May 2012
Cost £8.54

PhD Summary Report No. 20

Assessing the drought risk of oilseed rape to target future improvements to root systems

by
Linde Hess
University of Edinburgh and SAC

Primary supervisor:	Ian Bingham, SAC
Secondary supervisors:	Patrick Meir, University of Edinburgh
	William Spoor, SAC

This is the final report of a 48 month project (RD-2006-3260) which started in November 2006.

HGCA is the cereals and oilseeds division of the Agriculture and Horticulture Development Board.

CONTENTS

1. ABSTRACT

It has been suggested that root length density in the subsoil of many UK oilseed rape crops may be insufficient to fully explore the soil horizon and therefore limit supply of water to the crop (HGCA Project Report 402). Information on water relations of oilseed rape is, however, lacking.

The aim of the current project was to compare the water relations of oilseed rape and wheat. In an experiment to test the hypothesis that oilseed rape was more sensitive to drying soil than wheat, irrigated oilseed rape mini-crops transpired more water than wheat crops and showed a greater reduction in growth when water was withheld. In a separate experiment, the root hydraulic conductance of oilseed rape was about twice that of wheat. These results suggest that oilseed rape needs a less dense root system for water extraction than wheat.

When soil dries it also hardens and high soil strength is known to impede root growth and alter plant-water relations. At low soil strength, oilseed rape had a greater stomatal conductance than wheat but, as soil strength increased, stomatal conductance decreased to a greater extent in oilseed rape, indicating a more sensitive response.

Plants often rely on pores to explore the soil and to reach soil and water stored below a plough pan. The ability of oilseed rape and wheat to exploit soil pores to penetrate hard soil layers was compared in a pot experiment. Presence of pores in the hard layer led to a significant increase in number of roots in the deeper soil, of 29% for wheat and 54% for oilseed rape, compared to when no pores were present. This suggests that oilseed rape is better able to exploit soil pores than wheat.

This project has shown that the growth and distribution of oilseed rape roots under a range of soil conditions was similar to, if not better than, that of wheat, but that stomatal conductance and biomass production of oilseed rape reacted more sensitively to soil drying. Oilseed rape would therefore probably benefit from improved soil management to ensure greater access to deep soil water in the same way as wheat in drought prone areas. Additionally, using or developing oilseed rape varieties that maintain canopy function longer during a period of water limitation may also decrease yield loss to drought in future.

2. INTRODUCTION

Oilseed rape is becoming a more widely grown crop in the world and its area in the UK has increased steadily since the 1970s to 598,000 hectares in 2008 (DEFRA 2009). Oilseed rape yields in the UK have not increased on commercial farms during the last 20 years, despite an increase observed in Recommended List trials. In 2008, the yield was 3.3 t ha^{-1} and the yield has fluctuated around 3 t ha^{-1} since 1984 (Figure 1). In the same time period, the yield per hectare of cereals has increased (Figure 1). It appears, therefore, that the improved genetic potential of new varieties is not being exploited. One factor thought to be responsible for constraining the yield potential is low water availability, although at present only circumstantial evidence is available to support this hypothesis.

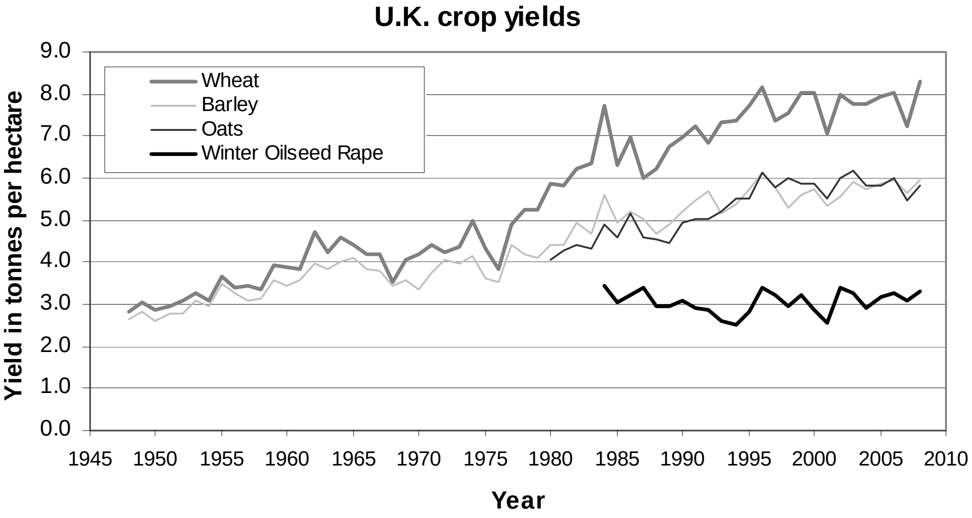

Figure 1. Yearly yield of four UK crops (DEFRA 2009).

The aim of this project is to investigate the crop water relations of oilseed rape and assess the risk of drought-limitation to yield in the UK In this thesis I will compare root functioning and drought sensitivity of oilseed rape with wheat. Wheat is used as benchmark because it is a more intensively researched crop species. Additionally, wheat and oilseed rape are grown in the same fields in the UK as oilseed rape often functions as a break crop in cereal rotations

The experimental approach involved controlled environment and open glass house experiments. Drought sensitivity was assessed by growing mini-crops in lysimeters in an open sided glasshouse and monitoring canopy function as a function of soil moisture deficit in Experiment 1.

Root system hydraulic conductivity was measured on young plants grown under controlled environment conditions (Experiment 2). Parallel measurements were made on wheat to facilitate comparison of results from these experiments with those published in the literature, the majority of which is on cereals.

Compaction problems have been widely encountered in the moist, temperate climatic zones of northern Europe and North America (Soane 1994). In drying or dense soils, in addition to water availability (soil matric potential), soil strength is a factor that can limit root growth and plant-water relations (Whitmore and Whalley 2008). When soil dries it also hardens and high soil strength is known to impede root growth and alter plant-water relations. The hypothesis that oilseed rape is more sensitive to increasing soil strength than wheat was tested in Experiments 3 and 4 in which soil bulk density and soil water content were varied to create a range of soil strengths.

In dense or strong soil, plants often rely on pores created by earthworms or roots of the previous crop to explore the soil volume. The ability of oilseed rape and wheat to exploit soil pores to penetrate hard soil layers was compared in a pot experiment (Experiment 5).

3. EXPERIMENT 1 – DROUGHT ONSET AND EFFECT OF WATER LIMITATION ON OILSEED RAPE AND WHEAT

The objective of this experiment was to test whether oilseed rape was more sensitive to drying soil than wheat, and whether water acquirement by the oilseed rape root system differed from that of wheat.

3.1. Experimental design and treatments

An experiment involving 24 lysimeters laid out in a randomised block design, with five blocks, was set-up in a glasshouse at Easter Bush, Penicuik, Scotland. The glasshouse was open-sided to encourage airflow and to avoid high temperatures. The lysimeters were constructed of pvc pipes of 30 cm internal diameter and 120 cm height (**Error! Reference source not found.**).

A sandy clay loam soil was packed into the lysimeters (**Error! Reference source not found.**). A 5 cm diameter access tube for a capacitance probe (Sentek diviner 2000, Kent Town, Australia) was placed into the centre of the lysimeter before packing the soil and the soil was packed around it. P, K and S fertiliser was applied before sowing. Nitrogen (NH_4NO_3) was applied to the soil surface once at a rate of 100 kg ha^{-1} nitrogen four days after sowing (DAS).

Figure 2. The lysimeters with oilseed rape and wheat plants at the day of harvest. The green mesh shading the mini crops during growth was slid down.

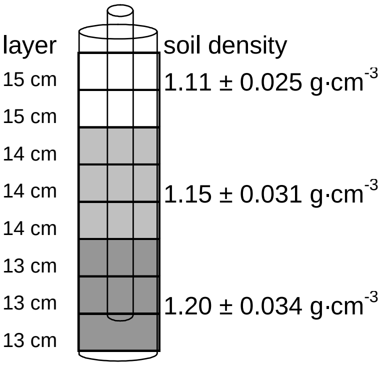

Figure 3. Packing of lysimeters, and measured soil bulk density.

Spring oilseed rape *Brassica napus* L. cv. SW Landmark seeds and spring wheat *Triticum aestivum* L. cv. Tybalt were used. These varieties were chosen because they have similar life-cycle duration. The target density for oilseed rape was 8 plants per lysimeter (113 plants m^{-2}); for wheat the density was 38 plants per lysimeter (552 plants m^{-2}).

For the plants in the non-irrigated treatment, water was withheld from 14 DAS. The plants in the irrigated treatment were given water once per week to return the soil to field capacity.

3.2. Measurements

Volumetric soil moisture content of the top 80 cm of soil was measured every Thursday and Friday during the experiment with a capacitance probe (Sentek Diviner 2000, Sentek pty ltd, Kent Town, Australia).

On 67 and 74 DAS, the leaf stomatal conductance (g_s) of the youngest fully expanded leaf in the top of the canopy of one plant per lysimeter was measured around midday with a portable IRGA (ADC-LCA4 Analytical Development Co. Ltd, Hoddesdon, Herts, UK).

On 84 DAS for wheat and 85 DAS for oilseed rape the plants were destructively sampled. The leaf, pod or ear and stem area of the subsample were determined with a LI-3100 leaf area meter (Li-Cor Biosciences, Cambridge, UK). The dry weights of the plant parts were determined after drying to constant weight in a fan-assisted oven at 80°C.

Root samples were taken after the lysimeters were laid down horizontally and cut open with a saw. Samples were taken at 10 cm depth intervals with a corer of a volume of 209.3 cm^3 and kept at -18°C until root washing took place. The roots of samples from 30-40 cm depth and 70-80 cm depth were washed out with a Delta-T root washer (Delta-T Devices Ltd, Cambridge, UK) and subsequently scanned with a Régent LA1600 scanner. The images were analysed with Winrhizo software (Régent Instruments Inc, Quebec, Canada).

3.3. Results

Day 14 was the last watering day and withholding water had a significant effect on plant water use rates from day 42 onwards, e.g. interval 38-45 DAS (Table 1). The transpiration rate of irrigated plants (taken to be the potential transpiration rate) was greater for oilseed rape than for wheat from DAS 42 onwards (irrigated treatments). Later on, during the interval 45-52 DAS, oilseed rape crops transpired more than wheat regardless of treatment. This coincided with a period of high relative humidity, following a period of low relative humidity, and even the well-watered control plants showed a drop in transpiration rate.

Table 1. Two-way ANOVA test results (p-values, five replicates) for water use rates, data represented in Figure 4.

Interval (DAS)	Midpoint interval	Species	Irrigation	Species x Irrigation
0-4	2	0.394	0.426	0.241
4-8	6	0.433	0.002	0.443
8-17	12.5	0.349	0.135	0.879
17-24	20.5	0.77	0.98	0.35
24-31	27.5	0.01	0.07	0.72
31-38	34.5	0.31	0.3	0.64
38-45	41.5	0.094	<.001	0.666
45-52	48.5	<.001	<.001	0.334
52-59	55.5	<.001	<.001	0.002
59-66	62.5	<.001	<.001	<.001
66-73	69.5	<.001	<.001	<.001
73-80	76.5	<.001	<.001	<.001

There was no difference in the timing of onset of drought stress between species. In both oilseed rape and wheat the transpiration rate of non-irrigated plants dropped below the potential transpiration rate (irrigated treatments) around day 42 (during the interval 38-45 DAS) (Figure 4 and Table 1). From day 56 onwards (52-59 DAS interval), withholding water had a significantly greater effect on oilseed rape than on wheat when compared to the irrigated controls.

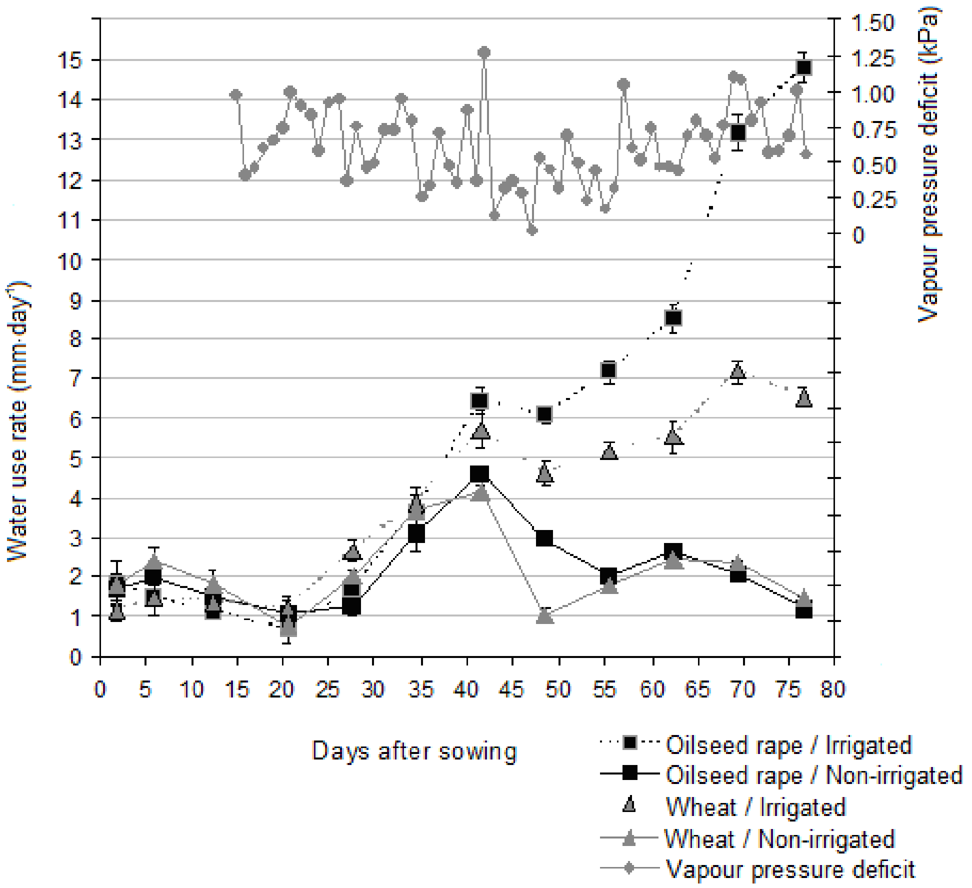

Figure 4. Transpiration rates of plants per lysimeter (mean of five replicates given and standard error of the mean (sem) in error bars). The data point is the mid-point of the interval (usually of seven days) over which transpiration rate was calculated. Potential transpiration rate is represented by symbols connected with intermittent lines. The vapour pressure deficit kPa is also plotted.

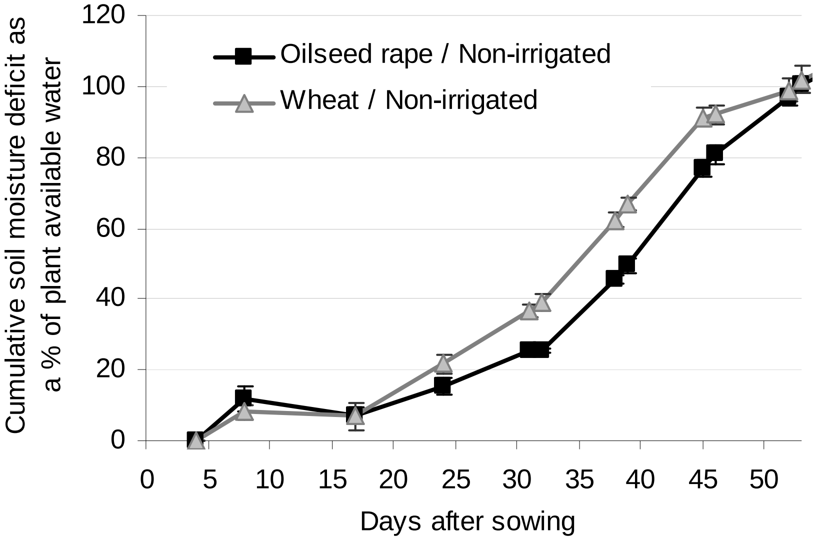

Figure 5. Cumulative soil moisture deficit of oilseed rape and wheat plants and unplanted lysimeters, as a percentage of plant available water over the total measured depth of 80 cm depth. Error bars represent sem.

In Figure 5, the cumulative soil moisture deficit of non-irrigated plants over a depth from 0 to 80 cm is expressed as a percentage of plant available water (that was held between field capacity and permanent wilting point). Between DAS 32 and 46, the cumulative soil moisture deficit of soil in lysimeters planted with wheat was significantly greater than that of lysimeters with oilseed rape (**Error! Not a valid bookmark self-reference.**).

Table 2. Results of ANOVA with repeated measures for testing of effects of species and time on cumulative soil moisture deficit measured from 0-80 cm soil depth, data from 0 to 53 days after sowing tested, original data in Figure 5.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F pr.**
block stratum	4	399.14	99.79	1.76	
block.Subject stratum					
species	1	1704.16	1704.16	30.05	0.005
Residual	4	226.85	56.71	2.41	
block.Subject.Time stratum					
Time	11	150659.5	13696.32	583.01	<.001
Time.species	11	1510.99	137.36	5.85	0.01
Residual	88	2067.34	23.49		
Total	119	156568			

3.3.1. Effects of withholding water on shoot growth

Withholding water reduced the above ground dry weight of oilseed rape significantly more than that of wheat (Tables 3 andTable 2). Total leaf area was reduced by the same degree in both species. Oilseed rape had a significantly lower total leaf area than wheat in both water treatments. Withholding water not only reduced dry weight of oilseed rape more than wheat, it also reduced pod dry weight significantly more than the ear dry weight of wheat. While pod dry weight of oilseed rape was halved, wheat ear dry weight was not significantly affected.

Table 1. Plant parameters of total number of plants per lysimeter at harvest. Plants were harvested on days 84 and 85 after sowing, the mean of five samples and the standard error are given, result of statistical tests given in Table 2.

	Oilseed rape		**Wheat**	
	Irrigated	**Non-irrigated**	**Irrigated**	**Non-irrigated**
Total above ground biomass (g)	144.9 ± 4.8	69.8 ± 1.9	108.5 ± 4.1	83.1 ± 3.1
Total leaf area (cm2)	5364 ± 596.2	1756 ± 88.8	5970 ± 428.2	2484 ± 145.2
Total pod or ear DW (g)	45.6 ± 3.0	21.9 ± 0.8	26.0 ± 0.8	25.1 ± 1.0
Stem or tiller number	9.4 ± 0.51	8.60 ± 0.75	66.0 ± 1.70	50.4 ± 2.50
Relative water content	0.84 ± 0.041	0.68 ± 0.061	0.93 ± 0.008	0.63 ± 0.038

Table 2. Two-way ANOVA test results for harvest data.

	Species	**Irrigation**	**Sp x Ir**
Total above ground biomass (g)	0.095	< 0.001	< 0.001
Total leaf area (cm2)	0.032	< 0.001	0.457
Total pod or ear DW (g)	< 0.001	< 0.001	< 0.001
Stem or tiller number	< 0.001	< 0.001	0.001
Relative water content	0.552	< 0.001	0.116

3.3.2. Root system influx rates

When irrigated, oilseed rape plants had a greater water influx rate per unit root length and root area, based on root measurements made on DAS 84 and DAS 85 (at harvest) and the change in soil water content between DAS73 and DAS 80 (Table 1). At both depths, this difference was significant.

Table 1. Influx rate of water at two depths at end of experiment, between DAS 73 and 80. Expressed on a root length (in ml m^{-1} day^{-1} and root surface area basis (in ml m^{-2} day^{-1}). Irrigated plants only. The mean of five samples and sem are given, result of two-way ANOVA tests given.

				p-values		
Root influx	**Depth**	**Oilseed rape**	**Wheat**	**Species**	**Depth**	**Sp x Depth**
per unit root length	30-40	0.52 ± 0.105	0.33 ± 0.055	0.019	0.699	0.527
	70-80	0.54 ± 0.079	0.24 ± 0.077			
Per unit root area	30-40	876 ± 195.1	521 ± 88.7	0.012	0.726	0.577
	70-80	908 ± 117.4	381 ± 120.6			

When averaged over irrigation treatments the stomatal conductance of oilseed rape was greater than wheat on both day 67 and 74 (**Error! Not a valid bookmark self-reference.**). Withholding water resulted in a significant decrease in stomatal conductance in both species on both dates. On the earlier date, drought treatment reduced stomatal conductance to a similar degree in each species (species x irrigation $p > 0.05$), but on the later date, oilseed rape plants responded to drought by closing their stomata more than wheat (species x irrigation $p < 0.001$, Table 3).

Table 2. Stomatal conductance (gs) in mol m^{-2} s^{-1} measured 67 and 74 days after sowing.

	Oilseed rape		**Wheat**	
	Irrigated	**Non-irrigated**	**Irrigated**	**Non-irrigated**
gs DAS 67	0.38 ± 0.102	0.14 ± 0.029	0.19 ± 0.003	0.05 ± 0.006
gs DAS 74	0.40 ± 0.023	0.06 ± 0.002	0.12 ± 0.024	0.03 ± 0.004

Table 3. Statistical results of two-way ANOVA tests on stomatal conductance (gs) data.

	Species	**Irrigation**	**Sp x Ir**
gs DAS 67	0.002	0.020	0.385
gs DAS 74	< 0.001	< 0.001	< 0.001

3.4. Key findings

- Water use of oilseed rape is relatively high when irrigated.
- Oilseed rape canopy parameters are more sensitive than wheat when water is withheld.
- The root system of oilseed rape acquires water as least as well as that of wheat and oilseed rape may not need a denser root system, but might benefit from deeper rooting.

4. EXPERIMENT 2 – HYDRAULIC CONDUCTIVITY OF THE ROOT SYSTEM

The objective of experiment in this section was to test whether the roots of oilseed rape roots are more efficient in transporting water than wheat roots.

4.1. Experimental design and treatments

In this experiment, hydraulic conductance of the root system (the ability of roots to transport water) of oilseed rape and wheat were measured using a technique in which pressure was applied to the root system and rate of out flow of water from the stem base was measured.

One spring oilseed rape or spring wheat seed was sown in a polypropylene tube of with a diameter of 32 mm and a depth of 10 cm. The growth medium consisted of a mixture of sharp washed sand and vermiculite. Nutrients, in the form of ten ml half strength Hoagland solution were given weekly (Epstein 1972) and water was supplied every other day to keep the growth medium moist. The hydraulic conductivity was measured when plants had two unfolded leaves and a third unfolding, three weeks after sowing. Plants were cultivated in a controlled climate growth chamber.

4.2. Measurements and analyses

Measurements were made within the period one hour before and one hour after the midpoint of the light period. The shoot was cut just below the first leaves, and the plastic bag including growth medium and root system was placed in the pressure vessel (ELE international ltd., Leighton Buzzard, U.K). The chamber was pressurised to 0.3 MPa and the root system was left for at least twelve minutes for a constant rate of water flow to establish from the cut surface. The water rate of water out flow over a further ten minute period was measured, see Gallardo et al (1996) for a comparable method.

After measurement, the root system was washed from the sand/vermiculite and spread in a transparent dish containing a film of water and scanned with a Régent scanner (LA1600, Epson expression, 836 XL) and analysed with Winrhizo software (Régent, Quebec, Canada). Leaf area was measured with a leaf area meter (LI-COR, Lincoln Nebraska, USA). After scanning, the root system was dried until constant weight and the dry weight determined.

4.3. Results

4.3.1. Plant characteristics

Oilseed rape plants were bigger than wheat plants. Spring oilseed rape plants had a significantly greater shoot area and greater root length (Table 8). While the root length per plant was significantly greater for oilseed rape plants, the root surface area did not differ significantly, this was because the wheat roots had a greater diameter; the dry weight of the wheat root system was also significantly greater. Oilseed rape’s root length per unit dry weight was about twice that of wheat. The leaf area:root length ratio of oilseed rape plants was greater than that of wheat but not significantly so.

4.3.2. Hydraulic conductivity

On a root area basis, the hydraulic conductance of spring oilseed rape roots was over two times greater than spring wheat (Table 8). The conductance per unit root length was also on average greater for oilseed rape roots, but not significantly so. The whole root system conductance of oilseed rape plants was two and a half times that of wheat plants in both experiments.

Table 1. Root and shoot parameters of oilseed rape and wheat plants measured for root hydraulic conductivity, mean of six replicates and sem are given. In the last column the p-value of a Kolmogorov-Smirnov test for difference between oilseed rape and wheat is given.

	Oilseed rape	**Wheat**	**p-value**
Total root system conductance (ml h^{-1} MPa^{-1})	1.02 ± 0.114	0.44 ± 0.078	0.002
Conductivity (ml h^{-1} MPa^{-1} m^{-1} root length)	0.080 ± 0.014	0.057 ± 0.011	0.223
Conductivity (ml h^{-1} MPa^{-1} m^{-2} root surface area)	113.1 ± 20.0	53.5 ± 10.6	0.016
Root diameter (mm)	0.224 ± 0.006	0.328 ± 0.007	0.002
Shoot DW (g)	0.090 ± 0.008	0.066 ± 0.007	0.223
Shoot area (cm^2)	19.6 ± 1.2	8.0 ± 0.2	0.002
Specific root length (m g^{-1})	589 ± 25.0	228 ± 24.9	0.002
Leaf area/root length (cm^2 m^{-1})	1.50 ± 0.132	1.05 ± 0.0.094	0.069

4.4. Key findings

- Oilseed rape roots had a greater ability to transport water than wheat roots.
- Oilseed rape crops may not need as dense a root system as wheat crops to extract all easily available water from the soil.

5. EXPERIMENT 3 – SENSITIVITY TO INCREASED SOIL BULK DENSITY

The sensitivity of oilseed rape and wheat to soil compaction were compared by measuring the root and shoot parameters in addition to water use of plants growing in a range of soil bulk densities.

5.1. Soil and packing regime

The experiment was laid out in a glasshouse in a randomised block design with five replicates per treatment. Sandy clay loam soil was sieved with a five mm sieve prior to packing into pots. Pots were constructed of polyvinyl chloride pipes, with an inner diameter of 7.6 cm and 50 cm depth. Pots were cut in half lengthwise and bound back together again. This was to facilitate recovery of the soil and root system after harvest. Plants were given water every few days, from the base of the pot, to bring the soil back to field capacity. Mineral nutrients were supplied to give applications equivalent to 120 kg ha^{-1} N, 83 kg ha^{-1} K and 30 kg ha^{-1} S. The bottom 44 cm of each pot was packed with soil to a dry bulk density of 1.1, 1.2, 1.3 or 1.4 g cm^{-3}.

5.2. Measurements

The pots were weighed every two to four days to determine plant water use and evaporation of soil water. The stomatal conductance of the youngest expanded leaf was measured with an AP4 porometer (Delta-T devices, Cambridge, UK), on days 12 to 21 after planting.

At harvest, 22 days after planting, the number of leaves, number of tillers (wheat only), shoot projected area and shoot fresh weight were measured. The shoot tissue was dried to constant weight to determine dry weight.

The containers with soil and root systems were kept at 4°C until washing and scanning of roots. The pot was opened length-wise and soaked in a tray of water to soften the soil. The depth of the deepest root was measured and the soil core was cut into four equal parts of 12 cm depth each. The soil was washed from the root system over a five mm and two mm sieve. Roots were placed in a tray of water and scanned with a Régent LA1600 scanner, the images were analysed with Winrhizo software (Régent Instruments Inc, Quebec, Canada).

5.3. Analysis

To test for the effects of species and the effects of increasing soil bulk density (i.e. soil strength) data were tested with two-way ANOVAs in GenStat (GenStat 11.1 2008, VSN International Ltd, UK). If there was a significant interaction ($p < 0.05$) of the factors species and bulk density on a parameter, it indicated that the species differed in their in sensitivity to soil bulk density.

5.4. Results

5.4.1. Plant growth

While oilseed rape shoots were larger, oilseed rape root length density, root area, root dry weight and the depth of longest root were not significantly different from wheat when averaged over soil bulk density.

An increase in soil compaction resulted in a significant decrease in total shoot area, shoot dry weight, specific shoot area, root length density, root area and depth of rooting for both species. The average root diameter of oilseed rape plants was not affected by soil compaction, while the root diameter of wheat plants increased with increasing soil compaction (Figure 6). Although total root length at high bulk density was smaller, the root length in the top 12 cm of soil was greater in the 1.4 g cm^{-3} treatments than in the less compacted treatments (data not shown).

For almost all parameters the interactions of the factors species and bulk density was not significant, implying that oilseed rape and wheat responded to bulk density in the same way. However, the average root diameter of oilseed rape plants did not respond in a clear pattern to increased soil compaction, while the root diameter of wheat plants increased with increased soil compaction giving a significant species x bulk density interaction ($p < 0.01$) (Figure 6).

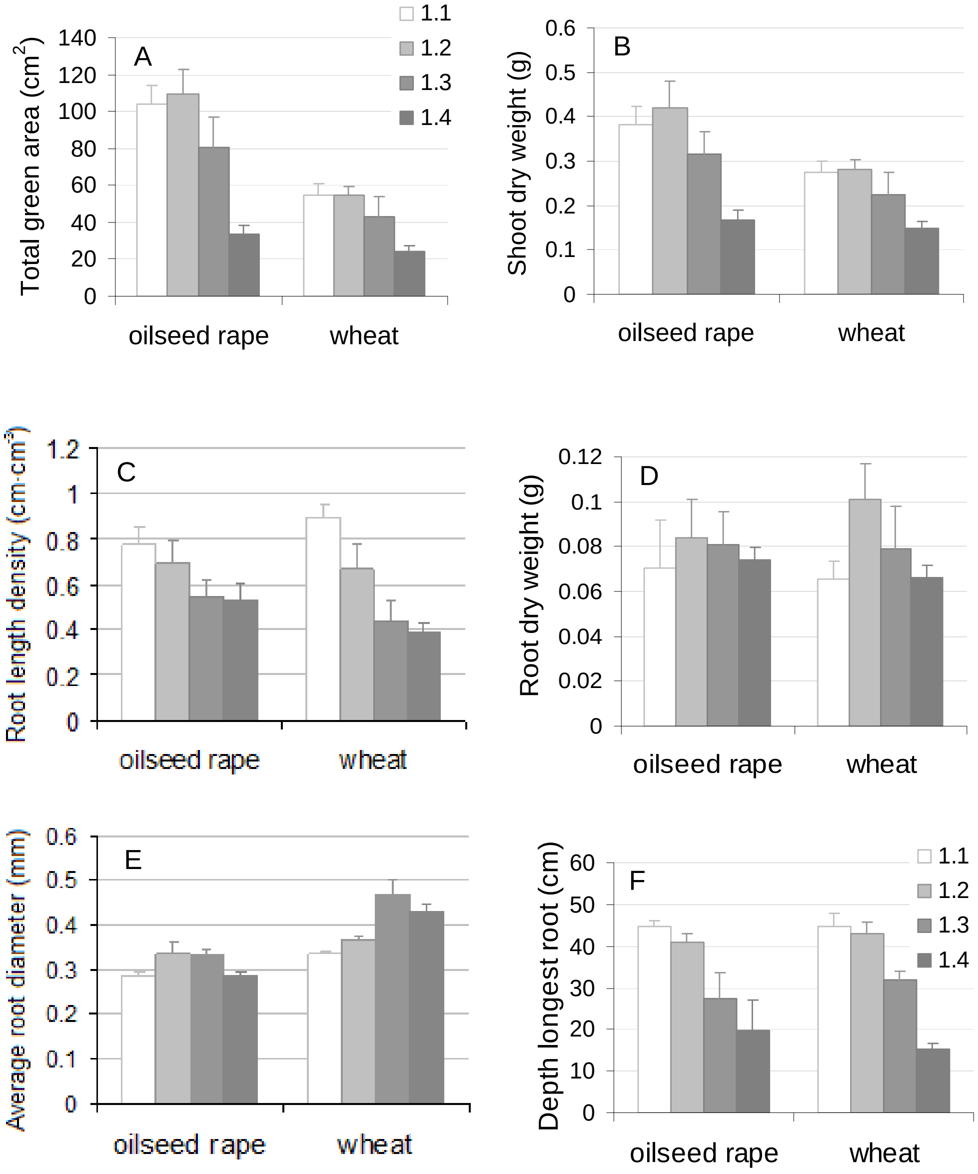

Figure 6. Influence of soil bulk density, varying from 1.1 to 1.4 g cm^{-3} (see key), on root and shoot properties of oilseed rape and wheat plants.

Table 1. Results of two-way ANOVA tests on growth and harvest data, p-values are given for species effect (oilseed rape and wheat), soil bulk density effect (1.1 to 1.4 g cm^{-3}) and interaction of those two factors.

Parameter	**species**	**bulk density**	**interaction**
Total green area	< 0.001	< 0.001	0.101
Shoot dry weight	0.002	< 0.001	0.452
Root length density	0.520	< 0.001	0.429
Root dry weight	0.968	0.314	0.819
Root diameter	< 0.001	< 0.001	0.002
Depth longest root	0.834	< 0.001	0.737
Specific shoot area (cm2 g-1)	< 0.001	< 0.001	0.252

5.4.2. Water use

The pots that were planted with oilseed rape lost more water by evapotranspiration than pots planted with wheat (Figure 7). Not only was the total evapotranspiration from oilseed rape greater than that wheat, its transpiration rate per plant and per unit root length were also significantly greater when averaged over soil bulk density treatments (Figure 7, Table 10). The water use by plants was affected significantly by soil bulk density, plants growing in more compacted soil transpiring less water in total and at a slower rate (Table 10).

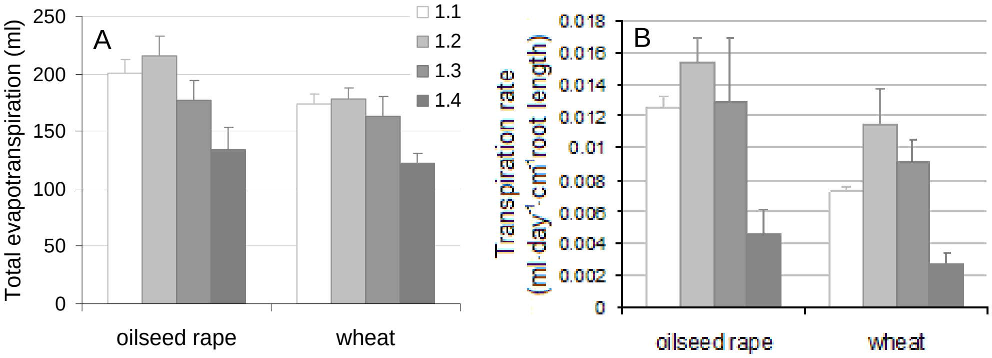

Figure 7. The influence of soil bulk density on transpiration and water status of oilseed rape and wheat plants. The error bar depicts sem of five replicates.

Table 1. Results of two-way ANOVA tests on water use data in Figure 6, p-values are given for species effect (oilseed rape and wheat), soil bulk density (1.1, 1.2, 1.3 and 1.4 g cm^{-3}) effect and the interaction of those two factors.

Parameter	**species**	**bulk density**	**interaction**
Cumulative evapotranspiration day 22	0.036	< 0.001	0.783
Transpiration rate day 20 to 22:			
Per unit root length	0.01	< 0.001	0.862

5.5. Key findings

- Both species are affected by soil compaction; compaction resulted in reduction in shoot weight and area and also in total root length.
- Oilseed rape was not significantly more sensitive to increased soil compaction than wheat in this experiment.

6. EXPERIMENT 4- SENSITIVITY TO INCREASE IN BULK DENSITY AND SOIL DRYING

In this experiment the sensitivity of oilseed rape and wheat to increasing soil strength were compared by measuring the relationship between stomatal closure and soil strength.

6.1. Plant growth conditions and experimental design

Details of soil preparation, fertiliser application, soil packing and seed germination are as described in the previous experiment, with the following modifications. Pots were 25 cm high and packed with soil to a depth of 24 cm. Two dry bulk density treatments were prepared, 1.2 and 1.3 g cm^{-3}. There was one oilseed rape or wheat seedling per pot.

The experiment was initially laid out in a glasshouse in a randomised complete block design with two plant species (oilseed rape and wheat), two soil bulk densities (1.2 and 1.3 g cm^{-3}) and two watering regimes (well watered and non-watered) within each of five blocks. After 24 days, the pots were transferred to a climate controlled growth room, where light intensity at plant height was greater. Pots were weighed every two to four days to determine water use. In the well-watered treatment, water was supplied to restore the soil to field capacity. In the non-watered treatment, water was withheld from day 30 onwards. The treatment was imposed after roots in pots pre-designated for both watering regimes had reached the base of the pot. This was to ensure that plants in each treatment had access to water throughout the whole soil depth before soil strength increased as a result of soil drying and thus minimize the possible differences in water use arising from differences in the depth of soil explored.

6.2. Plant measurements

Water use was measured by weighing the pots every two to four days and calculating the weight loss over the time interval. Stomatal conductance (gs) was determined on the youngest completely unfolded leaf with a portable IRGA (ADC-LCA4 Analytical Development Co. Ltd, Hoddesdon, Herts, UK). At harvest (day 43, Dec 22), the shoot area of each plant was measured separately, and for each plant the area of dead (non-green leaves and petioles either still on the plant or shed) and the live (green) parts were measured separately. The shoot area was measured with a LI-3100 leaf area meter (Li-Cor Biosciences, Cambridge, UK). The shoots were dried at 70°C in a fan-assisted oven to constant weight and weighed to determine dry weight.

Directly after harvest of the shoots, the pots with soil and root systems were put in a freezer at -18°C. After soaking overnight, the soil was washed from the roots with a Delta-T root washer (Delta-T Devices Ltd, Cambridge, UK). A subsample of the roots was scanned with a Régent

LA1600 scanner, the images were analysed with Winrhizo software (Régent Instruments Inc, Quebec, Canada).

6.3. Calculations and analysis

Soil sample rings with a diameter of 5.6 cm and a depth of 4.0 cm were packed with soil to dry bulk densities of 1.2 and 1.3 g cm-3 and put on tension tables at known tension to determine the relationships between soil moisture content, soil matric potential and soil strength. Soil physical properties were measured at the James Hutton Institute (formerly SCRI).

Soil strength was measured on the same cores with a penetrometer with a 1 mm diameter tip after equilibration at potentials of minus 10, 25, 50 and 200 kPa.

To eliminate the influence of time or plant age on stomatal conductance, the stomatal conductance of non-watered plants was expressed as a ratio of that of well-watered plants (referred to as the relative stomatal conductance).

6.4. Results

6.4.1. Soil physical properties

The relationship between soil volumetric water content (x) and soil strength in MPa (y) is described in Figure 8

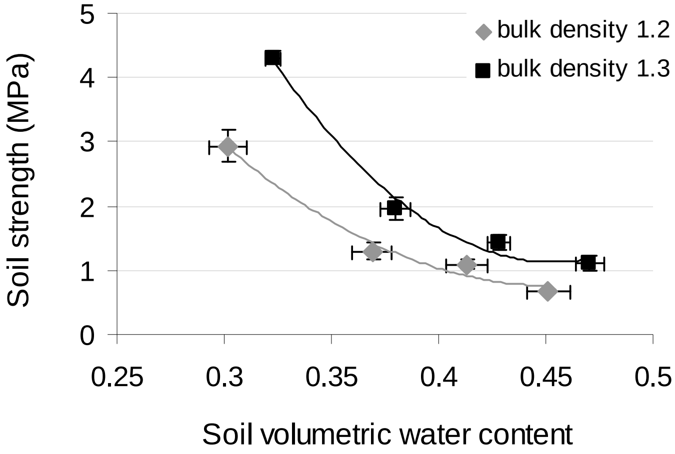

Figure 8. Relationship between soil strength and soil volumetric water (in cm^3 cm^{-3}) content of soil at bulk densities of 1.2 g cm^{-3} and 1.3 g cm^{-3}. Sample size was six and error bars depict standard errors of the mean. The fitted curves are second order polynomials.

6.4.2. Water use and stomatal response

Stomatal conductance decreased over time for plants in both the non-watered and well-watered treatments. At the start of the experiment, when plants were unstressed, oilseed rape plants had a greater stomatal conductance than wheat plants (ca. 0.4 and 0.3 mol m^{-2} s^{-1} respectively).
The response of the stomatal conductance (gs) of the youngest fully developed leaf of oilseed rape and wheat to increasing soil strength was plotted in Figure 9. Power function curves were fitted to compare the relative gs of oilseed rape and wheat to increasing soil strength.

Both oilseed rape and wheat started reducing their stomatal conductance relative to controls as the soil strength increased. The relative gs of oilseed rape showed a steep initial decline as soil strength increased. In wheat the decline was less pronounced. However, for both species there was a lot of variation not accounted for by the relationship (R2 = 0.62 and 0.25 for rape and wheat respectively).

Relative gs showed little further response to increases in soil strength above 6 MPa. There were no indications that one species began to respond to soil strength earlier than the other (i.e. at a lower threshold soil strength). Above a soil strength of 6 MPa, oilseed rape plants had significantly lower gs ratio than wheat (i.e. they closed their stomata more relative to well-watered controls) (Figure 9).

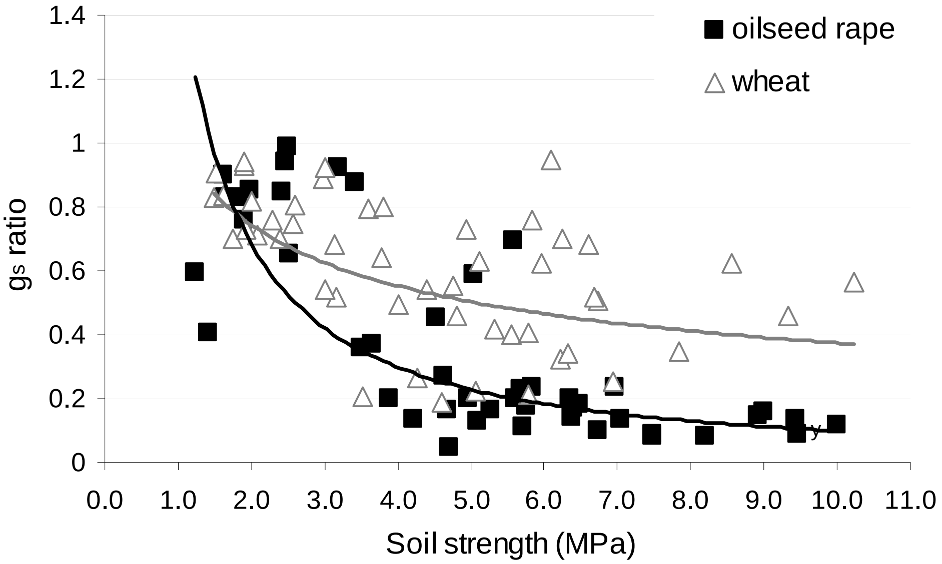

Figure 9. The relationship between the relative stomatal conductance of non-watered plants and soil strength. The stomatal conductance of non-watered plants is expressed as a ratio of the average stomatal conductance of well-watered plants in the same bulk density treatment on the same measurement occasion.

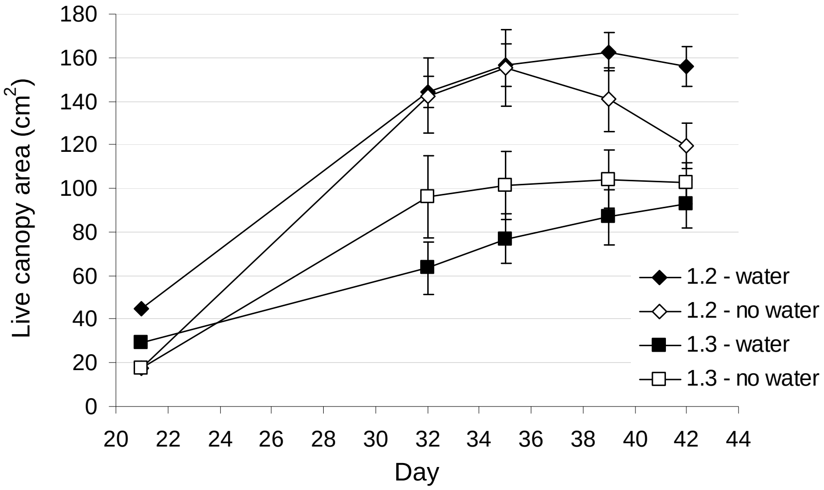

Figure 10. Total live (green) shoot area development in time for oilseed rape plants in different treatments.

6.4.3. Effect on other plant parameters

For both species an increase in soil bulk density from 1.2 to 1.3 g cm^{-3} resulted in a significant decrease in shoot dry weight, total leaf area, root length, root projected area and root dry weight (data not shown). The uptake rates of water per plant and per unit root length were significantly decreased by withholding water in both wheat and oilseed rape. Withholding water at soil bulk density of 1.2 g cm^{-3} had a significantly greater effect on dry weight of live leaves than at 1.3 g cm^{-3}. This trend can also be observed in Figure 11, where the live canopy development of oilseed plants was plotted. Water use parameters were equally sensitive to soil compaction within the time frame of the experiment.

6.5. Key findings

- At low soil strength oilseed rape had a greater stomatal conductance than wheat.
- As soil strength increased, stomatal conductance decreased to a greater extent in oilseed rape, indicating a more sensitive response.

7. EXPERIMENT 5 – THE ABILITY OF OILSEED RAPE AND WHEAT TO USE BIO-PORES

Plants often rely on pores to explore the soil and to reach soil and water stored below a plough pan. The ability of oilseed rape and wheat to exploit pores to penetrate hard soil layers was compared in a pot experiment.

7.1. Soil and packing regime

Pots made of polyvinyl chloride pipes. The twelve cm layer of sandy clay loam soil below and above the compacted layer in the centre of the pot was packed to a dry bulk density of 1.1 g cm^{-3}. The 5 cm thick compacted layer in the centre had a density of 1.5 g cm^{-3}. Initially, the pots consisted of two sections. Firstly the lower five cm of the top the section was packed in two layers of 2.5 cm, to a dry bulk density of 1.5 g cm^{-3} using a hydraulic press. With a power drill and a 2 mm drill bit, seven holes (pores) were drilled in an even pattern (see Figure 11) through the compacted layer of half of the number of pots.

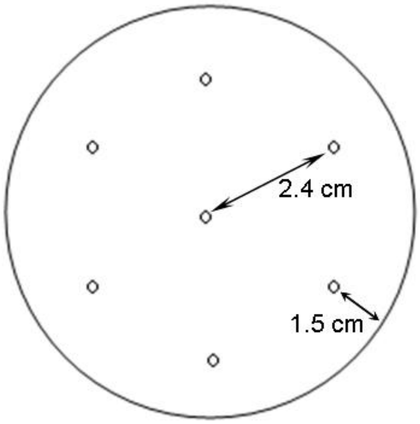

Figure 11. Location of the seven two mm diameter pores in the cross-section of the compacted layer. Roots that touched the pot edge and roots that were within two mm of the pot edge were counted as ‘edge’ roots.

7.2. Plant growth conditions

The number of seedlings was thinned down to two per pot, either oilseed rape or wheat. The experiment was laid out as a randomised block design with six replicates within a growth cabinet. The pots were watered from the top on 6, 12, 15 and 20 days after transplantation to bring the soil back up to field capacity, by calculating the loss of weight and re-supplying that amount of water. The experiment was terminated when all plants had lost turgor, as shown by visible wilting, 30 days after transplantation.

7.3. Measurements

Water loss from the soil and hence transpiration rate of the plants was determined by weighing of the pots.

At harvest time, the oilseed rape plants were at growth stage 1.4 to 1.7 (leaf production stage, 4th to 7th leaf exposed) (Letham-Shank-Farm 2010) and the wheat plants were at Zadoks growth stage 2.9 (late tillering) (Zadoks et al. 1974). After harvesting of the shoots, the pots with soil and root systems were frozen at -18°C. Three cross-sections were cut though the frozen pots with an industrial band saw. The first was through loose soil 2.5 cm above the compacted layer (named 'top' from here onwards), the second through the centre of the 5 cm thick compacted layer ('compacted') and the third through loose soil 2.5 cm below the compacted layer ('bottom').

The position of root-ends at the interfaces of the three cross-sections were viewed under a dissection microscope, traced on paper and counted. Additionally, the number of roots directly within two mm of the pot-edge and roots within the two mm pores were recorded. In the control pots, the roots that were in the corresponding area of where pores were situated in the pore-treatment were counted.

7.4. Results

7.4.1. Number of roots in bottom layer and effect of pores

Oilseed rape had more roots in the bottom layer and significantly fewer roots in the top layer than wheat. The presence of pores resulted in more roots in the bottom layer, for both oilseed rape and wheat (Figure 12, Table 11).The increase in the number of roots in the bottom layer in the presence of pores was significantly more with oilseed rape plants than wheat ($p < 0.05$ for species x pore interaction when edge roots excluded (Table 11).

Oilseed rape plants had significantly more roots in the cross-section of the compacted layer (Figure 11, Table 1). The presence of pores increased the number of roots in the compacted layer for both species, but not significantly so ($p=0.085$, Table 1). Wheat plants had a greater percentage of roots growing along the edge of the pot than rape (Table 1).

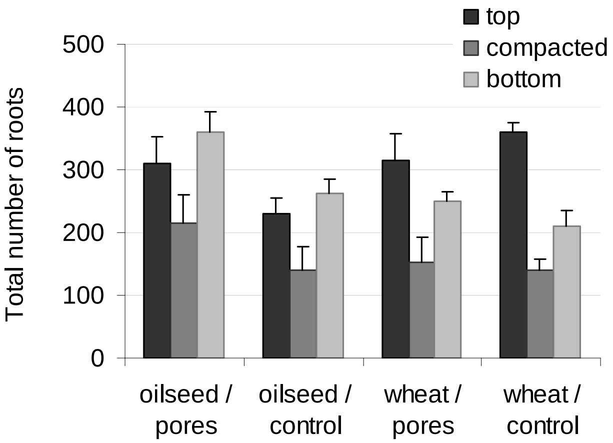

Figure 12. The total number of roots in a cross-section of the top, compacted (middle layer) and bottom layer. The roots growing along the edge of the pot were included, mean and sem of four replicates is given.

Table 1. Results (p-values) of statistical test testing for effect of species, presence of pores and the interaction of those factors on the number of roots in the cross-section of each layer, data in Figure 12.

	parameter	**Species**	**Pores**	**Species x pores**
All roots				
	Top	0.056	0.582	0.076
	Compacted	0.187	0.088	0.213
	Bottom	0.002	0.005	0.148
Roots along edge excluded				
	Top	0.04	0.518	0.061
	Compacted	0.065	0.386	0.296
	Bottom	< 0.001	<0.001	0.018
Roots along edge only				
	Top	0.433	0.894	0.424
	Compacted	0.640	0.028	0.210
	Bottom	0.451	0.626	0.870

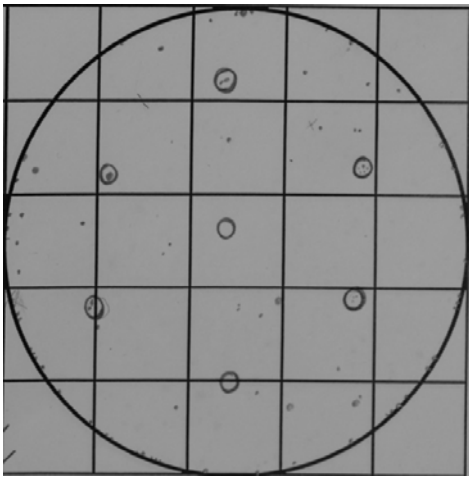

Figure 13. Diagram of location of oilseed rape root ends in a cross-section of a compacted layer with pores, pores are highlighted by the drawn circles.

7.4.2. Growth in bio-pores

Both species had roots growing in the pores. Figure 13 is an example of a root-count template. Here there were roots growing in five out of the seven pores. Oilseed rape had a greater number of roots growing in pores than wheat, both in absolute and relative terms (Figure 14). Almost 19% of oilseed rape roots in the compacted layer (roots growing along the edge were excluded from the count) were situated in pores, while for wheat this was only 10%. In the control treatments 2.6% and 1.5% of the total number of roots for oilseed rape and wheat respectively were situated in the areas where pores were drilled in the corresponding pore-treatment (Figure 1).

For both species a large number of roots were found in the compacted layer not associated with pores, indicating that roots of rape and wheat were able to grow into this dense layer (Figure 13).

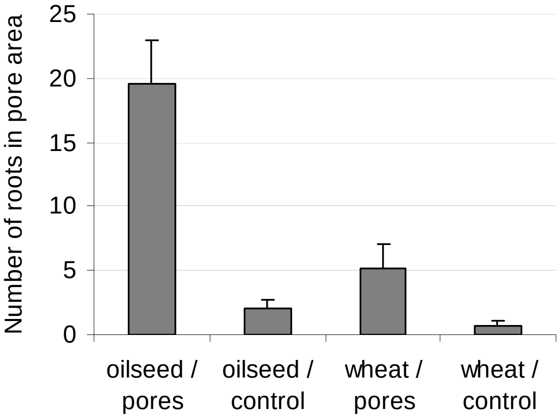

Figure 1. The number of roots in pores, or the in the corresponding area in control pots, mean of six replicates, vertical errors bars represent sem.

Table 1. Results (p-values) of two-way ANOVA testing for the effects of species and pores on the number of roots in the compacted layer and in the pores (six replicates), also see Figure 14.

	species	**pores**	**Species x pores**
Total root count (excl. roots at edge)	0.001	0.085	0.317
% of roots along edge of pot	0.001	0.535	0.943
Number of roots in pores	0.002	< 0.001	0.008

Oilseed rape plants had a greater shoot dry weight than wheat plants and the presence of pores had no significant effect on shoot dry weight (Table 2, 14). Oilseed rape plants had a significantly greater live shoot area and the area of dead leaves was also significantly greater than that of wheat. The plants in the control treatments had a significantly greater shoot area than the plants in treatment with pores when averaged across species. The area of dead canopy was significantly greater in treatments with pores, regardless of species. There were no significant species x pore interactions in any of these plant characteristics indicating that the oilseed rape and wheat responded in the same way to the presence of pores.

Table 2. Plant properties at the end of the experiment, 30 days after transplanting. Values are means per plant of six replicate pots and sem.

	Oilseed rape		**Wheat**	
	pores	**control**	**pores**	**control**
Dry weight shoot (g)	2.06 ±0.032	2.09 ±0.081	1.91 ±0.060	1.95 ±0.057
Number of unfolded leaves	5.4 ± 0.24	4.9 ± 0.08		
Number of tillers per plant			15.1 ± 1.06	17.0 ± 0.89
Live plant shoot area (cm^2)	181.7 ±4.68	194.7 ±5.95	171.2 ±2.45	184.3 ±3.76
Total shoot area (cm^2)	224.8 ±4.84	227.8 ±5.34	193.4 ±1.28	203.3 ±4.43
Dead shoot area (cm^2)	43.2 ±1.25	33.2 ± 4.56	22.2 ± 3.35	19.0 ± 1.28
Percentage dead area (cm^2)	19.5 ± 0.69	14.2 ± 1.91	11.5 ± 1.60	9.6 ± 0.44

Table 3. Results of statistical tests (p-values two-way ANOVA) on harvest data of oilseed rape and wheat plants, Data in Table 2.

P-values	**species**	**pores**	**Species x pores**
Dry weight shoot	0.003	0.488	0.907
Number of unfolded leaves (oilseed rape only)		0.076	
Number of tillers per plant (wheat only)		0.434	
Live plant shoot area	0.036	0.011	0.989
Total shoot area	< 0.001	0.173	0.415
Dead shoot area	< 0.001	0.029	0.232
Percentage dead area	< 0.001	0.013	0.209

7.5. Key findings

- Presence of pores in the hard layer led to a significant increase in number of roots in the deeper soil for both species.
- Oilseed rape had more roots growing in pores and its number of roots in the bottom layer was more increased. This suggests that oilseed rape is better able to exploit soil pores than wheat.

8. DISCUSSION AND CONCLUSIONS

8.1. Different strategies of water use by oilseed rape and wheat

When grown as individual plants or small populations, oilseed rape transpired at a faster rate than wheat when supplies of water were unlimited. This was found consistently across experiments incorporating plants at different growth stages and under different growth conditions (open-sided and closed glasshouses and controlled environment chambers). However, when the supply of water was restricted and the soil allowed to dry oilseed rape responded more sensitively than wheat. Stomata closed more rapidly as the soil dried and soil strength increased (Experiment 1 and 4) and where the duration of the experiment was long enough (Experiment 1), there was a greater reduction in growth relative to irrigated plants than was found in wheat. Thus, oilseed rape may be considered to be profligate in its use of water when the supply is ample, but more conservative than wheat when confronted with a restricted supply. Wheat by contrast appears to be less wasteful in its use of water when the supply is unrestricted, but also less sensitive to soil drying. Stomatal conductance was less responsive to changes in soil water content and soil strength and water appeared to be accessed from deeper soil layers sooner than by oilseed rape. Wheat may also allocate more energy to reproduction in response to water stress, since its ear dry weight was hardly reduced in non-irrigated treatments, while oilseed rape pod dry weight was halved (Experiment 1).

Oilseed rape can be seen as having an opportunist strategy of water use. When water is readily available its high stomatal conductance will permit high rates of photosynthesis, but at the expense of a high transpiration rate and large total water use and thus low WUE (Experiments 1, 2 and 4).

As the soils dries, closure of stomata and conservation of water could allow the plant to survive and complete its lifecycle, but at the expense of growth and yield. There was evidence that stomatal conductance was reduced (transpiration rate reduced below the potential rate) at a lower soil moisture deficit than in wheat (Experiment 1). Relative to oilseed rape, wheat is perhaps better-adapted to normal field conditions and slight water limitation by metering out finite supplies of water for longer through the season, but cannot profit as well from extremely fortunate conditions. Thus wheat may have a safer strategy which enables it to survive in adverse conditions and suffer less yield loss.

Oilseed rape was found to have a greater root hydraulic conductivity than wheat, at least when water supplies were unlimited (Experiment 2), facilitating higher rates of inflow per unit root length. Other aspects of the physiology of oilseed rape are consistent with the apparent opportunistic strategy of water use by this species. From the literature it is known that oilseed rape has a limited capacity for osmotic adjustment and this may contribute to the sensitivity of pod growth and development to drought (Jensen et al. 1996). Most plants are able to osmotically adjust to some degree by accumulating solutes, mainly sugars, organic acids and ions and thereby keep cells turgid for longer as tissue water potential declines. The maintenance of turgor ensures continuation of cell elongation and division and also of keeping stomata open (Taiz and Zeiger 1998). Wheat, on the other hand, is a relatively good adjuster (Cutforth et al. 2009), which could have contributed to the less severe reduction in canopy area of wheat when water was withheld in the lysimeter experiment in Experiment 1. Osmotic adjustment could have caused the leaves of wheat to remain turgid when water supply was limited and facilitate leaf expansion.

8.2. Root growth and response to soil physical conditions

Although water stress (low soil water potential) is the most intensively researched physical stress to root growth, field data show that it alone may not be the critical factor. Additional factors including lack of oxygen and mechanical impedance, may all act on the roots in combination or sequence with water potential as the soil water content or soil structure change (Whitmore and Whalley 2009). In tilled and untilled soil, soil strength (mechanical impedance) appeared to be the main soil physical factor controlling root growth of oat plants (Ehlers et al. 1983). Soil strength varied predominantly via changes in soil water content and, in this experiment, bulk density seemed to be of minor importance for root growth.

In the current project, uniform soil compaction reduced total root length and altered its distribution down the soil profile to a similar extent in both oilseed rape and wheat (Experiment 3). In each case compaction led to a shallower root system as reported for field grown plants.

In the relatively loose well watered soil in Experiment 1, oilseed rape was able to generate root length densities deep in the subsoil (70-80 cm) equivalent to those of wheat. Differences were observed in the temporal and spatial pattern of water extraction by oilseed rape and wheat when grown on stored water. Oilseed rape extracted water from each soil layer later than wheat, but at a faster rate so that all the available water was extracted by about the same time (Experiment 1, data not shown).

However, field soils are not uniform in structure or in the availability of water and nutrients. Plasticity of root growth and physiological activity is mechanism that enables plants to acquire resources from heterogeneous soil. Experiment 5 provided evidence that oilseed rape may also be better able to exploit spatial variation in soil structure. When a compacted layer was present in the soil, analogous to a plough pan in the field, oilseed rape benefited more from artificial bio-pores in the layer than wheat. Oilseed rape had a greater number of roots growing in the pores and more roots growing in the soil layer below the compacted layer. In this experiment, there was little benefit in terms of water extraction from having these extra roots in the subsoil, but the experiment was of short duration and the supplies of water were finite. If oilseed rape is also able to exploit pores in the field more effectively than wheat, greater differences in growth might be expected to occur over the course of the season, especially if there is adequate water available in the deep sub soil layers.

Currently little is known about the extent of genotypic variation in root plasticity of oilseed rape and whether this might be improved through breeding. Genetic differences in rooting may also exist between semi-dwarf, conventional and hybrid oilseed rape varieties (HGCA Project Report 402). Variation in root plasticity has been reported for wheat. Song et al (2010) compared the drought tolerance of modern and old wheat cultivars and came to the conclusion that modern cultivars have a greater plasticity in root morphology and have the ability to develop thinner roots when water is scarce.

8.3. Suggestions for crop management

The opportunist strategy and extravagant use of water by individual or small populations of oilseed rape plants is not something which was obvious from the literature relating to field crops. In this project, although care was taken to mimic field conditions, the boundary layer resistance around the canopy of the mini-crops could have differed from a field crop (Jarvis and McNaughton 1986). Thus the differences between wheat and oilseed rape in terms of water use are likely to be smaller in the field.

There is little known about genetic diversity of oilseed rape root growth. If there is variation in rate of root system development and in maximum rooting depth, it may be possible to select for greater access to subsoil water thereby increasing the crop’s ability to avoid drought. Additionally crops may benefit if canopy function could be maintained for longer as the soil begins to dry i.e. by having a less conservative stomatal response and or a greater degree of osmotic adjustment. This could ensure a lower loss of yield when water supply is limited.

To improve oilseed rape ability to capture water stored in the soil to avoid water limitation, the following actions could be taken (also see HGCA publication ‘Soil management for sustainable profit, 2005):

- Manage the soil in such a way that root systems are not hampered in their exploration of the soil, i.e. they are not impeded by poor soil structure due to soil compaction, for instance by adopting a controlled traffic policy.
- Taking remedial action such as sub-soiling, when compaction is found, to improve root growth to depth and soil drainage.
- Use or develop varieties which have deep root systems, so that water which is stored deep in the soil can be accesses when there is a period of low rain fall.

- In order to make an oilseed rape yield less sensitive to water limitation, the following actions could be taken:
- Use/develop varieties which are able to osmotically adjust and therefore maintain functions during drought spells instead of excising leaves.
- Develop varieties with yield components which are less sensitive to water limitation, as in Experiment 1 allocation to pods was severely reduced when water was limited.

In conclusion, oilseed rape appears to exploit the soil just as well or better than wheat. However its demand for water may be greater and oilseed rape’s shoot is more sensitive to water limitation and soil hardening. As UK summers are expected to become dryer and warmer oilseed rape, like wheat, could possibly benefit from deeper rooting. Greater access to subsoil water, coupled to a less sensitive stomatal response could lead to greater yields under mild drought conditions.

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