Available online at www.sciencedirect.com
ScienceDirect

Europ. J. Agronomy 28 (2008) 234–244

European Journal of Agronomy
www.elsevier.com/locate/eja

The effects of winter waterlogging and summer drought on the growth and yield of winter wheat (*Triticum aestivum* L.)

Edward Dickin[a,*], David Wright[b]

[a] *University of Wales, Bangor, Henfaes Research Centre, Abergwyngregyn, Llanfairfechan, Gwynedd LL33 0LB, United Kingdom*
[b] *University of Wales, Bangor, School of the Environment and Natural Resources, Deiniol Road, Bangor, Gwynedd, United Kingdom*

Received 9 March 2006; received in revised form 22 June 2007; accepted 24 July 2007

Abstract

Winter waterlogging and summer drought may become more prevalent as a result of climate change. Their effects on the growth and yield of winter wheat were investigated. Wheat was grown in lysimeters in an unheated glasshouse, over two seasons. Seed rate was included as an additional factor in the first season, and cultivar in the second. Root growth was investigated in both seasons using mini-rhizotrons. Waterlogging for 44 days at 93 days after sowing in 2002, and 58 days at 64 days after sowing in 2003, decreased grain yield by 20% and 24%, respectively. Drought during grain filling further decreased yields but there was no evidence that winter waterlogged plants were more susceptible to damage from drought the following summer, the effects of the two stresses being additive. Waterlogging decreased the total length, but not the final depth of the root system. Plots with a lower plant density demonstrated a smaller decrease in yield due to waterlogging. There was a significant positive linear relationship between the number of shoots per plant and nodal root axes per plant. There appeared to be a difference between cultivars in root system architecture, and in their response to waterlogging, but these differences were not reflected in grain yield.

Keywords: Waterlogging; Drought; Grain yield; Root growth; Winter wheat

1. Introduction

Climate change models predict that UK rainfall may increase in winter whilst that in summer is likely to decrease, thus increasing the risks of both waterlogging and drought (Dai et al., 1998; Hulme et al., 2002). Waterlogging has been shown to decrease wheat grain yields in the UK (Cannell et al., 1980; Belford, 1981), North America (McKersie and Hunt, 1987; Musgrave, 1994) and Australia (McDonald and Gardner, 1987; Melhuish et al., 1991). Many farmers believe that winter waterlogging leaves plants more vulnerable to subsequent drought through inhibition of root development, although previous experiments have not validated this, and also suggested that cereals in the UK are much more likely to experience winter waterlogging than summer drought (Cannell et al., 1984; Gales et al., 1984). This paper reports the results of two experiments designed to study the effects of winter waterlogging and summer drought, alone and in combination, on the growth, development and grain yield of winter wheat.

To decrease the cost of crop establishment farmers are encouraged to decrease seed rates, and rely on the tillering capacity of winter wheat to achieve target ear populations at harvest (HGCA, 2000). Although waterlogging during establishment has been shown to decrease plant populations (Cannell et al., 1980; Belford, 1981), there are no published reports of the interaction between waterlogging and seed rate (Setter and Waters, 2003). Seed rate was therefore included as a subplot factor in the first experiment.

Taking root measurements *in situ* presents substantial practical difficulties (Wellbank et al., 1973; Monteith, 1994), so soil-filled glass rhizotron chambers (after Riedacker, 1974) were set up in parallel with the lysimeter experiments to observe the impact of waterlogging on root systems. In the second season cultivar differences were investigated both in the lysimeters and rhizotrons. Previous workers have reported differences in tolerance to waterlogging between cultivars (Musgrave, 1994; Musgrave and Ding, 1998; Setter et al., 1999), but evidence of significant differences between varieties in root systems is not compelling (Wellbank et al., 1973; Hoad et al., 2001). Wheat

---

[*] Corresponding author. Tel.: +44 1248 689106; fax: +44 1248 354997.
E-mail address: e.t.dickin@bangor.ac.uk (E. Dickin).

1161-0301/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.eja.2007.07.010

roots are usually classified as seminal or nodal axes, although this description is not entirely accurate (Klepper et al., 1984), and the two classes have differing sensitivities to waterlogging (Trought and Drew, 1980). The greater sensitivity of the seminal root system to waterlogging is explained by their lack of adaptability to environmental stress, since the first four axes are determined in the seed (Wiedenroth and Erdmann, 1985). Aerenchyma tissue allows transport of oxygen to the root apices (Drew, 2000; Gibberd et al., 2001), and wheat varieties with more aerenchymatous nodal roots are more tolerant of waterlogging (Huang et al., 1997). In some cases waterlogging acts as a stimulus to nodal root production, especially in *Triticum aestivum*, and to a lesser extent in diploid and tetraploid *Triticum* species (Erdmann and Wiedenroth, 1986). The production of nodal roots, after the coleoptile pair, is associated with tiller production (Gregory et al., 1978); hence a prolifically tillering cultivar may have more of the waterlogging tolerant nodal roots. Therefore, in the second season two cultivars with different tillering habits were tested in the rhizotron and lysimeter experiments. These were Deben, which is a prolifically tillering cultivar, and Xi-19, which is less so (NIAB, 2002).

2. Materials and methods

2.1. 2002 lysimeter experiment

The experiment was conducted in 20 concrete lysimeters, each of approximately 1 m^3 (surface area = 1.2 m × 0.9 m, depth = 1 m). They were filled with local clay loam topsoil—a fertile alluvial loam with a high content of stones (Rheidol series) classified as a Dystric Cambisol, pH 6.2. The lysimeters were situated in an unheated glasshouse, with no supplementary lighting. The bottom of each lysimeter was filled with a 30 cm layer of coarse gravel, separated from the soil by a water-permeable membrane to allow free drainage. Drainage holes in the waterlogged lysimeters were blocked with rubber bungs and silicone sealant. All lysimeters were treated with bituminous paint, to prevent seepage through the concrete blocks. The experimental design was a split-plot arranged in five randomised complete blocks. The main plot treatments applied to each whole lysimeter were: control, winter waterlogged, summer drought, winter waterlogged followed by summer drought. Each lysimeter was split into two subplots. The split-plot treatment was sowing density, either 264 plants/m^2 or 132 plants/m^2. Plots were hand sown with winter wheat cv. Claire, on 24 October 2001 using a template to produce 10 rows of plants 12 cm apart. Seeds were sown 4 cm deep and 3 cm apart within rows at the high seed rate and 6 cm apart at the lower rate. Two seeds were sown in each position and the plots thinned to the desired plant population when the seedlings reached the first leaf fully emerged stage, GS 11, after Zadoks (Tottman et al., 1979).

Phosphorus and potassium fertilizers were applied to the seedbed at the rate of 40 kg P_2O_5/ha, and 40 kg K_2O/ha. Nitrogen (N) was applied as ammonium nitrate at a total rate equivalent to 150 kg N/ha, in two equal splits at GS 30 and 32. No N was applied during waterlogging. Weeds were removed by hand. Foliar disease was controlled by applications of 0.67 g/ha cyprodinil as Unix (Syngenta plc) and 125 g/ha epoxiconazole + 125 g/ha kresoxym-methyl as Landmark (BASF (UK) Ltd.) at stem extension (GS 31) followed by a further 125 g/ha epoxiconazole + 125 g/ha kresoxym-methyl as Landmark at flag leaf emerged stage (GS 39). Disease levels were low, with mildew (*Blumeria graminis*) early in the spring being the only one observed.

Table 1 shows the calendar dates, days after sowing (DAS) and Zadoks growth stages (Tottman et al., 1979) of the plants at the start and end of the waterlogging and drought periods, and mean air temperatures during these periods.

Sufficient water was applied to waterlog from the top down, by applying water in excess of the rate at which it could infiltrate the soil, indicated by surface pooling. Lysimeters were checked daily, and water added as required.

Drought treatments were applied, initially by withholding water completely, then watering twice weekly from 20 May

Table 1
Timings, duration and mean air temperatures during the waterlogging and drought treatments in the 2001/2002 and 2002/2003 lysimeter experiments

	2002	2003
Start of waterlogging		
Date/days after sowing	25/1/02; 93 DAS	1/1/03; 64 DAS
Growth stage	25	25
End of waterlogging		
Date/days after sowing	10/3/02; 137 DAS	1/3/03; 122 DAS
Growth stage	30	30
Mean air temperature during waterlogging	Max 10.7, min 4.2	Max 9.6, min 2.5
Start of drought		
Date/days after sowing	29/4/02; 187 DAS	12/5/03; 195 DAS
Growth stage	45	61
End of drought (grain maturity)		
Date/days after sowing	Drought 6/6/02; 225 DAS No drought 4/7/02; 253 DAS	3/7/03; 247 DAS 8/7/03; 252 DAS
Mean air temperature during drought	Max 29.8, min 10.9	Max 30.4, min 12.7

onwards. The control treatments were watered to field capacity as required. In all treatments watering was gradually decreased as the plants approached maturity.

Destructive growth analyses were conducted at the end of waterlogging on 11 March 2002 and at ear emergence on 7 May 2002. Sample size was 15 plants from the 132 plants/m^2 subplots and 30 plants from the 264 plants/m^2 subplots. Plants were cut at the stem base. At the first growth analysis the total shoot number and total plant above-ground biomass were measured. At the second growth analysis live shoots were divided into those which had formed a spike and those which had not. Green leaves were removed from the shoots that had formed a spike and the area measured with an optical area meter (LI-3000A, LI-COR). All plant fractions were dried in an oven at 80 °C for 48 h and dry weights recorded.

At maturity a subsample was taken, consisting of the middle row of each subplot. The remaining plants were harvested and grains removed using a Wintersteiger laboratory thresher. The subsample was divided into mature ears and dead tillers. Mature ears were cut from the stems at the collar. A subsample of ears was hand threshed and grain fresh and dry weight determined to calculate grain moisture content. A random subsample of five stems was taken to measure straw length. Dry weight of all plant fractions was recorded after drying in an oven at 80 °C for 48 h. Droughted and waterlogged plus droughted plots attained maturity and were harvested on 6 June 2002; controls and waterlogged plots on 4 July 2002.

Dried grain samples were milled and the nitrogen content determined by a semi-automatic Kjeldahl method (Kjeltech, Foss). Crude grain protein concentration was calculated by multiplying the nitrogen percentage by 5.83 (Sylvester-Bradley et al., 1997).

2.2. 2003 lysimeter experiment

In this experiment the structure and main plot treatments were the same as used in 2002. Split-plot treatments differed from the previous season, with cultivar instead of sowing rate. Each lysimeter was divided, with half being sown with Deben and half with Xi-19. Plots were sown on 29 October 2002 using the 264 seeds/m^2 template from 2001 to 2002.

Waterlogging was imposed from 1 January (64 DAS) for 58 days to 28 February (Table 1). Drought was applied by reducing watering of selected plots to twice a week from anthesis (GS 61) on 12 May 2003, 195 DAS to harvest (Table 1). Fertilizers and fungicides were applied at the same rates and growth stages as 2002.

Non-destructive tiller counts were made *in situ* on random samples of five plants from all plots during and at the end of the waterlogging period. The length of the pseudostem and lamina length of the youngest fully emerged leaf was measured at the end of the waterlogging period. Drought and waterlogged plus drought plots were harvested on 3 July 2003: control and waterlogged plots on 8 July 2003. Harvest at maturity followed the same protocol as in 2002.

2.3. Rhizotron experiments

Twelve rhizotron chambers were constructed in autumn 2001 using a method based on that described by Riedacker (1974). Each consisted of two sheets of glass, 120 cm long and 30 cm wide, with 2 cm of soil between the sheets. Even spacing between the sheets was achieved using two 20 mm square sections of soft wood as spacers. The sheets were secured with four layers of waterproof tape, with the spacer in place, and filled with sieved soil, dried in an oven at less that 35 °C. The soil was from the same source as that used in the lysimeters. The wooden bases of six control chambers were drilled to facilitate free drainage, whilst the six to be waterlogged were sealed with tape.

Seeds of winter wheat cv. Claire were sown on 6 December 2001, one plant per chamber. Each chamber was securely wrapped in black polythene to exclude light. The rhizotron experiment was in the same unheated glasshouse as the lysimeters. The rhizotrons were arranged on a frame inclined 30° from the vertical, to allow root growth on the ventral pane to be traced onto clear acetate sheets for measurement using a map pen. New growth was recorded weekly using a different coloured pen for each observation.

Waterlogging was obtained by watering daily until the water table was at the soil surface. This treatment was applied from 18 January 2002 to 19 February. The chambers were harvested at grain maturity on 16 July, washed carefully to remove soil and the root weight in each 20 cm horizon determined.

In 2003 a second rhizotron experiment was conducted, testing two varieties, Deben and Xi-19. There were four replicates of each treatment combination. Each chamber was held in a cradle to provide support and exclude light from the ventral glass pane. Only the dorsal pane was covered with black polythene, so the root growth could be traced by removing the rhizotron from its cradle. Seeds were sown on 4 December 2002. The waterlogging period was from 27 January to 26 February 2003.

Root growth was traced before, during and after the waterlogging period as 2001–2002 but no destructive samples were taken. All plants were harvested at anthesis, on 13 May 2003, and root growth was measured as in 2002. Additionally, shoots and nodal root axes were counted.

2.4. Statistical analysis

All data were subjected to analysis of variance using Genstat 7 (Lawes Agricultural Trust). Where significant, differences between means were compared by determining values of the least significant difference (standard error of the difference between means × t (5%)). Data are presented for the main effects of the main and subplot treatments (waterlogging, drought, seed rate in 2001/2002; waterlogging, drought, cultivar in 2002/2003) and the interactions that the experiments were established to investigate (waterlogging × drought in both years; waterlogging × drought × seed rate in 2001/2002; waterlogging × drought × cultivar in 2002/2003). Interactions between waterlogging × seed rate, drought × seed rate, waterlogging × cultivar and drought × cultivar were not significant in both years and are therefore not presented.

3. Results

3.1. Impact of waterlogging on vegetative growth

In 2002, waterlogging significantly ($P < 0.05$) decreased the total above-ground biomass of the plants but had no effect on shoot number (Table 2). Although the lower density treatment had a significantly smaller shoot dry weight and number per unit area, this was greater than half that of the high seed rate indicating that these plants had compensated to some extent. There was no significant interaction between waterlogging and seed rate and there was no loss of plants caused by waterlogging (data not presented). In 2003, waterlogging significantly decreased in comparison with the drained controls the number of shoots during and at the end of the waterlogging period (Table 3). Deben produced more shoots than Xi-19, both under control and waterlogged conditions, but the difference between the cultivars was smaller at the end of waterlogging. The number of shoots from waterlogged plants did not increase between the two sampling dates, whilst that of the controls of both cultivars did. The measurements of leaf lamina and pseudostem length illustrate the marked restriction of shoot growth in response to waterlogging stress (Table 3) (see also, Table 4a).

Table 2
Impact of winter waterlogging (drained control (C); waterlogged (W) for 44 days, starting 93 DAS) and seed rate (132 plants/m^2 or 264 plants/m^2) on vegetative growth of winter wheat, cv. Claire, as observed at the end of the waterlogging period in 2002

Treatment	Shoots/m^2	Shoot dry weight (g/m^2)
Waterlogging ($n = 20$, data are the means of 2 seed rates)		
C	437	119.8a
W	415	94.9b
Seed rate ($n = 20$, data are the means of 2 waterlogging treatments)		
132	345b	81.9b
264	507a	132.8a
Waterlogging × seed rate ($n = 10$)		
132C	335	87.9
132W	355	75.9
264C	539	151.7
264W	475	114.0
Significance		
Waterlogging	NS	*
Seed rate	***	**
Waterlogging × seed rate	NS	NS

Between waterlogging, or seed rate treatments, means followed by the same letter are not significantly different ($P = 0.05$) according to L.S.D. (t). NS, not significant.

[*] Significant at the 0.05 probability level.

[**] Significant at the 0.01 probability level.

[***] Significant at the 0.001 probability level.

3.2. Residual effect of waterlogging on plant growth at ear emergence

In 2002, both waterlogging and drought significantly decreased the number of ears per unit area, the total number of shoots and number of ears at ear emergence (Table 4b). This is in contrast to the observations at the end of the waterlogging period, where the decrease in shoot number per unit area was not significant. Waterlogging and drought significantly decreased shoot dry weight and green area (Table 4b). The deleterious effects of both stresses appeared to be additive, with the plants that were waterlogged and then droughted having the lowest means for all characteristics. Decreasing seed rate significantly decreased shoot and ear number, shoot dry weight and green area

Table 3
Impact of winter waterlogging (drained control (C); waterlogged (W) for 58 days starting 64 DAS) and cultivar (Deben or Xi-19) on tillering of winter wheat as observed, during and at the end of the waterlogging period in 2003, and the length of the youngest lamina and pseudostem of the primary stem

Treatment	Shoots/m^2, 21/1/03	Shoots/m^2, 10/3/03	Lamina length (mm)	Pseudostem length (mm)
Waterlogging ($n = 20$, data are the means of 2 cultivars)				
−	475a	660a	325a	14.7a
+	370b	343b	266b	8.0b
Cultivar ($n = 20$, data are the means of 2 waterlogging treatments)				
Deben	554a	581a	286b	11.0b
Xi-19	290b	422b	305a	11.7a
Waterlogging × cultivar ($n = 10$)				
Deben C	634	713	318	14.7
Deben W	449	422	254	7.4
Xi-19 C	290	581	333	14.8
Xi-19 W	264	264	278	8.6
Significance				
Waterlogging	**	**	***	***
Cultivar	***	**	**	*

Between waterlogging or cultivar treatments, means followed by the same letter are not significantly different ($P = 0.05$) according to L.S.D. (t). All interactions were not significant.

[*] Significant at the 0.05 probability level.

[**] Significant at the 0.01 probability level.

[***] Significant at the 0.001 probability level.

Table 4a
The statistical significance of the effects of winter waterlogging (W), summer drought (D) and seed rate (SR) on shoot and ear populations, shoot dry weight, green area index (GAI), ear length and the percentage (by length) of the ear emerged from the boot at ear emergence (GS 55) of winter wheat, cv. Claire

	Shoots/m^2	Ears/m^2	Shoot dry weight	GAI	Ear length	% Ear emerged
W	***	***	***	***	***	***
D	***	***	***	***	***	NS
W × D	*	NS	*	NS	NS	NS
SR	***	***	*	*	**	NS
W × SR	NS	NS	NS	NS	NS	NS
D × SR	NS	NS	NS	NS	NS	NS
D × W × SR	NS	NS	NS	NS	NS	NS

W, waterlogging, D, drought, SR, seed rate. NS, not significant.
* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

(Table 4b). Observations showed that waterlogging delayed ear emergence, in that at the time of sampling the non-waterlogged plants had almost completed emergence from the boot, in contrast to the ears of the waterlogged plants, of which two thirds of the length was still inside the boot, thus indicating a suppressive effect on development, but drought had no effect. There were no interactions between seed rate and waterlogging treatment for any of the variables recorded at ear emergence.

3.3. Grain yield and yield components at harvest

Both waterlogging and drought had significant ($P < 0.05$) effects on wheat grain yield in both years, although their relative impacts varied between years. In 2002, compared to the unstressed control, waterlogging decreased grain yield by 20% whilst drought decreased grain yield by 53% (Table 5b). The grain yield of the waterlogged plus drought treatment was not significantly different to that of drought alone, in contrast to the situation at ear emergence, when drought and waterlogging in combination caused greater losses than either stress alone (Table 5b, cf. Table 4b).

In 2003, the effect of waterlogging was similar whilst drought was less deleterious than in 2002. These factors resulted in decreases in grain yield of 24% and 17% respectively (Table 5c). Waterlogging plus drought decreased grain yield by 37% but the waterlogging × drought interaction was not significant. As at ear emergence in 2002 (Table 4b), the effects of waterlogging and drought in 2003 appeared to be additive (Table 5c); in con-

Table 4b
Impact of winter waterlogging (drained control (C); waterlogged (W) 44 days starting 93 DAS); summer drought (no drought (C); droughted (D) from mid booting 197 DAS); and seed rate (132 plants/m^2 or 264 plants/m^2) on reproductive growth of winter wheat, cv. Claire 2002

Treatment	Shoots/m^2	Ears/m^2	Shoot dry wt (g/m^2)	GAI	Ear length (mm)	% Ear emerged
Waterlogging ($n = 20$, data are the means of 2 drought treatments and seed rates)						
C	649a	512a	1584a	8.3a	137.8a	86.3a
W	458b	359b	1009b	6.2b	123.6b	35.5b
Drought ($n = 20$, data are the means of 2 waterlogging treatments and seed rates)						
C	633a	507a	1586a	9.8a	137.8a	60.3
D	474b	365b	1007b	4.7b	123.0b	61.5
Waterlogging × drought ($n = 10$, data are the means of 2 seed rates)						
C	757a	590a	1949a	11.0	143.0	81.9
W	508b	423b	1222b	8.6	133.8	38.8
D	541b	434b	1219b	5.5	132.6	90.8
WD	407c	295c	796c	3.8	113.4	32.1
Seed rate ($n = 20$, data are the means of 2 drought and waterlogging treatments)						
132	448b	350b	1083b	6.2b	134.7a	59.4
264	658a	522a	1511a	8.3a	126.7b	62.4
Waterlogging × drought × seed rate ($n = 5$)						
C132	623	492	1639	9.8	147.8	79.9
W132	421	328	1049	7.0	138.8	37.1
D132	454	366	1040	5.1	135.4	90.1
WD132	295	213	603	2.8	116.8	30.6
C264	891	689	2259	12.3	138.2	83.9
W264	421	519	1396	10.1	128.8	40.5
D264	628	503	1398	6.0	129.8	91.5
WD264	519	377	989	4.9	110.0	33.6

Between waterlogging, drought or seed rate treatments, means followed by the same letter are not significantly different ($P = 0.05$) according to L.S.D. (t).

Table 5a
The statistical significance of the effects and interactions of winter waterlogging (W), summer drought (D), seed rate (SR) and cultivar (V) on grain yield, ear population, thousand grain weight and grain number per ear of winter wheat

	Grain yield	Ears/m^2	Thousand grain weight	Grains/ear
2002				
W	***	*	NS	NS
D	***	***	***	***
W × D	***	*	NS	NS
SR	**	NS	NS	NS
W × SR	NS	NS	NS	NS
D × SR	*	NS	NS	NS
D × W × SR	**	NS	NS	NS
2003				
W	***	**	NS	NS
D	*	NS	**	NS
W × D	NS	NS	NS	*
V	*	*	**	NS
W × V	NS	NS	NS	NS
D × V	NS	NS	NS	NS
D × W × V	NS	NS	NS	NS

W, waterlogging, D, drought, SR, seed rate, V, variety. NS, not significant.
* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

Table 5b
Effects of winter waterlogging (drained control (C); waterlogged (W) 44 days starting 93 DAS); summer drought (no drought (C); droughted (D) from mid booting 197 DAS); and seed rate (132 plants/m^2 or 264 plants/m^2) on grain yield, ear population, thousand grain weight (TGW) and grain number per ear of winter wheat, cv. Claire in the 2001/2002 lysimeter experiment

Treatment	Grain yield (t/ha)	Ears/m^2	TGW (g)	Grains/ear
Waterlogging ($n = 20$, data are the means of 2 drought treatments and seed rates)				
C	10.51a	374a	47.4	55.2
W	8.46b	347b	46.8	56.5
Drought ($n = 20$, data are the means of 2 waterlogging treatments and seed rates)				
C	12.90a	417a	52.1a	63.6a
D	6.07b	304b	42.1b	48.0b
Waterlogging × drought ($n = 10$, data are the means of 2 seed rates)				
C	14.97a	445a	50.5	62.5
W	10.83b	390b	52.0	63.5
D	6.05c	304c	42.6	47.9
WD	6.08c	305c	41.6	48.3
Seed rate ($n = 20$, data are the means of 2 waterlogging and drought treatments)				
132	8.90a	347	46.9	56.6
264	10.06b	374	47.3	55.1
Waterlogging × drought × seed rate ($n = 5$)				
C 132	13.21b	415	49.2	63.9
W 132	10.72c	385	52.2	67.0
D 132	6.00d	294	43.5	48.6
WD 132	5.69d	296	40.2	48.0
C 264	16.73a	475	51.8	61.2
W 264	10.95c	395	51.9	60.0
D 264	6.10d	314	41.7	47.1
WD 264	6.48d	314	43.0	48.5

Between waterlogging, drought, seed rate or variety treatments, means followed by the same letter are not significantly different ($P = 0.05$) according to L.S.D. (*t*).

trast to the situation at maturity in 2002 (Table 5b), by which time the more severe drought had masked the effects of previous waterlogging.

In 2002, grain yield was significantly ($P < 0.01$) higher at the high seed rate than the low seed rate in the control treatment only (Table 5b). In 2003, although grain yield of Xi-19 was significantly higher than that of Deben, no significant interactions occurred between cultivar, waterlogging and drought (Table 5c).

In both years the decrease in yield due to waterlogging was due to a significant decrease in the number of ears/m^2, other yield components being unaffected. However, in both years the thousand grain weights of waterlogged plants were slightly lower than those of non-waterlogged, although the differences were not significant (Tables 5a–5c). Drought resulted in a significant decrease in all yield components in 2002 (Table 5b). In 2003, when smaller drought effects were seen, the only significant reduction was in thousand grain weight (Table 5c).

In 2002 waterlogging significantly decreased both grain protein concentration and the total amount of nitrogen incorporated into the grain (Table 6). Drought significantly increased grain protein concentration, but total nitrogen content of the grain per unit area was decreased by drought, due to the lower grain yield.

3.4. Rhizotron experiments

In both seasons, rate of elongation of the root systems of the waterlogged plants quickly decreased at the start of waterlogging. In 2002, it continued to decline throughout the treatment period (Fig. 1a), but in 2003, after the initial sharp decrease, there was a steady recovery, markedly so for Deben (Fig. 2a). The decrease in growth rate of the controls at the end of January in 2003, and on 7 March 2003 (Fig. 2a) was probably due to frost and low light levels at these times. In 2002, recovery began approximately one month after the end of waterlogging, growth following an exponential curve similar to that of the control. The growth rate of the waterlogged plants did not recover to that of the controls during the period when measurements were taken (Figs. 1a and 2a). In both seasons the total length of the control root system increased linearly until February, when growth became exponential (Figs. 1a and 2b). The waterlogged roots followed a similar pattern, but growth virtually ceased during the waterlogging period in 2002 and in Xi-19 in 2003, and the exponential growth phase began a month later. The data for root dry weight in each 20 cm soil horizon presented in Fig. 3a and b were collected at grain maturity, approximately five months after the end of the waterlogging period in 2002 and at anthesis, three months after the end of waterlogging in 2003. A comparison with the data in Figs. 1b and 2b, shows that considerable compensatory growth occurred between the measurements being taken, as at the end of the waterlogging period total root length of waterlogged plants was only around half that of the controls. In 2002 (Fig. 3a), differences between waterlogging and controls were significant only in the 20–40 cm ($P = 0.04$, L.S.D. = 0.35) and

Table 5c
Effects of winter waterlogging (drained control (C); waterlogged (W) for 58 days starting 64 DAS); summer drought (control (C); droughted (D) from anthesis 195 DAS); and cultivar (Deben or Xi-19) on grain yield, ear population, thousand grain weight (TGW) and grain number per ear of winter wheat in the 2002/03 lysimeter experiment

Treatment	Grain yield (t/ha)	Ears/m^2	TGW (g)	Grains/ear
Waterlogging ($n = 20$, data are means of 2 drought treatments and cultivars)				
C	9.99a	408a	43.3	53.5
W	7.62b	334b	40.8	49.6
Drought ($n = 20$, data are the means of 2 waterlogging treatments and cultivars)				
C	9.53a	361	45.7a	53.0
D	7.89b	384	37.5b	49.8
Waterlogging × drought ($n = 10$, data are the means of 2 cultivars)				
C	10.84	393	46.6	57.4a
W	8.23	328	44.9	48.5b
D	8.93	426	39.3	48.5b
WD	6.85	342	35.7	51.0ab
Cultivar ($n = 20$, data are the means of 2 waterlogging and drought treatments)				
Deb	8.26a	392a	39.3a	48.8
Xi	9.35a	350a	44.9b	54.3
Waterlogging × drought × cultivar ($n = 5$)				
C Deb	10.43	423	43.3	56.9
W Deb	7.39	334	41.7	43.4
D Deb	8.42	456	36.8	42.9
WD Deb	6.45	362	33.5	51.2
C Xi	11.24	364	49.8	58.0
W Xi	9.06	322	48.1	53.6
D Xi	9.44	395	41.8	54.1
WD Xi	7.26	323	37.9	50.9

Between waterlogging, drought, seed rate or variety treatments, means followed by the same letter are not significantly different ($P = 0.05$) according to L.S.D. (t).

Table 6
Effects of winter waterlogging (drained control (C); waterlogged (W) 44 days starting 93 DAS); summer drought (no drought (C); droughted (D) from mid booting 197 DAS) on the grain protein concentration of winter wheat, cv. Claire, in 2002

Treatment	Grain protein concentration (% of dry matter)	Total N content of grain (g m^{-2})
Waterlogging ($n = 20$, data are the means of 2 drought treatments and seed rates)		
C	11.34a	95.7a
W	10.12b	80.7b
Drought ($n = 20$, data are the means of 2 waterlogging treatments and seed rates)		
C	9.76b	114.2a
D	11.70a	62.2b
Significance		
Waterlogging	***	*
Drought	***	***

Between waterlogging, or drought treatments, means followed by the same letter are not significantly different ($P = 0.05$) according to L.S.D. (t). The effect of seed rate, and all interactions were not significant.

[*] Significant at the 0.05 probability level.

[***] Significant at the 0.001 probability level.

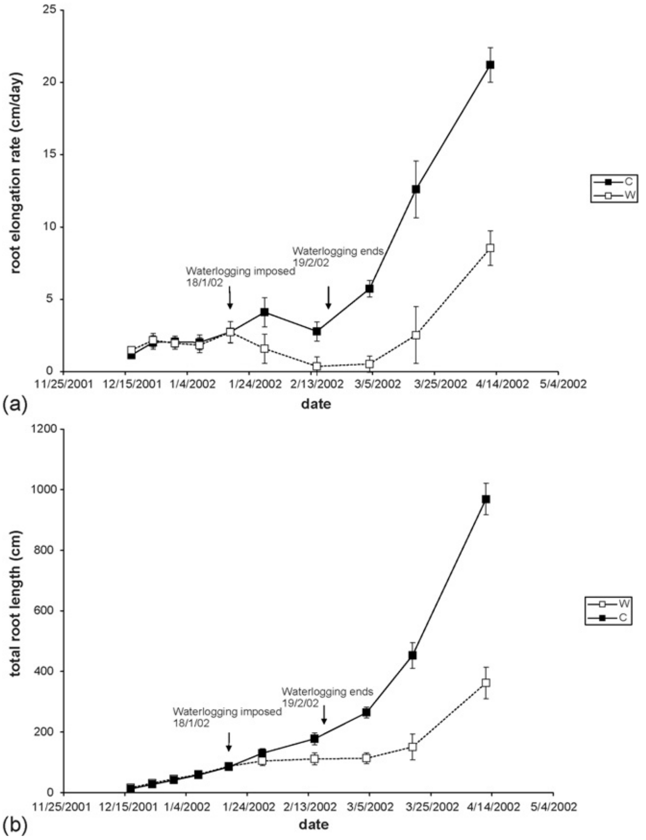

Fig. 1. (a) Root elongation rate in centimetres per calendar day of the root system of Claire winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was imposed 43 DAS for 32 days from 18 January 2002 to 19 February 2002; means ± S.E.M. (b) Total length of the root system of Claire winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was imposed 43 DAS for 32 days from 18 January 2002 to 19 February 2002; means ± S.E.M.

40–60 cm ($P = 0.03$, L.S.D. = 0.38) soil layers. In 2003 (Fig. 3b), differences between waterlogged and controls were only significant in the 0–20 cm ($P = 0.02$, L.S.D. = 1.56) and 80+ cm ($P = 0.003$, L.S.D. = 0.71) layers. The data presented in Fig. 3b are the pooled means for both cultivars, as differences between cultivars were only significant ($P = 0.01$, L.S.D. = 0.26) in the 60–80 cm soil layer, where Deben had 1.45 g root dry weight and Xi-19 0.6 g. There was no significant interaction between waterlogging and cultivar in any soil layer.

Visually Claire and Deben appeared to have similar fine fibrous root systems, with much higher level branching, whilst Xi-19 tended to exhibit secondary branching from a smaller number of thick primary roots. By the end of the waterlogging period some of the deep seminal roots appeared brown and necrotic, in contrast to the nodal roots, which generally appeared white and healthy.

There was a strong positive linear relationship between the number of shoots (both with and without ears) and nodal root axes observed at when the plants were harvested at anthesis (Fig. 4). Waterlogging significantly ($P < 0.05$) decreased the number of shoots and nodal roots of waterlogged relative to control plants. Control plants had a mean of 9.9 shoots and 39.9 nodal root axes per plant compared to 5.1 shoots and 25.9 nodal

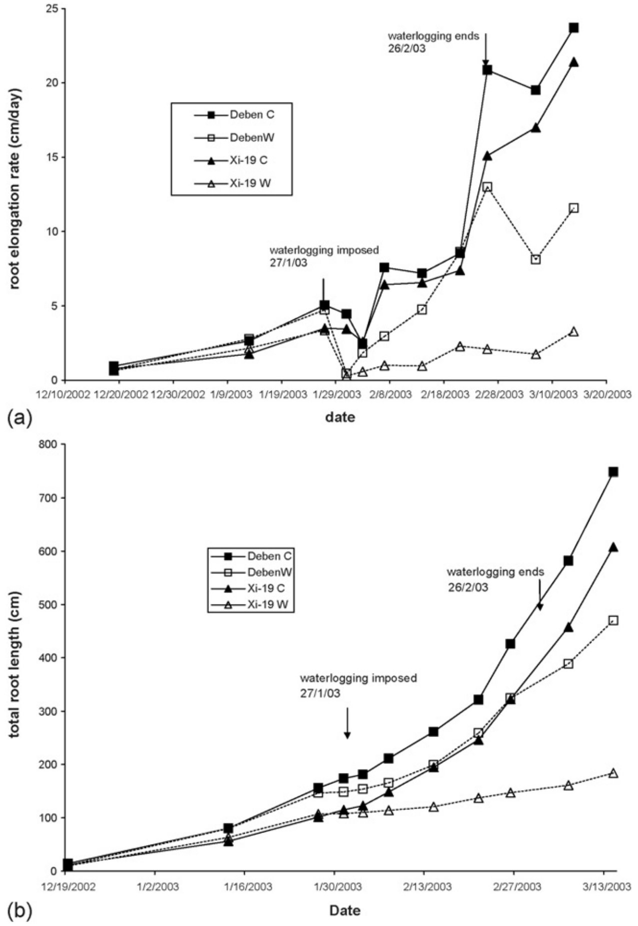

Fig. 2. (a) Root elongation rate in centimetres per calendar day of the root system of Deben and Xi-19 winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was imposed 54 DAS for 30 days from 27 January 2003 to 26 February 2003; means ± S.E.D. (b) Total length of the root system of Deben and Xi-19 winter wheat grown in rhizotrons containing drained or waterlogged soil. The waterlogging period was imposed 54 DAS for 30 days from 27 January 2003 to 26 February 2003; means ± S.E.D.

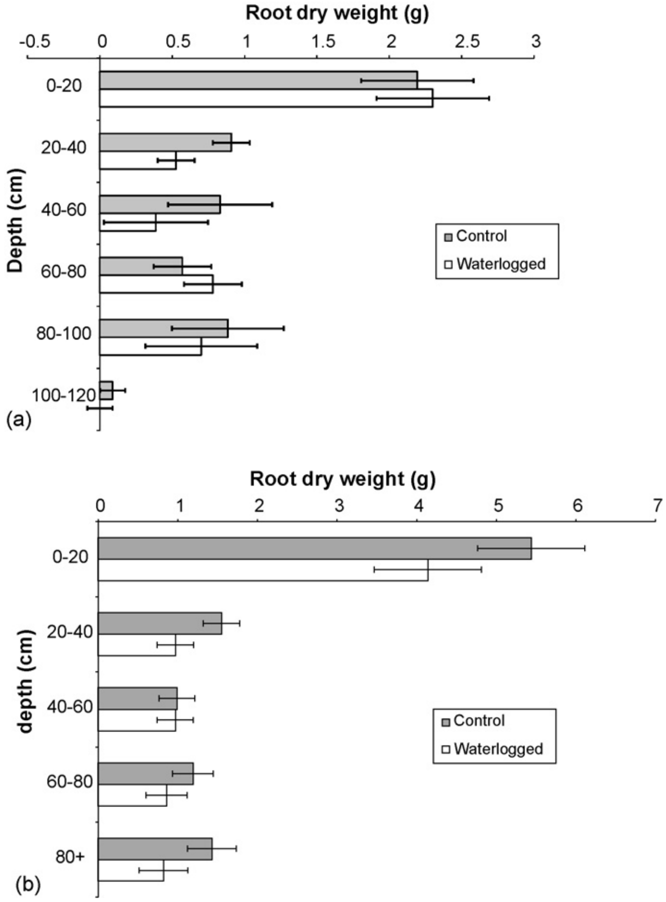

Fig. 3. Dry weights of roots in each 20 cm soil horizon of winter wheat grown in drained or waterlogged conditions over winter, harvested at grain maturity in 2002 (a) and anthesis in 2003 (b). Waterlogging was imposed 43 DAS for 32 days in 2002 and 54 DAS for 30 days in 2003. Data for 2003 (b) are the means of both cultivars; means ± S.E.M.

root axes for waterlogged plants. There was no difference in shoot number per plant between cultivars, though Deben (38.9) had more nodal root axes than Xi-19 (26.9). There was no significant interaction between waterlogging and cultivar for either of these characteristics.

4. Discussion

4.1. The effects of waterlogging

Yield losses due to waterlogging reported in this paper were in the range of those found in the experiments using UK cultivars of winter wheat at Letcombe grown in outdoor lysimeters (Cannell et al., 1980, 1984; Belford, 1981; Belford et al., 1985).

The decreased grain yield resulted from a decrease in the number of ears per plant, rather than the number of grains per ear or thousand grain weight, in agreement with previous workers (Belford et al., 1985). In both years waterlogging significantly reduced the total number of tillers produced (Tables 3 and 4b) so that the reduction of ear number at harvest (Tables 5b and 5c) was due to the inhibition of tiller initiation rather than an increased rate of tiller abortion. Although the effect of waterlogging on thousand-grain weight (TGW) was not significant, in both years waterlogged plants had slightly lower TGWs (Tables 5b and 5c).

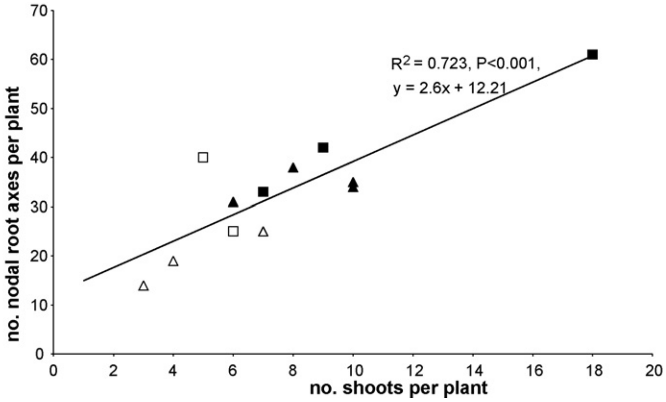

Fig. 4. The relationship between the number of shoots per plant (x) and number of nodal root axes at maturity (y), of winter wheat. $P < 0.001$, percentage of variation accounted for 72.3, standard error of observations 6.42, $y = 2.6x + 12.21$. Closed symbols: controls; open symbols: waterlogged; □: Deben; △: Xi-19.

Decreased vegetative growth was possibly a result of waterlogging restricting the supply of nitrogen to the shoot in early spring, which was observed in an earlier experiment by Trought and Drew (1980), and which had a residual effect in decreased grain protein concentration at maturity. Nitrogen deficiency would be expected to slightly accelerate plant development (Mirshel et al., 2005), however in this study waterlogging delayed shoot development slightly as waterlogged plants showed delayed ear emergence and maturity. This contrasts with the effects of drought, which accelerated leaf senescence and caused earlier grain maturity (Table 1). This observation suggests that any nitrogen deficiency caused by a limited period of winter waterlogging is a minor stress, and its effects on development are far outweighed by the decrease in plant development rate as a stress response during waterlogging. Belford (1981) also found that 120 days waterlogging in mid winter delayed ear emergence by 2 days compared to drained controls.

4.2. The effects of drought and the interaction with waterlogging

In 2002, the drought treatment was sufficiently severe to mask some of the effects of preceding waterlogging, resulting in a lack of significant differences in yield and yield components between the droughted plus waterlogged and drought only plots. This resulted in a significant interaction between waterlogging and drought (Tables 5a and 5b). Hence although the waterlogging × drought interaction was significant, the effects of waterlogging plus drought were not greater than the combined effects of waterlogging and drought alone. The less severe drought treatment in 2003 (Table 5c) and the 2002 ear emergence data (Table 4b) reveal the cumulative effect of waterlogging and drought. The results, using the three cultivars tested here, suggest that the effects of the stresses on grain yield are additive. In this study waterlogging or drought each caused around 2 t/ha grain yield loss as a single treatment or 4 t/ha when combined (Table 5c). These findings are in agreement with those of Cannell et al. (1980) in suggesting that there was no interaction between waterlogging and drought. Both the size of the root system (Figs. 1b, 2b, and 4a and b) and the foliage canopy (Table 4b) were decreased by waterlogging, so that the decreased capacity for water uptake was possibly balanced by the decreased transpiration area, as suggested by Gales et al. (1984). However, it should be noted that this work, and that of Cannell et al. (1980) and Gales et al. (1984) all used lysimeters, and that therefore different conclusions could potentially be reached *in situ* using natural field soils where the soil volume available for root exploration and exploitation is not artificially restricted.

Drought also decreased ear number in 2002, but not 2003 (Tables 5b and 5c). This was because in the 2003 experiment drought was applied later, during grain fill only, and so did not cause tiller abortion. This also explains the less severe yield loss due to drought observed in 2003. In 2002, fewer tillers in total were observed at harvest on droughted plants (data not shown), although this was a result of small aborted tillers sloughing away from the main stem and being lost.

Although waterlogging does not appear to affect the ability of a wheat crop to cope with subsequent drought, a wet winter and spring, when the soil remains at or near field capacity (but not waterlogged), may make plants more vulnerable to summer drought. Wheat roots will preferentially use water from the top 20 cm or so of the soil when frequent rain replenishes the surface layers, rather than seeking water from the water table deeper down (Gregory, 1994). Approximately half of the total root dry matter is found in the top 20 cm layer and easy availability of water here will not encourage partitioning of resources into the deeper roots needed in the summer. Winter waterlogging changes the pattern of water extraction in spring (Gales et al., 1984). Previously waterlogged plants demonstrated increased water extraction from the top 20 cm of soil on clay, or the top 40 cm on sand, and decreased extraction from the soil layers below this depth. The results of the study reported here and other published work suggest that this observation is due to increased reliance on nodal roots, which are formed in response to waterlogging. These roots form the root crown – a cone of roots which anchors the plant – which is found in the upper 20 cm or so of soil. The deeper seminal roots are responsible for deep extraction of water, and it is these that are most likely to be killed by waterlogging, as although both seminal and nodal roots of wheat are able to form aerenchyma, they must be exposed to hypoxia before they reach 100 mm (Thomson et al., 1990). These workers also report that nodal roots may possess some aerenchyma tissue when grown in aerated media, which would explain the observation that the seminal root system is more vulnerable to waterlogging damage (Trought and Drew, 1980).

Cannell et al. (1984) concluded that waterlogging was more likely to be a problem for cereal growers in the UK than drought, although climate change was not considered at that time. The reduction in yield potential due to waterlogging may be more serious than that due to drought. Drought generally causes a slow linear decrease in yield potential as the stress progresses, and once water becomes available significant recovery may occur, providing stress does not coincide with a sensitive stage in development; loss in yield potential due to hypoxia is sharper and recovery slower (Sojka et al., 1975).

Waterlogging delayed development slightly, illustrated by the delay in ear emergence (Table 4b). Heading date is one important characteristic in determining drought tolerance in barley; earlier maturing cultivars avoid the worst of late season droughts (Stanka et al., 2003). Therefore by delaying development winter waterlogging could potentially cause crops to be more vulnerable drought later in the summer. A caveat is that in these glasshouse experiments maturity was approximately a month earlier than normal for these cultivars in the UK, and so these findings need to be further investigated with field experiments.

4.3. The effects of seed rate and the interaction with waterlogging

This experiment set out to investigate the interaction between waterlogging and seed rate, and to find whether lower seed rates lead to unacceptable losses in waterlogged conditions. By the time of harvest the plants in the low seed rate plots had shown some ability to compensate by producing a larger weight of grain per plant. The decrease in grain dry weight due to waterlogging of the low seed rate plots was only half of that of the high seed rate plots, when compared to their respective drained controls. This resulted in a statistically significant interaction between waterlogging, drought and seed rate (Tables 5a and 5b).

At present there is incomplete evidence to confidently predict whether waterlogging will damage plant populations beyond the point where compensatory tillering can maintain grain yield. Evidence from this work indicates that decreasing sowing density relieves interplant competition, so at low plant populations waterlogging may not cause further loss of plants. As the difference in ear number between the two seed rates was not significant at harvest (Tables 5a and 5b), it can be estimated that the plants in the 132 plants/m^2 plots produced almost twice as many ears per plant than those in the 264 plants/m^2 plots. The positive relationship between numbers of shoots and nodal axes (Fig. 4) implies that the plants in the low seed rate plots produced more nodal roots. Use of lower seed rates is a strategy advocated to decrease the risk of root lodging by encouraging the development of a robust root crown (Baker et al., 1998; Berry et al., 1998). This would increase the numbers of the more waterlogging tolerant nodal roots (nodal roots = crown roots) thereby inadvertently producing plants with a greater waterlogging tolerance.

4.4. *The effects of cultivar and the interaction with waterlogging*

There was a significant difference in grain yield between the two cultivars used in these experiments, with Xi-19 having a greater yield than Deben. However, there was no interaction between waterlogging and cultivar. The very hot conditions in the glasshouse favoured Xi-19, which has more stem soluble carbohydrate (NIAB, 2002) and a faster winter growth rate, possibly allowing it to accumulate resources in the early spring before temperatures high summer temperatures occurred.

Although comparisons between the two seasons must be treated with caution, in the rhizotrons the root systems of Claire in 2002 and Deben in 2003 showed better recovery after waterlogging than Xi-19 in 2003 (Figs. 1a and b, and 2a and b). This observation may be linked with differences in root system architecture, Claire and Deben having finer roots with greater higher level branching and more nodal roots (Fig. 3), although this was not reflected in improved grain yield (Table 5c). Differences between cultivars in root dry weight were also not significant at anthesis (Fig. 4b). Interestingly, Deben and Claire share the variety Wasp in their parentage and are products of the same breeding programme (Anon., 2004). As discussed above, both the range of yield losses and the mechanism of these losses, by a decrease in ear number, agree with results of the 1970s experiments in the UK (Cannell et al., 1980; Belford, 1981), indicating that the modern cultivars tested here respond to waterlogging in a very similar way to their predecessors 30 years ago.

To enable a greater appreciation of the interaction between waterlogging and cultivar, a greater number of cultivars would need to be screened. This was done in a parallel series of experiments, which will be reported in a forthcoming paper.

4.5. *Use of lysimeters and rhizotrons*

Abiotic stresses, such as waterlogging and drought, can be applied with a greater degree of control using single plants grown in small containers. Unfortunately, such experiments often do not provide an adequate replication of field conditions, both by artificially restricting soil volume and removing interactions between plants. For example, it is well understood that the resource capture by the whole canopy composed of a population of cereal plants is more important than that of individual plants or leaves in determining yield. It would be logical to assume that roots behave in a similar way to shoots, and form an 'inverted canopy', whereby both the resource capture of individual plants and the interactions between plants determine total resource capture of the crop. The lysimeters used in this experiment were an attempt to provide the control offered by container experiments with a larger soil volume to better approximate field conditions. It would be preferable to use undisturbed soil cores, as used at Letcombe (Cannell et al., 1980), but unfortunately these require heavy machinery to extract. The rhizotron root chambers yielded useful data, albeit using single plants. Further investigations using larger root chambers *in situ* with an undisturbed soil profile as part of a field experiment would be technically demanding but would provide valuable insights into the crop 'root canopy', discussed above.

5. Conclusions

The glasshouse-based experiments reported here do not suggest that winter waterlogging increases plant susceptibility to subsequent drought. Further work is needed to confirm these findings in a field situation. Unfortunately, it is difficult to compare the effects of the two stresses fairly, as waterlogging is most likely to occur during the vegetative phase of growth for autumn sown wheat during which growth rates are slow. In contrast, drought is most likely during the later reproductive phase which is more crucial in determining grain yield and hence more sensitive to stress. If winter waterlogging and summer drought become more prevalent as a result of climate change a major challenge is posed to plant breeders: adaptations to one stress may increase susceptibility to the other. For example, prolific tiller production facilitates compensation if waterlogging decreases plant populations and may be associated with increased nodal root initiation, but filling the increased number of ears and hence grains would tax the resources of drought stressed plants. Increased cultivation of spring cereals may not offer a solution, as winter waterlogging would delay sowing, leaving crops more vulnerable to summer drought. Other potential effects of climate change, outside the scope of this paper, could interact with waterlogging; for example, increased winter soil temperatures and resulting changes in soil microbial activity and gas and nutrient flux. Further work is needed urgently to investigate the physiological and morphological traits required in plants that are better adapted to future climate and soil environments.

Acknowledgements

The authors wish to thank Mrs. Llinos Hughes for technical help and advice, Mr. W. Handley at NIAB for seeds and the trustees of the William Roberts Scholarship that provided funding for Edward Dickin.

References

Anon., 2004. http://www.nickersonuk.com, accessed on 1/6/04.

Baker, C.J., Berry, P.M., Spink, J.H., Sylvester-Bradley, R., Griffin, J.M., Scott, R.K., Clare, R.W., 1998. A method for the assessment of the risk of wheat lodging. J. Theor. Biol. 194, 587–603.

Belford, R.K., 1981. Response of winter wheat to prolonged waterlogging under outdoor conditions. J. Agric. Sci. 97, 557–568.

Belford, R.K., Cannell, R.Q., Thomson, R.J., 1985. Effects of single and multiple waterloggings on the growth and yield of winter wheat on a clay soil. J. Sci. Food Agric. 36, 142–156.

Berry, P., Sylvester-Bradley, R., Scott, R.K., Clare, R.W., Spink, J.H., Baker, C.J., 1998. Factors affected lodging. In: Proceedings of the Sixth HGCA R&D Conference on Cereals and Oilseeds. Home Grown Cereals Authority, London, pp. 11.1–11.11.

Cannell, R.Q., Belford, R.K., Gales, K., Dennis, C.W., Prew, R.D., 1980. Effects of waterlogging at different stages of development on the growth and yield of winter wheat. J. Sci. Food Agric. 31, 117–212.

Cannell, R.Q., Belford, R.K., Gales, K., Thomson, R.J., Webster, C.P., 1984. Effects of waterlogging and drought on winter wheat and winter barley grown on a clay and a sandy loam soil. Plant Soil 80, 53–66.

Dai, A., Trenberth, K.E., Karl, T.R., 1998. Global variations in droughts and wet spells: 1990–1995. Geophys. Res. Lett. 25, 367–370.

Drew, M.C., 2000. Programmed cell death and aerenchyma formation in roots. Trends Plant Sci. 5, 123–127.

Erdmann, B., Wiedenroth, E.M., 1986. Changes in the root system of wheat seedlings following root anaerobiosis: II. Morphology and anatomy of evolution forms. Ann. Bot. 58, 607–616.

Gales, K., Ayling, S.M., Cannell, R.Q., 1984. Effects of waterloggging and drought on winter wheat and winter barley grown on a clay and a sandy loam soil: II. Soil and plant water relationships. Plant Soil 80, 67–78.

Gibberd, M.R., Gray, J.D., Cocks, P.S., Colmer, T.D., 2001. Waterlogging tolerance among a diverse range of *Trifolium* accessions is related to root porosity, lateral root formation and 'aerotrophic rooting'. Ann. Bot. 88, 579–587.

Gregory, P.J., McGowan, M., Biscoe, P.V., Hunter, B., 1978. Water relations of winter wheat. 1. Growth of the root system. J. Agric. Sci. 91, 91–102.

Gregory, P.J., 1994. Resource capture by root networks. In: Monteith, J.L., Scott, R.K., Unsworth, M.H. (Eds.), Resource Capture by Crops. Nottingham University Press, Nottingham.

HGCA, 2000. Optimum Winter Wheat Plant Population. Topic Sheet 36. HGCA, London.

Hoad, S.P., Russell, G., Lucas, M.E., Bingham, I.J., 2001. The management of wheat, barley, and oat root systems. Adv. Agron. 74, 193–246.

Huang, B., Johnson, J.W., NeSmith, D.S., 1997. Responses to root-zone CO_2 enrichment and hypoxia of wheat genotypes differing in waterlogging tolerance. Crop Sci. 37, 464–468.

Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Murphy, J.M., Hassell, D., Boorman, P., McDonald, R., Hills, S., 2002. Climate Change Scenarios for the United Kingdom: The UKCIP02 Scientific Report. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK.

Klepper, B., Belford, R.K., Rickman, R.W., 1984. Root and shoot development in winter wheat. Agron. J. 76, 117–122.

McDonald, G.K., Gardner, W.K., 1987. Effect of waterlogging on the grain yield response of wheat to sowing date in south-western Victoria. Aust. J. Exp. Agric. 27, 661–670.

McKersie, B.D., Hunt, L.A., 1987. Genotypic differences in tolerance of ice encasement, low temperature flooding, and freezing in winter wheat. Crop Sci. 27, 860–863.

Melhuish, F.M., Humphreys, E., Muirhead, W.A., White, R.J.G., 1991. Flood irrigation of wheat on a transitional red-brown earth. I. Effect of duration of ponding on soil water, plant growth, yield and N uptake. Aust. J. Agric. Res. 42, 1023–1035.

Mirshel, W., Wenkel, K.-O., Schultz, A., Pommerening, J., Verch, G., 2005. Dynamic phenological model for winter rye and winter barley. Eur. J. Agron. 23, 123–135.

Monteith, J.L., 1994. Principles of resource capture by crop stands. In: Monteith, J.L., Scott, R.K., Unsworth, M.H. (Eds.), Resource Capture by Crops. Nottingham University Press, Nottingham.

Musgrave, M.E., 1994. Waterlogging effects on yield and photosynthesis in eight winter wheat cultivars. Crop Sci. 34, 1314–1318.

Musgrave, M.E., Ding, N., 1998. Evaluating wheat cultivars for waterlogging tolerance. Crop Sci. 38, 90–97.

NIAB, 2002. Cereal Varieties Handbook. NIAB, Cambridge.

Riedacker, A., 1974. Un nouvel outil pour l'etude des raciness et de la rhizosphere: le minirhizotron. Ann. Sci. Fores. 31 (20), 129–134.

Setter, T.L., Burgess, P., Waters, I., Kuo, J., 1999. Genetic diversity of barley and wheat for waterlogging tolerance in Western Australia. In: Proceedings of the 9th Australian Barley Technical Symposium, 1999.

Setter, T.L., Waters, I., 2003. Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil 253, 1–34.

Sojka, R.E., Stolzy, L.H., Kaufmann, M.R., 1975. Wheat growth related to rhizospere temperature and oxygen levels. Agron. J. 67, 591–596.

Stanka, A.M., Romagosa, I., Takeda, K., Lundborg, T., Terzi, V., Cattivelli, L., 2003. Diversity in abiotic stress tolerance. In: von Bothmer, R., van Hintum, T., Knupffer, H., Sato, K. (Eds.), Diversity in Barley (*Hordeum vulgare*). Elsevier Science, Amsterdam, pp. 179–199.

Sylvester-Bradley, R., Watson, N.A., Dewes, M.E., Clare, R.W., Scott, R.K., Dodgeson, G. (Eds.), 1997. The Wheat Growth Guide. HGCA, London.

Tottman, D.R., Makepeace, R.J., Broad, H., 1979. An explanation of the decimal code for the growth stages of cereals, with illustrations. Ann. Appl. Biol. 93, 221–243.

Thomson, C.J., Armstrong, W., Waters, I., Greenway, H., 1990. Aerenchyma formation and the associated oxygen movement in seminal and nodal roots of wheat. Plant Cell Environ. 13, 395–403.

Trought, M.C.T., Drew, M.C., 1980. The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.). Plant Soil 54, 77–94.

Wellbank, P.J., Gibb, M.J, Taylor, P.J., Williams, E.D., 1973. Root growth of cereal crops. Rothamsted Experimental Station Report 1973, Part 2, pp. 26–66.

Wiedenroth, E.M., Erdmann, B., 1985. Morphological changes in wheat seedlings (*Triticum aestivum* L.) following root anaerobiosis and partial pruning of the root system. Ann. Bot. 56, 307–315.