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Effects of waterlogging on soil aeration and on root and shoot growth and yield of winter oats (*Avena sativa* L.)

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Summary Winter oats were grown outdoors in lysimeters containing monoliths of a sandy loam soil. The soil was either freely-drained throughout the experiment or waterlogged to the soil surface from mid-January until mid-April. After the start of waterlogging the oxygen flux density decreased most rapidly nearer the soil surface and in the upper 50 cm declined to zero. At 80 cm depth the oxygen flux density at the end of the waterlogging still had not diminished to zero. While the soil was waterlogged root growth was negligible in the 20–50 cm zone of the soil profile, whereas below that depth root growth continued, reaching 95 cm by the end of the treatment. During the latter part of the waterlogging period root growth resumed in the upper 10 cm, and in the upper 2.5 cm was greater than in the freely-drained treatment.

At the end of the waterlogging period, the total root length and shoot dry weights were 77 and 60% of those in the freely-drained treatment, tillering was restricted and leaf area index diminished. However, by anthesis, root length and shoot weights of the plants that had been waterlogged were only 10 and 12% less respectively than for the freely-drained plants. At harvest, total dry matter and grain yields were only 9% less, the latter largely through fewer grains per panicle.

Introduction

The heavier crop yields that can result from drainage[11] must be caused in part by improved root growth or function. Widely quoted publications on drainage and soil management[16,20], suggest that deeper rooting, facilitating access to water during dry weather, is one of the main advantages of draining the soil. In experiments in lysimeters, pea

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roots extracted less total water from the soil after waterlogging, especially from the deeper parts of the profile[1], suggesting that the capacity of the roots to absorb water had been impaired; but winter wheat that had been waterlogged extracted more water from the upper 20–40 cm and less from below those depths than wheat that had grown in freely-drained soil[13]. Root growth of peas is greatly restricted by waterlogging[9], and in controlled environments anaerobiosis inhibited root growth of winter oats[4] and winter wheat[18]. However little information exists on effects of anaerobic soil conditions on the root growth of cereals in the field. Recent field studies with winter wheat[10] showed that after the water-table in an undrained clay soil had been about 20 cm below the surface for three months in the winter compared with 45 cm in a drained treatment[15], root density in April when the water-tables had fallen was greater in the deeper parts of the drained profile[12]; subsequently more water was extracted[15], and grain yield was about 10% heavier[12]. In this paper we report the results of an experiment on winter oats, grown outdoors in lysimeters where effects of prolonged winter waterlogging on soil aeration, and on root and shoot growth and yield were examined.

Methods

A description of the experimental system of lysimeters, the moveable shelter to exclude unwanted rainfall, the irrigation facilities, the means of controlling the depth of the water-table and of the sandy loam soil, a gley podzol (or aquentic haplorthod), used in this experiment has already been published[6]. Winter oats, cv. Pennal, were grown in 1980–81 in 32 lysimeters, each 80 cm diameter and 135 cm deep, containing soil monoliths.

There were two treatments: (i) freely-drained, with the water-table at 50 cm until mid-January, at 90 cm thereafter in winter, and draining below that depth when water was extracted by roots in the spring and summer, and (ii) waterlogged to the soil surface for 90 days from mid-January, also with the water-table at 50 cm before waterlogging and afterwards at 90 cm as in (i). In earlier work on this soil the oxygen flux density at 50 cm depth had remained relatively large during waterlogging when oxygen concentrations were small[3]. This large flux may have been caused by occluded gas and larger porosity in the subsoil[3], and may in part explain why wheat crops on this soil have been less affected by waterlogging than those on an adjacent clay soil[7]. To lessen the possibility of oxygen trapped in the deeper parts of the profile offsetting the otherwise damaging effects of waterlogging, the water-table was maintained at 50 cm depth in all lysimeters until the differential treatments started in mid-January. Sixteen replicates of the two treatments were allocated to the thirty-two lysimeters.

The soil and plants were destructively sampled on 5 occasions during the growth of the crop (the number of replications on each occasion is given in parenthesis):- at the start of waterlogging, 15 January (1); at the end of the phase of rapid decline in oxygen partial pressure and flux density, 2 February (2); when the oxygen concentration had reached a minimum in the upper part of the soil profile, 12 March (2); at the end of the waterlogging, 14 April (2); and at anthesis, 26 June (2). The remaining 7 replicates were used for yield estimation at maturity. At each sampling measurements of the shoots and roots were made. Shoot measurements were number of tillers, area of leaves and dry weight. At maturity the grain and straw yields, yield components and nutrient concentration were measured. Root measurements, made after washing 8 cores (10 cm diameter) per lysimeter, were length and dry weight in the depth zones 0–2.5 cm, then at 5 cm increments to 37.5 cm, 37.5–45 cm and at 10 cm increments to 115 cm. In the waterlogged lysimeters concentration of dissolved oxygen was measured in samples collected at 5, 20, 50 and 80 cm depth using a membrane covered electrode[2], and oxygen flux density and redox potential were measured at 5, 20, 35, 50 and 80 cm using platinum electrodes[2]. Soil temperature was measured at all depths using thermistors connected to a data-logger; this information also allowed correction of the measurements of dissolved oxygen concentration to the equivalents at soil temperature[2]. From other experiments using this soil[1,3,7,8] it is known that when the soil is freely-drained the oxygen concentration is close to atmospheric. Soil moisture content was measured at regular intervals at 5 cm depth increments to 20 cm, and at 10 cm increments below that depth with a neutron moisture meter in an access tube located in the centre of each lysimeter, enabling the pattern of soil water extraction to be assessed.

Details of the agronomic practice are summarised in Table 1. Before seeding, the nematicide oxamyl was incorporated into the topsoil to control free-living eelworms (particularly *Trichodorus cylindricus*) which had previously been found, and which can feed on roots. Fungicides and insecticides were used as necessary.

The annual total rainfall (858 mm) (including any necessary irrigation to reach the monthly target) was within the upper quartile rainfall for the Oxford area and about the median rainfall for Gloucester[17]. The monthly distribution was based on that for the Gloucester area (Table 2). All lysimeters received the same rainfall.

Results

Soil temperature

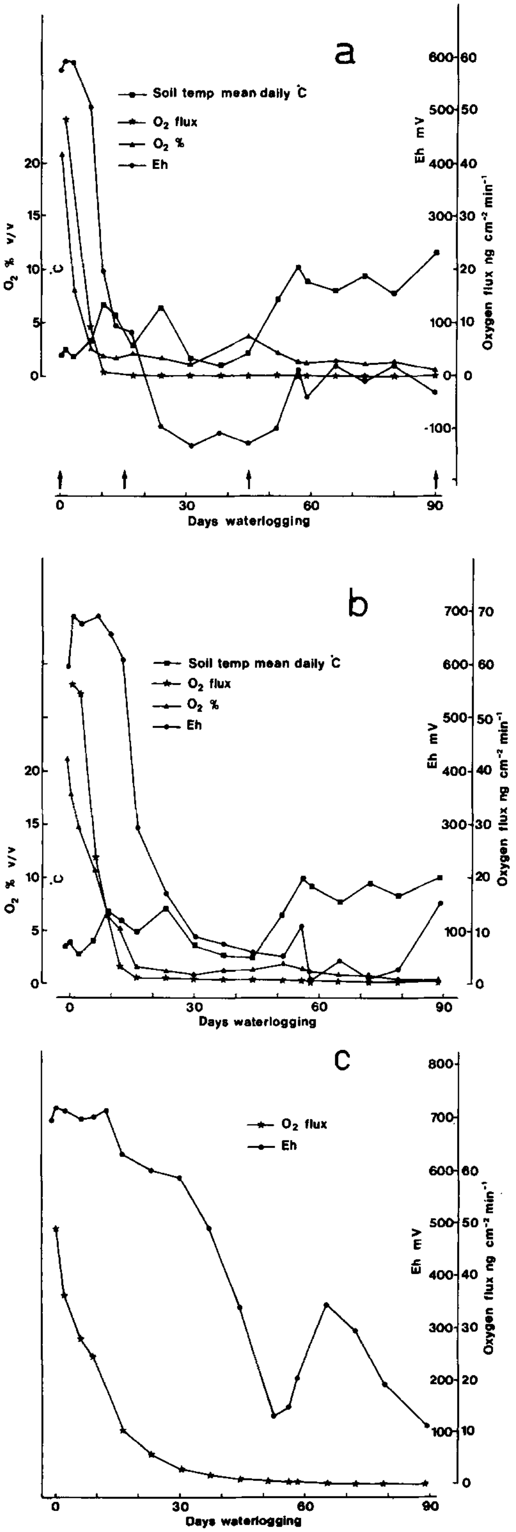
The soil temperature at 5 cm was mainly in the range 2–5°C from the start of waterlogging in mid-January until the beginning of March, rising to about 10°C for the last 40 d of the waterlogging (Fig. 1a). At 20 cm depth the temperature during January and February was slightly warmer (Fig. 1b), and at 50 and 80 cm the temperature remained above 5°C, rising more slowly in late March and April to 9°C (Figs. 1d and e). These values were within the interquartile range for the Oxford area[17].

Table 1. Agronomic practice

Fertilizer (kg/ha),	
Seed-bed, N, P, K	0, 50, 50
Top dressing of N	100 on 21 April
Sowing date	21 October
Plant population (per m^2)	397
Harvest date	10–13 August

Table 2. Monthly and annual rainfall (mm) used in experiment

Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Total
59	80	73	123	39	110	70	71	38	68	42	85	858


a
Soil temp mean daily °C
O₂ flux
O₂ %
Eh
O₂ % v/v
°C
Eh mV
Oxygen flux ng cm⁻² min⁻¹
600 60
500 50
400 40
300 30
20
100 10
0 0
-100
20
15
10
5
0
0
30
60
90
Days waterlogging
b
Soil temp mean daily °C
O₂ flux
O₂ %
Eh
700 70
600 60
500 50
400 40
300 30
20
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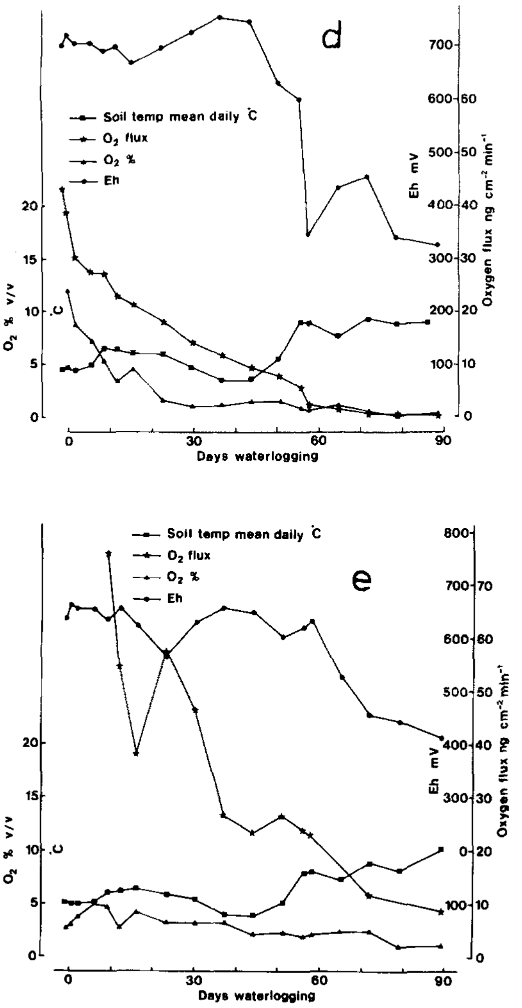

Fig. 1. Effect of waterlogging a sandy loam from 15 January to 14 April on redox potential, oxygen flux density, and concentration of dissolved oxygen. Also shown is the mean daily soil temperature. Measurements for the different depths in the soil profile: a) 5 cm, b) 20 cm, c) 35 cm (redox potential and oxygen flux density only), d) 50 cm and e) 80 cm. *Vertical arrows* in Fig. 1a indicate times of root sampling.

Aeration status of the waterlogged soil

Oxygen flux. The oxygen flux density declined most rapidly near the soil surface. The flux reached almost zero at 5, 20, 35 and 50 cm depths after 10, 16, 50–60 and 70 d respectively from the start of waterlogging (Figs. 1a–d). At 80 cm on day 90, at the end of the waterlogging, it was about 9 ng cm^{-2} min^{-1} and still declining (Fig. 1e).

Oxygen concentration. At 5 and 20 cm the dissolved oxygen concentration reached minima of 1–2% after 10 and 16 d respectively (Figs. 1a and b). At 50 cm the minimum was reached after 30 d (Fig. 1d), but at 80 cm the concentration was less than 5% from the time the water-table was raised from 50 cm to the soil surface at the start of the waterlogging treatment (Fig. 1e).

Redox potential. Redox potential declined in a pattern relating to the oxygen flux, declining faster nearer the surface, and reaching smaller values in the upper layers. Minima at 5, 20, 35 and 50 cm were reached after 30, 50, 50 and 60 d of waterlogging respectively, with the corresponding Eh being −120, 0, 100 and 300 mV (Figs. 1a–d). At 80 cm redox potential at the end of the waterlogging was 400 mV and still declining (Fig. 1e).

Root growth and function

Root growth. At the start of the waterlogging treatment in January the maximum depth of roots was 75 cm (Fig. 2a). Root length density continued to increase at all depths throughout the winter in the freely-drained controls, and by the end of the waterlogging treatment period, roots of freely-drained plants reached 95 cm. In the waterlogged treatment, root density between 20 and 50 cm did not increase, but below 50 cm there was a slight increase in root density while the soil was waterlogged. However, the maximum depth of root growth was not affected by waterlogging. The largest effect was to restrict root growth between 5 and 35 cm, (Figs. 2b–d). By mid-March, the total length of roots in the waterlogged treament was only 43% of that in the freely-drained lysimeters (Fig. 2c). However, in the uppermost layer (0–2.5 cm) between mid-March and mid-April, root length density increased faster in the waterlogged soil, and was significantly greater there than in the freely-drained soil at the end of the treatment period (Fig. 2d). The difference in total root growth between treatments diminished, so that at the end of the waterlogging the treated lysimeters had 77% of the root length in the freely-drained (Fig. 2d), but only 56% of the root weight (Table 3).

After the waterlogging treatment had ended, root density and weight increased below 5 cm, especially in the plants that had been waterlogged; at anthesis the total length of roots in the profile that had been waterlogged was 90% of that in the controls (Fig. 2e), but the weight of roots was still only about two thirds (Table 3).

Water extraction. During May and June the soil moisture deficit

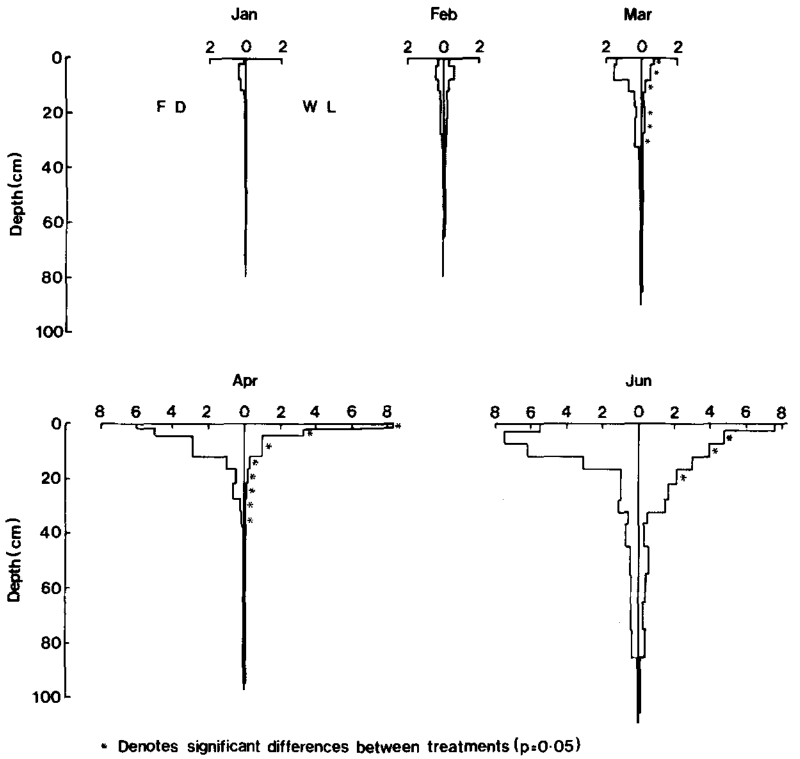

Fig. 2. Effect of waterlogging a sandy loam soil on length of winter oat roots per unit volume of soil (cm/cm^3): a) at start of waterlogging, 15 January, b) at end of phase of rapid decline in oxygen status, 2 February, c) 12 March, d) at end of waterlogging, 14 April, and e) at anthesis, 26 June. FD freely-drained; WL waterlogged. * indicates significant difference (P = 0.05).

was greater in the soil that had been freely-drained. The largest difference in soil moisture deficit between treatments was on 23 June, when the deficits were 56 and 43 mm on the freely-drained and waterlogged treatments respectively, and by which date significantly more water had been extracted from the upper 15 cm, and from below 60 cm in the freely-drained soil (Fig. 3). The maximum soil moisture deficit of about 160 mm was on 26 July, but on that date treatments did not differ in the total or in the distribution of the deficit down the profile (Fig. 3).

Shoot growth

Shoot number. The number of plants established, 397 m^{-2}, was similar on all lysimeters. Tillering was most rapid from January to March, but was restricted by waterlogging (Fig. 4), especially the higher order tillers. After the end of the waterlogging in April when

Table 3. Effect of waterlogging on root weight (g/m²)

	2 Feb		12 March		14 April		26 June	
Depth (cm) in soil	Freely-drained	Water-logged	Freely-drained	Water-logged	Freely-drained	Water-logged	Freely-drained	Water-logged
0 – 2.5	0.60	0.83	2.68	3.02	10.73	11.23	45.85	34.00
2.5– 7.5	1.90	2.00	4.20	3.05	20.15	11.95	62.30	20.00
7.5–12.5	1.10	0.95	2.35	1.05	14.05	3.00	28.70	15.75
12.5–17.5	0.75	0.55	1.35	0.50	6.15	1.20	14.75	11.90
17.5–22.5	0.55	0.40	1.10	0.45	2.95	0.40	6.00	9.25
22.5–27.5	0.60	0.35	1.00	0.45	2.75	0.25	5.65	7.15
27.5–32.5	0.45	0.30	0.75	0.45	1.90	0.20	6.65	7.60
32.5–37.5	0.30	0.20	0.35	0.30	0.95	0.20	2.90	2.85
37.5–45	0.30	0.22	0.22	0.45	0.37	0.22	4.20	2.02
45 –55	0.20	0.20	0.20	0.50	0.80	0.10	5.50	3.10
55 –65	0.05	0.08	0.20	0.30	0.80	0.20	4.60	2.80
65 –75	0.01		0.06	0.08	1.30	0.10	5.40	2.50
75 –85					0.06	0.01	5.10	2.10
85 –95							0.70	0.60
Total weight	6.76	6.08	14.5	10.6	63.5	40.3	198.3	121.6

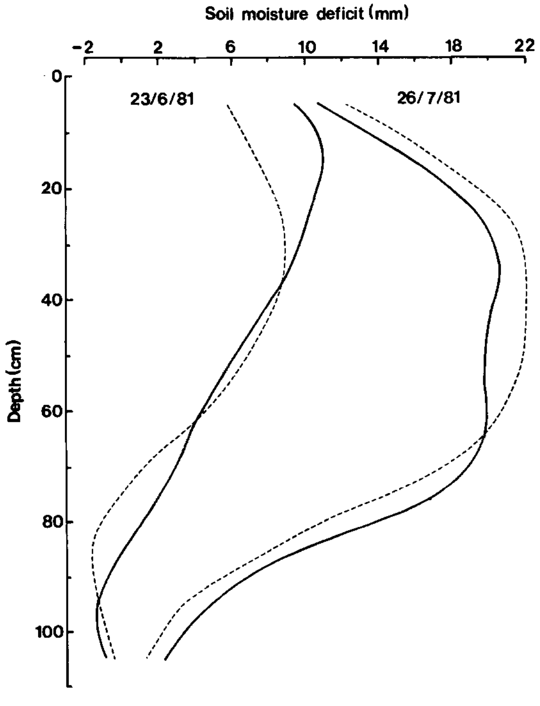

Fig. 3. Effect of waterlogging winter oats in winter on the pattern of soil water extraction on 23 June and 26 July. ——— freely-drained, ------ waterlogged.

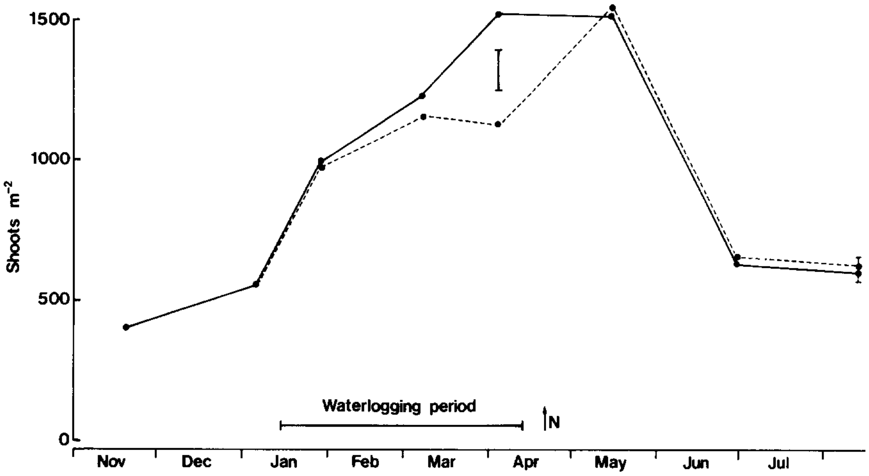

Fig. 4. Effect of waterlogging winter oats on number of shoots. ——— freely-drained, ----- waterlogged. *Arrow indicates* date that nitrogen fertilizer was applied. *Vertical bar* indicates least significant difference ($P = 0.05$).

Table 4. Effect of waterlogging on shoot dry weight and leaf area index

	15 Jan	2 Feb	12 March	14 April	26 June	Harvest
Shoot weight (g/m^2)						
Freely-drained	13.0	19.4	29.1	128.0	835	1490
Waterlogged		17.3	32.5	76.9	735	1370
Leaf area index						
Freely-drained	0.20	0.30	0.42	1.29	6.42	
Waterlogged		0.30	0.37	0.62	5.57	

nitrogen fertilizer was applied tillering was resumed on the waterlogged lysimeters (Fig. 4) so that by harvest time the maximum number of shoots and the number of ears were unaffected by the treatment.

Shoot weight, leaf area and nutrient concentration. In the early part of the waterlogging when shoot growth was slow, dry weight was unaffected, but by the end of the treatment the freely-drained plants were 40% heavier, and with a corresponding difference in leaf area index (Table 4). Subsequently the difference diminished, and at harvest, shoot weight was only 9% heavier. Stem extension was delayed by waterlogging, but at harvest the length of straw (mean 107 cm) was not affected.

The weight of grain also was 9% less after waterlogging, largely through fewer grains per panicle (Table 5).

The concentration of nitrogen, phosphorus and potassium in the grain, chaff and straw at harvest did not differ between treatments, except that potassium was more abundant in the chaff of the plants that had been waterlogged (Table 6).

Discussion

As expected the total size of the root system was restricted by waterlogging (Fig. 2), and although root growth virtually ceased in the zone 20 cm below the soil surface, and was much restricted from 35 to 50 cm, it continued in the deeper horizons. This result is consistent with the availability of oxygen in the soil profile, but contrasts with the commonly held opinion that root growth ceases in a waterlogged soil. In experiments in controlled environments, at temperatures of 7–10°C, where roots could be observed through perspex tubes, Blackwell and Wells[4] found that extension of seminal roots of oat seedlings (also cv. Pennal) was slower in waterlogged soil than in freely-drained soil at oxygen flux densities less than 56 ng cm^{-2} min^{-1}; a smaller limiting value would be expected in the slightly cooler conditions, 2–5°C, in the upper 20 cm during the early phase of waterlogging in our experiment (Fig. 1a and b). In Blackwell and Wells' work root extension stopped only when oxygen flux was effectively zero. In the work reported here the oxygen flux density in the upper 50 cm declined to about zero during the treatment (Fig. 1a–d), but at 80 cm although it declined from about 80 ng cm^{-2} min^{-1} it did not become much less than 10 ng cm^{-2} min^{-1} by the end of the treatment on 14 April (Fig. 1e). At 20 cm the oxygen flux density had reached zero on 15 February; root length did not increase at that depth until after the waterlogging had ended (Figs. 2b and c) when the oxygen supply was restored. This confirms the finding that root extension of oats ceases at zero flux density of oxygen; however since we made no direct observation of root growth, death and initiation of roots may possibly have been taking place simultaneously, although it seems unlikely.

Earlier measurements on this soil had shown that the oxygen flux density declined more slowly than the concentration of dissolved oxygen[3]. This effect was also evident at 50 cm depth in the present experiment (Fig. 1e). At 5 and 20 cm depth where both oxygen flux and concentration declined to zero in about 10 and 16 d respectively the limited sampling frequency did not permit the comparison. At 80 cm the soil had already been waterlogged from early November until the water-table was raised from 50 cm to the soil surface at the beginning of the treatment, and thus the concentration of dissolved oxygen was already down to about 5% (Fig. 1e).

Table 5. Effect of waterlogging on yield and yield components

	Freely-drained	Waterlogged	SE
Straw weight (g/m^2)	735	678	30.1
Chaff weight (g/m^2)	57.6	37.7	4.22
Grain weight (g/m^2)	701	654	14.1
Grain yield at 85% DM (t/ha)	8.24	7.68	0.17
Ears/m^2	595	610	14.0
Grains/panicle	37.5	34.7	1.45
1000 grain weight (g)	31.4	30.9	0.29

Table 6. Effect of waterlogging on concentration (mg/g) of nitrogen, phosphorus and potassium of winter oats

	Grain			Chaff			Straw		
	N	P	K	N	P	K	N	P	K
Freely-drained	15.0	3.11	3.80	6.94	0.85	7.12	2.64	0.70	10.1
Waterlogged	14.9	3.18	3.95	7.27	0.77	10.8**	2.85	0.42	13.0

** Significant at 1% level. Other treatment values not significantly different.

Nevertheless the oxygen flux at 50 and 80 cm at the beginning of the waterlogging period (Figs. 1d and e) was still sufficient for root growth. It is not surprising therefore that a few roots had reached 75 cm at the start of the waterlogging treatment (Fig. 2a). The small number of roots at 80 cm during the waterlogging period would have had only a small respiratory demand for oxygen. Thus the oxygen present and presumably trapped in these deeper parts of the profile was sufficient to ensure oxygen flux densities greater than zero, and so permitted root growth.

The increase in root length density in the upper 10 cm during the latter part of the waterlogging treatment, making it significantly greater than in the freely-drained treatment in the upper 2.5 cm on April 14 (Fig. 2d), probably resulted from the initiation and growth of nodal roots. Such roots growing in poorly aerated conditions can develop aerenchymatous tissue to provide sufficient internal diffusion of oxygen from the aerial parts of the plant to enable the roots to extend several centimetres into anaerobic media[18]. However, annual species such as tobacco that do not have these adaptive mechanisms and are more sensitive to waterlogging than small-grained cereals do not usually grow much below a water-table[5,14].

In field conditions root growth of winter wheat has also been found to continue in the zone 50 to 100 cm below the soil surface when the water-table was at 20 cm throughout a three month period in winter[12]; the number of roots in that deep zone also was small, however. In that work the concentration of dissolved oxygen or flux density were not measured, but in a subsequent year at the same site they remained above zero in the deeper parts of that soil also when the water-table was at 20 cm (P.S. Blackwell and P. Colbourn, AFRC Letcombe Laboratory, personal communication).

Nutrient uptake by the younger plants may have been affected by waterlogging, as has been found in wheat seedlings in laboratory conditions[18], but smaller differences have been found in the field[12] and in lysimeters[7]. In the present experiment the concentrations of nitrogen, phosphorus and potassium in the mature crop were not affected by waterlogging (Table 6), and the total uptake of nutrients was thus proportional to shoot dry matter yield. As root weight of the waterlogged plants was proportionally less than the shoot weight of the freely-drained plants at anthesis (Tables 3 and 4) the specific uptake rate of nitrogen, phosphorus and potassium by the roots integrated over the whole growing season was greater in the waterlogged treatment.

The effect of waterlogging on extraction of soil water (Fig. 3) was less than had been found with winter wheat on this soil[13] but the maximum soil moisture deficit of 160 mm was similar to the maximum amount of water that winter wheat could extract from the soil[13].

The overall effects of waterlogging on vegetative growth reported here for winter oats (Table 4; Fig. 4) are similar to those for winter wheat given similar treatments[7,8]. We have grown winter oats in only one other experiment in this series. In that case the oats were grown on the adjacent clay soil[6]. However, after a prolonged winter waterlogging, growth was also restricted, and subsequently compensated for in a similar manner to that found here, with grain yield being depressed by 6% (R.K. Belford and E. J. Gussin, AFRC Letcombe Laboratory, personal communication) compared with 9% in the present experiment (Table 5). In past work with winter wheat in these lysimeters waterlogging has tended to depress yield more on the clay soil than on the sandy loam[7,8], and the loss in grain yield with wheat from prolonged winter watelogging has ranged from 10 to 30%. Thus we conclude that winter oats can compensate for the effects of waterlogging on vegetative growth to a greater extent than winter wheat, so that grain yield is less affected. This conclusion is consistent with results from pot experiments[19].

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