yields greatly because the RLDs in the additional horizons were so small. The average RLD on a
medium soil type resulted in a predicted yield of 10.2 t ha$^{-1}$. The smallest yield increased by 0.1 t ha$^{-1}$ to 7.6 t ha$^{-1}$ on the low AWC soil type and the greatest predicted yield increased by 1.3 t ha$^{-1}$ to 13.8 t ha$^{-1}$ with maximum rooting on the high AWC soil type.

Oilseed rape rooting

The total root lengths measured in the 40 experiments carried out between 2004 and 2013 (Tables 2 and 4) demonstrate a very wide range, from 2.8 km m$^{-2}$ to 26.7 km m$^{-2}$. The mean total root length for the 40 crops was 26.7 km m$^{-2}$. The lowest estimated percentage of roots in the top 0.5 m was 61% and the greatest was 96%. The RLDs in each of all horizons (including extrapolated values for some horizons at 21 sites) are summarized in Fig. 2. There were more roots in the top-soil for OSR than for winter wheat, with average RLDs of 2.66 cm cm$^{-3}$ and 1.69 cm cm$^{-3}$ in the 0–20 and 20–40 soil horizons. RLD decreased down the soil profile, with average RLDs of 0.68, 0.63, and 0.55 cm cm$^{-3}$ in the lowest three horizons. As for wheat, the rate of decrease in the amount of roots in the lower horizons was less than that between the two upper horizons. The maximum RLD in the topsoil of 7.43 cm cm$^{-3}$ was much greater than the average (Fig. 2), and maxima in the 40–60 and 60–80 cm soil horizons were very similar at 1.95 cm cm$^{-3}$ and 1.89 cm cm$^{-3}$, respectively. The minimum RLD in the topsoil was 0.55 cm cm$^{-3}$, with 0.07 cm cm$^{-3}$ in the 80–100 cm soil horizon, so was less than the minimum RLD for wheat. Barraclough et al. (1989) reported an RLD of 7.97 cm cm$^{-3}$ for OSR in the top 0.2 m of soil, which is 2.7 times greater than the average RLD here, but similar to the maximum RLD. In the lower soil layers, the published reference RLDs are similar to the mean values presented here.

There are limited data available on rooting in OSR, and no published cRLD for OSR. If the same cRLD of 1 cm cm$^{-3}$ as for wheat is assumed, Fig. 2 indicates that average root intensity for winter OSR became inadequate below ~0.4 m soil depth. There was sufficient rooting in the top two soil horizons; however, in the lower horizons the average RLD was around half of the critical value. The minimum measured RLDs were adequately rooted in the 0–0.2 m soil horizon, but this was not the case further down the soil profile. The maximum measured RLDs exceeded the cRLD value at all soil depths. The depths to which the roots exceeded 1 cm cm$^{-3}$ at each site, estimated using Gale and Grigal’s model (1987), are given in Table 2 and summarized in Table 4; values tended to be slightly greater than for wheat and showed similarly wide variation from 0.17 m to 0.77 m (Table 4). Again, there was little obvious association between these depths and recorded growing conditions.

Modelled water-limited OSR yield

The predicted yield for OSR with median RLDs to 1 m on a medium AWC soil type was 5.2 t ha$^{-1}$ (Table 6). The predicted yields ranged from 3.9 t ha$^{-1}$ for a crop with minimum RLDs grown on a low AWC soil type to 6.6 t ha$^{-1}$ with maximum RLDs on a high AWC soil type. The predicted yield with reference RLD values grown on a medium AWC soil was the same as with the median RLD values. Increasing rooting depth and extrapolating the RLDs below the measured depth to 1.8 m resulted in a 2.1 t ha$^{-1}$ yield increase to 7.2 t ha$^{-1}$ with median RLDs on the medium AWC soil type. The lowest yield was 4.4 t ha$^{-1}$ for the minimum RLD crop on the low AWC soil type, 0.5 t ha$^{-1}$ more than with 1 m depth. The maximum RLD crop on the high AWC soil type gave a predicted yield of 10.1 t ha$^{-1}$ which was 3.5 t ha$^{-1}$ more than with rooting to 1 m.

Discussion

The measured RLDs from 17 wheat experiments were much less than the average published reference RLD values from the 1970s and 1980s (Gregory et al., 1978b; Barraclough et al., 1989, 1991), especially in the top 0.6 m of soil (Fig. 1). In the top 0.2 m, the average RLD was four times less than the reference values. Other recent studies (Hoad et al., 2004; Pillinger et al., 2005) have shown average topsoil RLDs from 3 cm cm$^{-3}$ to 10 cm cm$^{-3}$, comparable with the reference values but, in all of the deeper soil horizons, average RLDs were consistent with the average RLDs found here. Note that in general these RLDs are large compared with those from drier climates; for example, Atta et al. (2013), investigating the root systems of 15 wheat genotypes in Australia, found RLDs in the top 0.15 m of soil ranging between 0.6 cm cm$^{-3}$ and 2 cm cm$^{-3}$; on the other hand, Wasson et al. (2012) stated that RLDs for most Australian wheat crops were 3–5 cm cm$^{-3}$ in the surface layers.

Hoad et al. (2004) found that the total root length of field-grown wheat crops ranged between 7 km m$^{-2}$ and 28 km m$^{-2}$, consistent with the range of total root lengths reported here. Other publications generally report greater total root lengths with a smaller range; for example, Barraclough et al. (1989) report a total root length range between ~22 km m$^{-2}$ and ~35 m m$^{-2}$, while Barraclough and Weir (1988) report 27–32 km m$^{-2}$, and Barraclough and Leigh (1984) found a range between 22.2 km m$^{-2}$ and 29.8 km m$^{-2}$. As with the proportion of root in the top 0.5 m of soil reported here, Gregory et al. (1978b) found ~65% of the total root dry weight in the top 0.3 m of soil after April.

It is possible to be reasonably confident that the large differences between the RLDs presented here and some of the previously published values are not due to variations or limitations in methodology. The methods have already been described as comparable. The two main differences were merely in the diameter and number of the cores. More recent studies have tended to use smaller cores and fewer cores per treatment (Svoboda and Haberle, 2006; Kirkegaard et al., 2007; Atta et al., 2013) than in the reference publications. The majority of studies used 0.5 mm mesh sieves; Barley (1970; cited in Gregory et al., 1978b) estimated that field-grown wheat root systems had a diameter of 0.5–1 mm for primary axes and 0.2–0.5 mm for primary laterals. Gregory et al. (1978b) tested their sampling system with known lengths of root and concluded that roots were unlikely to pass straight through the sieve, and similar sieve sizes were used here.
Additionally, the relatively high OSR RLD values measured in the upper soil horizons here demonstrate the method to be capable of capturing and measuring large densities of root. If methodological causes of the relatively small RLDs found here are discounted, other causes can be considered. Clearly the old studies were not derived from as many crops as the more recent studies, and neither set of data can be taken as properly representative of crops grown in either era, so any conclusions from these comparisons must be treated with caution. However, given the size of the differences and the vital importance of adequate rooting to sustainable intensification (Sylvester-Bradley, 2010), it is important to register
that the recent data for both wheat and OSR crops appear to show quite shallow depths to which soil water capture may be incomplete, and to note the possible impacts of this, particularly in dry seasons.

It appears likely that poor rooting of wheat and OSR crops resulted from poor soil conditions perhaps brought about by heavier machinery used in a less timely manner due to larger farms with increased cultivation areas per tractor (Knight et al., 2012). Compaction is commonly associated with soil beneath the plough layer, where soil strength can increase and inhibit root growth (Whitmore and Whalley, 2009). However the apparent decrease in topsoil rooting noted here (Fig. 1) may also relate more to reduced intensity of topsoil cultivation over recent decades, particularly a reduction in ploughing (Knight et al., 2012). Additional factors may contribute to these effects, such as inadequately maintained field drains and poor agronomic management. In reality, it is likely that a combination of factors will have contributed to poor crop rooting in recent years.

Because wheat and OSR crops are grown on the same land, it might be expected that RLDs for wheat and OSR would be similarly small. However, the topsoil RLDs for OSR (Fig. 2) were larger than those for wheat (Fig. 1), the largest of these being consistent with the reference values. Whether this difference is due to different topsoil cultivations for the two species or to inherent interspecific differences is unclear. However, the OSR RLDs for the lower soil horizons were similarly small as those for wheat and consistent with the low reference RLDs reported by Barraclough et al. (1989). Perhaps it is inherent that RLDs for OSR diminish more with depth than those for for wheat.

Table 3. The root assessment methods used in the reference publications cited here

| Reference                  | No. of cores | Core diameter | Core depth | Core position | Minimum sieve width | Root length determination                              |
|----------------------------|--------------|---------------|------------|---------------|---------------------|--------------------------------------------------------|
| Gregory et al. (1978b)     | 2 or 1       | 10 cm         | 2 m        | Touching the row | 0.5 mm             | Machine to count the number of intersections described by Rowse and Phillips (1974) |
| Barraclough et al. (1991)  | –            | –             | –          | –             | –                   | Intersect method                                        |
| Barraclough et al. (1989)  | 12           | 7 cm          | 1.8 m      | –             | 0.5 mm             | Comair scanner                                         |
| Barraclough et al. (1989)  | 8            | 7 cm          | 1.8 m      | Above the plant, between plants in same row, between rows |                     |                                                        |

Table 4. Summary statistics for rooting measurements taken at 17 wheat sites and 40 oilseed rape (OSR) sites in the UK

|                                | Mean | Min | Q1 | Median | Q3 | Max  |
|--------------------------------|------|-----|----|--------|----|------|
| Winter wheat (n=17)            |      |     |    |        |    |      |
| Total RL, km m⁻² per m depth   | 9.8  | 2.9 | 6.3| 8.5    | 12.8| 18.2 |
| Roots to 0.5 m                 | 75%  | 63% | 72%| 74%    | 78%| 88%  |
| Depth (cm) with >1 cm m⁻³      | 32.2 | 18  | 31 | 47     | 47 | 60   |
| Oilseed rape (n=40)            |      |     |    |        |    |      |
| Total RL, km m⁻² per m depth   | 12.4 | 2.8 | 8.4| 11.0   | 16.6| 26.7 |
| Roots to 0.5 m                 | 83%  | 61% | 76%| 83%    | 92%| 96%  |
| Depth (cm) RLD >1 cm m⁻³       | 46.9 | 17  | 39 | 44     | 58 | 77   |

Results were derived from data including some extrapolated values, where measurements were not made for some (shallow or deep) horizons; this affected four wheat sites and 21 OSR sites.
(1998) noted that UK wheat breeding had decreased the ability of varieties to capture soil-derived N (which tends to be held in subsoil; Sylvester-Bradley et al., 2001). Interestingly, Siddique et al. (1990) compared roots of modern and older wheat varieties in a sand over clay soil in Western Australia and found that older varieties had greater root dry matter and RLDs in the top 40 cm of soil. These authors attributed the apparent reduction in rooting to increased HI and better water use efficiency. It may be that modern wheat varieties have been inadvertently selected to have fewer roots than those previously reported (Gregory et al., 1978b; Barraclough et al., 1989, 1991) because the conditions in which they have been selected have imposed few water or nutrient stresses. Certainly, at deeper soil depths (i.e. 0.4 m), it does appear that modern wheat crops are not rooting adequately to extract the available soil water, and this would also seem to be the case for OSR crops, assuming a similar cRLD to that for wheat. However, Hess (2012) compared the hydraulic conductance of wheat and OSR roots from plants grown in PVC tubes in controlled environment conditions and found that, when water was not limiting, OSR had a greater conductance than wheat, suggesting that OSR might require a less dense root system to extract a similar amount of water.

Undoubtedly, the adoption of a single value as the cRLD for both wheat and OSR and for all soil types here (and by King et al., 2003) is simplistic; many factors are expected to cause cRLD to vary, including soil hydraulic conductivity and moisture content (Bailey, 1990), the period of water extraction (Passiouera, 1983), the uniformity of root distribution (Gardner, 1960), the hydraulic conductance of roots and stems (as above), and the transpiration demand of the leaf canopy. Also, current justification for taking cRLD as 1 cm cm⁻³ is based on limited empirical evidence; Barraclough et al. (1989) studying field-grown wheat in the UK and Gregory and Brown (1989) studying field-grown barley in Syria both showed that, for droughted crops at anthesis, this was the RLD that approximately coincided with full water extraction. While cRLD has clearly been a useful tool for modelling (e.g. King et al., 2003), more confidence could be placed in model predictions, and in interpreting field observations, if cRLD values were validated more thoroughly, particularly for the major crop species and for the major soil types.

For winter wheat in the UK, average rainfall in the spring and summer is ~130 mm less than average evapotranspiration (Jones and Thomasson, 1985, cited in Foulkes et al., 2001). Despite UK soils being almost always returned to field capacity over winter, a significant minority of arable crops are grown on shallow or sandy soils which, without deep rooting, do not store sufficient moisture to meet this shortfall. Therefore, although a minority of wheat crops will experience drought in an average year, a majority will do so in a dry year (Foulkes et al., 2001). Foulkes et al. (2001) estimated that 34% of the wheat acreage in the UK are affected by at least 10 d of drought, and it is expected that this proportion will increase due both to an increased demand for water by crops with increased genetic potential for biomass production (e.g. Shearman et al., 2005) and to the effects of climate change.

Gregory et al. (1978a) observed that wheat, with limited rainfall, extracted soil water initially from the upper layers but, when water here was insufficient to meet plant demand, it was taken from deeper layers. In a dry period in late June their results showed that the soil below 1 m, which contained 3% of the total root dry weight (Gregory et al., 1978b), supplied almost 20% of evapotranspiration. This finding emphasizes the importance of a few deep roots in supplying water during a dry period (Gregory et al., 1978a). In Australia, Kirkegaard et al. (2007) estimated that an additional 10.5 mm of water available in the subsoil (1.35–1.85 m) after anthesis in wheat increased yield (in a moderate drought stress treatment) by 0.62 t ha⁻¹, and concluded that relatively small amounts of water in the subsoil can be highly valuable to grain yield.

## Table 5. Modelled water-limited yields (t ha⁻¹) of winter wheat with minimum, median, and maximum measured RLDs (root length density) and reference RLDs from Gregory et al. (1978b) and Barraclough et al. (1989, 1991) to 100 cm depth on three soil types of differing AWC (available water capacity)

| Soil type           | AWC (mm, 0–100 cm) | Predicted yield (t ha⁻¹) at 85% DM | Min RLD | Mean RLD | Max RLD | Reference RLD |
|---------------------|--------------------|-----------------------------------|---------|----------|---------|---------------|
| Silt loam           | 223                |                                   | 9.0     | 11.4     | 12.5    | 12.5          |
| Clay loam           | 166                |                                   | 8.3     | 10.1     | 10.9    | 10.9          |
| Loamy medium sand   | 102                |                                   | 7.5     | 8.7      | 9.2     | 9.1           |

## Table 6. Modelled water-limited yields (t ha⁻¹) of winter oilseed rape with minimum, median, and maximum measured RLDs (root length density) and reference RLDs from Barraclough et al. (1989) to 100 cm depth on three soil types of differing AWC (available water capacity)

| Soil type           | AWC (mm, 0–100 cm) | Predicted yield (t ha⁻¹) at 85% DM | Min RLD | Mean RLD | Max RLD | Reference RLD |
|---------------------|--------------------|-----------------------------------|---------|----------|---------|---------------|
| Silt loam           | 223                |                                   | 4.6     | 5.9      | 6.6     | 5.8           |
| Clay loam           | 166                |                                   | 4.4     | 5.2      | 5.7     | 5.2           |
| Loamy medium sand   | 102                |                                   | 3.9     | 4.5      | 4.8     | 4.4           |
Also with winter OSR, an experiment in Cambridgeshire UK (with below average rainfall in May and June) showed that RLD from 0.4 m to 1 m depth of soil accounted for 54% of the variation in yield (Blake et al., 2006).

Several studies have correlated deep rooting with root activity in extracting water and with crop performance ( Gregory et al., 1978; Gales, 1983). A good recent example is in the introduction of a deep rooting quantitative trait locus (QTL; DRO1) in rice (Oryza sativa L.) into a shallow rooting cultivar (IR64) to form a near-isogenic line (NIL) homozygous for the allele of DRO1. This NIL had more roots in lower soil layers and ~10% more grain yield than the shallow rooted line (Uga, 2013; Arai-Sanoh et al., 2014). Marker-assisted backcrossing was used in Eastern India to introgress four QTLs for root traits into an upland rice cultivar, and (in combination) these QTLs significantly increased root length during tillering and grain yield by 1 t ha⁻¹; this work has resulted in the release of a new upland rice cultivar ( Steele et al., 2013), demonstrating the feasibility of successfully manipulating crop rooting to increase cereal yields.

The modelling scenarios used herein explored the link between crop RLD, water uptake, and yield, with the best rooted crops yielding more than average rooted crops due to increased access to and uptake of soil water. The models for both crops that assumed 1 m root depth suggested that an increase in RLD would result in a yield increase compared with less well rooted crops, as was expected. Interestingly, however, this did not apply if the larger RLD values for the reference crops were assumed, because all of the available water had been extracted. The effects of increasing rooting depth to 1.8 m depended on whether sufficient RLDs were presumed in the additional depths; extending the depths of poor root systems had little effect because the deep RLDs were so small, whereas root systems with more significant RLDs at depth showed more substantial effects. The modelling exercise thus emphasized the importance of addressing inadequate rooting depths under commercial conditions, if increased yields are to be attained.

To improve crop rooting on-farm in order to support yield stability and enhancement, the research and agricultural communities must find ways of more frequently assessing rooting in field crops, so that they can investigate various engineering, chemical, and genetic solutions to improve rooting on-farm. Modern farmers are still largely unaware of how well their crops are rooting, so some form of on-farm monitoring will be crucial for the recognition of rooting problems and rooting improvements.

Digging soil pits is a simple but unattractive monitoring method; there is a need for easier, routine, high-throughput methods to estimate the size and activity of root systems in the field. Perhaps visual scoring of roots in a spit of soil (Trachsel et al., 2011) offers some scope, but ultimately remote sensing techniques should provide the most acceptable approach; for example, electrical resistance tomography (ERT) and electrical magnetic induction (EMI) have recently been used to map soil moisture and root biomass of herbaceous crops in the field (Sayeeddin and Doussan, 2009; R. Whalley and A. Binley, personal communication).

Once researchers have validated methods to monitor and assess crop rooting, these methods can be used to investigate and encourage agronomic practices that promote deeper healthier root systems. In addition, the potential benefits of genetic- and chemical-induced variation in crop root architecture and water extraction ( Blake et al., 2006; Manschadi et al., 2006; Berry and Spink, 2009; Lopes and Reynolds, 2010; Song et al., 2010) and crop rooting depth and vigour ( Gregory et al., 2005) can be exploited more effectively through breeding programmes and through rotational choices for specific environments.

While the levels of crop rooting deduced from work reported here are disappointing, they reveal a concomitantly large scope for progress through further research and innovation. It will be particularly important for this to be underpinned by re-exploration of some of the fundamental assumptions and data surrounding crop rooting and water uptake. As an important example, the cRLDs for OSR ( Blake et al., 2006) and other crops need to be identified, while the cRLD for wheat needs to be validated for modern wheat varieties and conditions. Overall, it will be important to establish a sufficient number of observations for patterns of variation to be observed; it is clear that the few data sets derived from field conditions over recent decades have created a potential for both science and industry to be misled about the adequacy of crop rooting.

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