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# Effects of waterlogging on young wheat plants (*Triticum aestivum* L.) and on soil solutes at different soil temperatures

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**Summary** We report a study of the mechanism by which the response of plants to waterlogging can be modified by soil temperature. Wheat was grown initially in well-aerated soil in a controlled environment room before the soil was flooded with aerated, deionized water. The soil temperature was maintained constant in the range 6–18°C while the air temperature was at 14°C. Waterlogging damage was greater in plants at the higher soil temperatures when the plants were compared at the same chronological age. However, when compared at the same growth stage, the response to soil temperature was little different *i.e.* plants subjected to waterlogging for a long time at low soil temperatures exhibited a similar reduction in growth and other properties as those subjected briefly at higher temperatures. The concentration of dissolved oxygen in the soil solution declined rapidly at all temperatures, being almost zero after 36 h waterlogging. Temperature affected rates of change of the concentrations of dissolved carbon dioxide, ethylene, nitrous oxide, nitrite, nitrate, calcium and potassium. The importance of soil-and plant-determined properties in the waterlogging response of plants at different temperatures are discussed.

## Introduction

For many dryland species, poor soil aeration resulting from saturation of the soil by water (waterlogging) can rapidly cause abnormal vegetative growth[11,14]. Typically, leaf extension and shoot fresh weight gain are slowed and tillering in Gramineae is partially suppressed. The older (lower) leaves sometimes become yellow, indicating premature senescence. Such signs of 'waterlogging damage' to shoots may have a variety of causes. Lack of oxygen around the root can impair uptake of water[20] and nutrient ions[16] and inhibit the supply to shoots of growth substances usually produced in the roots[23]. The anaerobic soil can accumulate reduced organic and inorganic substances, sometimes to phytotoxic concentrations[11]. Simultaneously, the concentrations of nutrient ions in the soil solution may change; nitrate especially may decrease enough to cause plant nitrogen deficiency[13,14].

In earlier studies of the response of wheat and barley to poor aeration, we related the time-course of the onset of waterlogging damage to shoots to the depletion of oxygen from the soil water and the accumulation of various

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potentially toxic solutes[12,31,32]. For two soils of small organic matter content, we established that waterlogging damage was linked most closely with the early depletion of oxygen from the soil water. Plants showed damage before any soil solutes attained injurious concentrations, and while soil nitrate was still present in appreciable concentrations.

Temperature can greatly modify the response of crop plants to waterlogging[34]. In temperate climates, the tolerance of waterlogging-susceptible species is generally greater during winter and cool springs than in warmer spring or summer temperatures[3,24]. But how far temperature and plant growth stage interact to determine the response to waterlogging under field conditions is often unclear[24,34]. In experiments in controlled environments with legumes, waterlogging damage occurs most rapidly at higher temperatures, with more severe, long-term effects on growth and survival[5,15,29]. The effect depends more on soil temperature than on air temperature[5,15]. For wheat, the pattern of response has been less consistent. In some investigations, high temperatures exacerbated the detrimental effects of low oxygen concentrations on shoot growth[25,35] but in experiments with soil exposed to controlled gas mixtures with various concentrations of oxygen, it was at lower temperatures (9°C) that plants with roots in anaerobic media showed the greatest inhibition relative to well-oxygenated controls[27].

The mechanisms of the apparent tolerance to waterlogging that plants sometimes show at low temperatures has been the subject of few experiments, but possible explanations include:

(1) Low temperatures slow the rate of depletion of oxygen from the soil water by roots and soil micro-organisms[18]. Adequate oxygen diffusion rates through the soil to individual roots may thus continue for a longer time before lack of oxygen limits root activities.

(2) Because low temperature slows the rate of oxygen consumption, loss of dissolved nitrate from the soil water through microbiological activity would be delayed, as also would any accumulation of potential toxins while the soil slowly became anaerobic[22].

(3) Some dryland species are able to adapt, physiologically and anatomically, to oxygen deficiency and thereby improve their tolerance to waterlogging[6,9,11]. Plants may have an extended period in which to adapt while the oxygen concentration declines slowly at lower temperatures.

(4) Shoot growth rate at lower root temperatures may be slowed such that a greatly diminished rate of supply of inorganic nutrients, water and growth substances by the roots could meet more nearly the requirements of the shoot.

(5) Root metabolism may be slowed at low temperatures such that the transport of oxygen from the atmosphere *via* the intercellular spaces of the plant is adequate for respiration, and consequently root growth and function.

The aim of the present investigation was to examine the waterlogging tolerance of young wheat plants at different soil temperatures and to attempt to distinguish broadly between the foregoing possible mechanisms. Two experimental procedures were used. In the first, plants grown initially at 14°C were subjected to soil temperatures between 6° and 18°C before waterlogging began. Plants were sampled at the same chronological age. In the second procedure, plants were grown throughout with soil temperatures of 10° or 14°C, and sampled when at the same growth stage.

## Methods

### *Experimental methods*

Winter wheat (*Triticum aestivum* L., cv. Capelle Desprez) was grown in a sandy soil (Skipwith series), obtained from a site known to be frequently subjected to waterlogging. The soil was air-dried and packed at a bulk density of 1.27 g cm$^{-3}$ into plastic cylinders 31 cm deep and 6.5 cm diameter, sealed at the base by a rubber bung to make them watertight. Once packed, the soil was brought to its approximate field capacity by adding deionized water to the soil surface. Germinated wheat seeds were then sown singly in the cylinders and these were put into tanks of water in a controlled environment cabinet, as described in detail elsewhere[30,31]. At this stage, the cylinders were kept sealed to prevent the entry of water. The cabinet provided a constant temperature of 14°C with a 16 h photoperiod of 100 W m$^{-2}$ and a relative humidity of 75%. Evapo-transpiration losses from the cylinders were replaced by watering daily to constant weight. To flood the soil, the rubber bung was removed from the base of the cylinder, so that aerated, deionized water (from the tanks) entered the soil, saturating it to the surface. The bung was then replaced and the cylinders were removed briefly from the water-tank and weighed. The cylinders were weighed daily and any losses corrected by addition of deionized water to the soil surface.

Leaf length was measured from the soil surface to the tip of the lamina. When plants were sampled, the roots were washed from the soil and the weights of roots and shoots were recorded. Dried shoot material was wet ashed in nitric and perchloric acids and analysed for phosphorus, calcium and potassium[32]. Total nitrogen in the dried shoot material was estimated by an automated Dumas procedure (Carlo-Erba, Italy).

### *Extraction and analysis of soil solution*

Sampling probes, comprising polyethylene tubing (20 mm long × 5 mm diameter) filled with glassfibre wool, were placed in the soil at 15 cm below the surface during the initial packing. A 1.5 mm diameter capillary tube led from the probe to the soil surface where the tube was closed by a 3-way tap. Following waterlogging, samples of the soil water were removed using a hypodermic needle and syringe, thus avoiding any contamination with air. The concentrations of dissolved oxygen, carbon dioxide, nitrous oxide and ethylene were measured by gas chromatography[31]. The concentrations of gas are expressed as the per cent (v/v) in the equilibrium gas phase. The concentrations of dissolved inorganic ions were measured by standard procedures using automated methods[31], and expressed as mol l$^{-1}$ of soil solution.

### *Methods for controlling soil temperatures*

Soil and air temperatures of 14°C were provided by the controlled environment cabinet. Where other soil temperatures were required, the water surrounding the cylinders contained in each tank was adjusted by circulation over a cooler and a heater. The water was continuously pumped out of the tank and into a commercial 'beer cooler', which lowered the temperature below that required for the treatment. In the bowl of the cooler was a heater unit, connected to a thermostat located in the returning flow of water to the water-tank. By controlling the temperature of the water as it entered the tank, the soil temperatures were maintained at ± 0.5°C of that required. To minimise heat exchange between the tanks and the controlled environment cabinet, the watertanks (other than that at 14°C) were encased in a 2.5cm thick, expanded polystyrene jacket. The same material was used as a cover, with circular holes provided for the cylinders so that seedlings were fully exposed to the light. The surface of the soil was covered by a layer of white polyethylene beads to reduce surface heating and algal growth. Although the technique gave adequate soil temperature control, the air temperature just above the tanks of water was slightly modified when these were appreciably below that of the controlled environment cabinet. At 5 cm above the water-tank held at 6°C, the air temperature was lowered from 14° to 12°C during the dark, and 13°C during the light periods.

Soil temperature was varied experimentally in two different ways. In the first, plants were all grown at the same temperature (14°C) for the initial 9 d in well-aerated soil, before being flooded for 14 d at various soil temperatures (6, 10, 14 or 18°C). To minimize stresses from sudden change, the transfer from 14°C to other temperatures was done in stages before flooding, as follows: 1: the soil temperature was lowered to 10°C for 24 h and then to 6°C for the period 24–48 h before flooding the soil at 6°C: 2: the soil temperature was lowered to 10°C for 48 h before flooding at 10°C: 3: the soil temperature was raised to 18°C for 24 h immediately before flooding at 18°C: 4: plants were kept at 14°C throughout.

The object of the second experimental procedure was to maintain plants at different, constant soil temperatures (14° and 10°C) throughout their development, both before and during flooding. We appreciated that temperature would markedly affect growth rates during the initial stage in well-aerated soil. However, we wished to subject plants from different soil temperatures to waterlogging on the same day when they were of similar size and at the same growth stage. Preliminary measurements of relative growth rates indicated that for plants at 10° and 14°C the same growth stage would be reached after, respectively, 13 and 9 d and the germination of seed was staggered accordingly by 4 d.

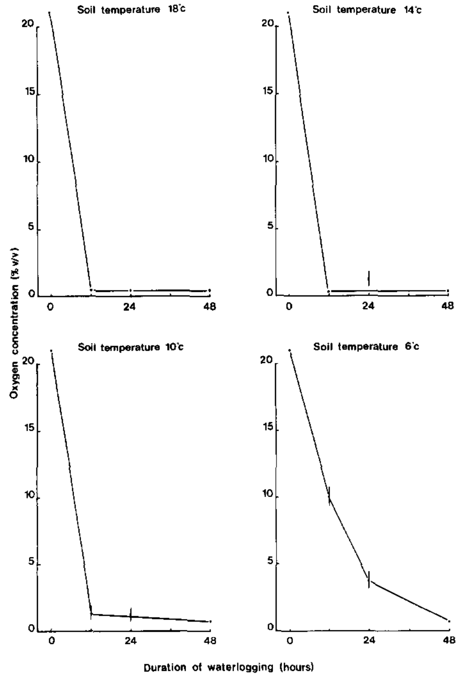

Fig. 1. Dissolved oxygen concentration in the soil solution with duration of waterlogging at 4 soil temperatures. The concentration is given as per cent (v/v) in the equilibrium gas phase. Values are means of duplicate determinations; the vertical bars give the range where this exceeds symbol size.

## Results

### *The effect of temperature on concentrations of oxygen and other dissolved substances in the soil solution during waterlogging (Experiment 1)*

The changes in the concentrations of various solutes in the waterlogged soil solution were markedly affected by soil temperature. Although the soil was flooded with fully-aerated water, the dissolved oxygen concentration declined from 21% to 1% or less within 12 h at 10°C and above, while at 6°C the same decline took 36 h (Fig. 1). Concentrations of carbon dioxide increased approximately linearly with time to 7, 11, 14 and 17% at temperatures of 6, 10, 14 and 18°C, respectively, after 14 d (Fig. 2). The accumulation of ethylene was most rapid at 18°C, rising to 5 $\mu l\ l^{-1}$ at 7 d (Fig. 2) but then declining to very small concentrations by 14 d. At 14° and 10°C ethylene slowly accumulated to 4 and 2.5 $\mu l\ l^{-1}$ respectively after 14 d. At 6°C, ethylene (0.9 $\mu l\ l^{-1}$) was first detected after 14 d.

The concentrations of nitrous oxide and nitrite in the waterlogged soil solution increased most rapidly at the higher temperatures (Fig. 2). The nitrite concentration was maximal after 2, 3, 6 and 7 d at 18, 14, 10 and 6°C respectively, subsequently falling to low or undetectable levels. Likewise, the nitrous oxide concentrations reached a peak earlier at the higher temperatures, subsequently

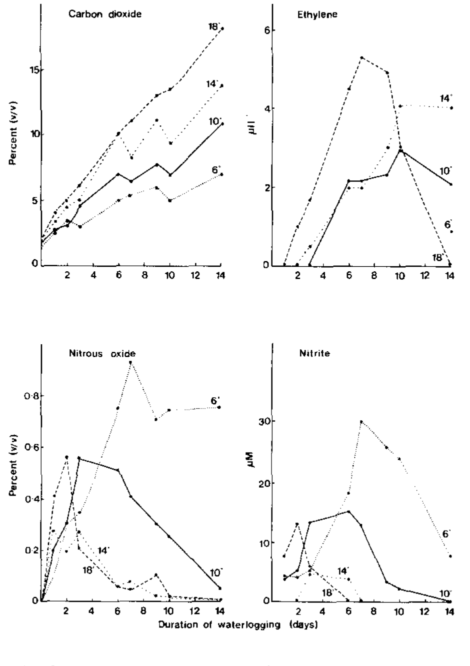

Fig. 2. Concentrations of dissolved carbon dioxide, ethylene, nitrous oxide and nitrite in the soil solution with duration of waterlogging at 4 soil temperatures. The concentrations of dissolved gases are given as those in the equilibrium gas phase.

falling. Despite the slower rates of accumulation of both these solutes in the waterlogged soil at 6°C, the greatest concentrations were attained at this low temperature, 7 d after the start of waterlogging, when nitrous oxide reached 0.96% and nitrite 0.03 m*M*.

While the products of denitrification were accumulating in the soil water, the nitrate concentrations in the soil solution were declining (Fig. 3), the rate being most rapid at 18°C. The linear regressions indicate little difference between the rates of nitrate disappearance from soils at temperatures between 14° and 6°C. Concentrations of calcium and potassium declined also, these changes being in proportion to those for nitrate at most temperatures. At 18°C both the calcium and potassium concentrations fell linearly with time; the equations of the linear regressions were:

$[\mathrm{Ca}^{+++}] = -0.30\ \mathrm{t} + 5.92;\ \mathrm{r} = -0.784; \mathrm{n} = 21; P\,0.01$

$[\mathrm{K}^{+}] \quad = -0.033\,\mathrm{t} + 1.378; \mathrm{r} = -0.710; \mathrm{n} = 21; P\,0.01$

(where square brackets denote the concentrations (m*M*) of ions in the soil solution, t the number of days after the start of waterlogging, r the correlation coefficient and P the probability, based on n observations).

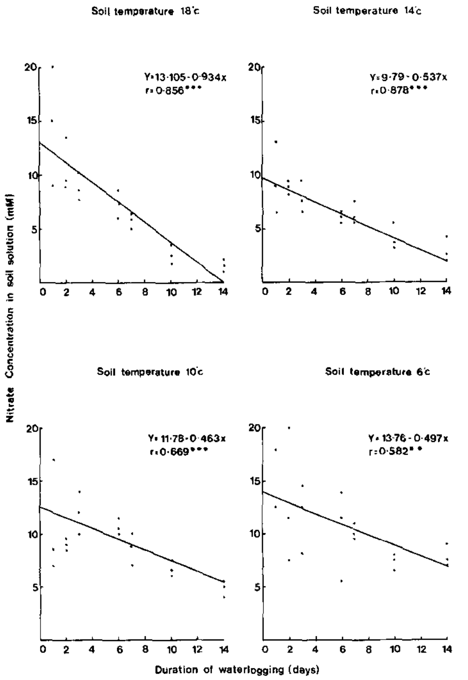

Fig. 3. Concentration of dissolved nitrate in the soil solution with duration of waterlogging at 4 soil temperatures. Each point is a measurement made on soil solution extracted from different soil columns. The lines and equations represent linear regressions, where Y is the nitrate concentration, x is time, r is the correlation coefficient. Statistical probability ($P$) is indicated by $^{**}P < 0.01$, $^{***}P < 0.001$.

At 6°C the rate of fall of calcium was slower, while the change in the potassium concentration was not significant

$[Ca^{++}] = -0.16t + 5.89;\ r = -0.496;\ n = 20;\ P < 0.05$

$[K^{+}] = -0.012t + 1.102;\ r = -0.356;\ n = 20;\ P = \mathrm{NS}$

The different soil temperatures did not affect the concentrations of phosphate in the soil solution which remained between 3 and 4 $\mu M$ for the duration of the experiment at all 4 temperatures.

### *Plant growth and nutrient uptake*

*Soil temperature treatments imposed two days before the start of flooding (Experiment* 1) Waterlogging at all soil temperatures caused the shoot fresh and dry weights, final leaf lengths and total root dry weight to be smaller than in the aerated controls (Fig. 4). However, plant growth in absolute terms was greater in waterlogged soil at the higher temperatures than in well aerated soil at lower temperatures. The inhibitory effects of waterlogging generally were greater at higher soil temperatures, compared with controls in well-aerated soil (Table 1). Waterlogging caused an increase in the per cent dry matter content of shoots, at the three upper temperatures (Table 2). As a consequence, the effect of waterlogging on shoot was not as severe as that on the fresh weight.

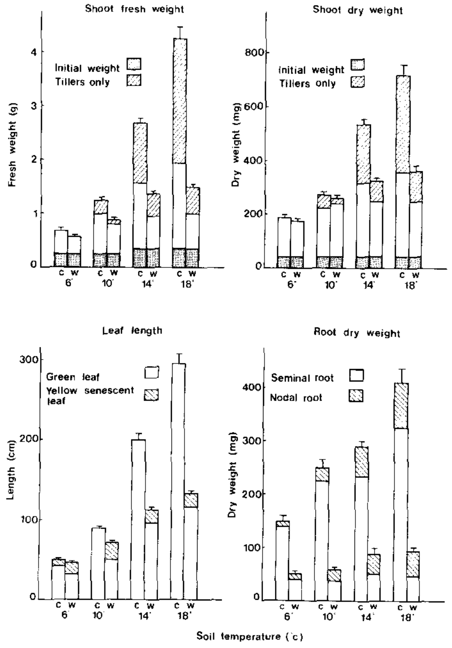

Fig. 4. The response of wheat to waterlogging at 4 soil temperatures. Plants were exposed to the stated temperatures shortly before the onset of waterlogging, and plants were sampled after 14 d waterlogging. Values are means per plant with S.E.

Table 1. Effect of soil temperature on the growth of young wheat plants in waterlogged soil. Values are expressed as percentage of the controls in non-waterlogged soil

| Plant parameter | Soil temperature (°C) | | | |
|---|---|---|---|---|
| | 6 | 10 | 14 | 18 |
| Total shoots | | | | |
| Fresh weight | 82 | 65 | 42 | 30 |
| Dry weight | 90 | 94 | 62 | 45 |
| Tillers | | | | |
| Fresh weight | – | 40 | 31 | 22 |
| Dry weight | – | 56 | 43 | 34 |
| Leaf extension rate* | | | | |
| 3rd oldest leaf | 82 | 78 | 81 | 68 |
| 4th oldest leaf | – | 56 | 55 | 42 |
| Root dry weight | | | | |
| Seminals | 31 | 18 | 21 | 13 |
| Nodals | 67 | 71 | 61 | 63 |

* Values are for the linear phase of leaf extension, obtained from daily measurements of leaf length.

Table 2. Dry matter content of the shoots (main shoot and tillers) of young wheat plants grown at different temperatures in waterlogged soil. Values give the per cent dry matter*

| Treatment | Soil temperature (°C) | | | |
|---|---|---|---|---|
| | 6 | 10 | 14 | 18 |
| Non-waterlogged (control) | 29 | 22 | 18 | 17 |
| Waterlogged | 30 | 29 | 24 | 23 |

* Per cent dry matter = (dry weight/fresh weight) × 100

Waterlogging exerted little effect on the dry weight of the main shoot alone (*i.e.* excluding the tillers), at soil temperatures between 10° and 18°C (Fig. 4) and any increase in the total shoot dry weight with temperature was due mainly to increased tiller growth. However, tiller growth as fresh or dry weight gain relative to the controls, was more severely affected by waterlogging at the higher temperatures (Table 1).

Leaves extended more rapidly with warmer soil temperatures, and at each temperature waterlogging retarded extension, the greatest inhibition relative to the controls being at 18°C (Table 1).

The initial development of premature senescence in waterlogged plants was affected by soil temperatures. At 14° and 18°C, yellowing started to be visible after five days in the oldest leaf, while at the two lower temperatures it was seen between 6 and 7 d. By 14 d, the length of yellow, senescent leaf per shoot was approximately the same at all 4 temperatures (Fig. 4). The colour of the younger emerging leaves was also affected, being a pale green at the three higher temperatures, and dark green at 6°C.

Growth of the seminal roots was severely restricted by waterlogging at all temperatures (Fig. 4; Table 1). When roots were washed out of the soil after 14 d, the main apex of those waterlogged at 6° and 10°C appeared healthy, but we did not test whether these roots could resume elongation when the soil drained. At 14° and 18°C the seminal root apices had started to decay.

Nodal roots which developed from the base of the shoots during the waterlogging treatments grew into the anaerobic soil, but at all temperatures the length of the longest, and their total dry weight were less than in controls, (Table 3; Fig. 4). At the two higher temperatures, waterlogging also diminished the number of nodal roots that emerged from the shoot base (Table 3).

Table 3. Effect of waterlogging on the growth of the nodal roots of young wheat plants at different soil temperatures

| Plant parameter | Treatment | Soil temperature (°C) | | | |
|---|---|---|---|---|---|
| | | 6 | 10 | 14 | 18 |
| Number of emerged nodal roots per plant | Control | 2.8 | 5.0 | 10.3 | 13.0 |
| | Waterlogged | 2.8 | 4.8 | 7.5* | 9.7* |
| Length of longest nodal root (cm) | Control | 11.5 | 23.9 | 33.6 | 34.4 |
| | Waterlogged | 6.9* | 13.3* | 17.9* | 18.5* |

* Indicates statistically significant difference between control and waterlogged ($P$ 0.05).

The accumulation of nitrogen, phosphorus and potassium by the shoots was more inhibited by waterlogging at all soil temperatures than was dry matter accumulation, resulting in a decline in the average concentration in the shoots (Table 4). This reduction in nutrient concentration with waterlogging, relative to controls, was least at the lower temperature (6°C). By contrast, accumulation of calcium was little affected by waterlogging, in accord with previous observations[32].

*Soil temperature kept constant at* 10° *and* 14°*C.* (*Experiment* 2) The response to waterlogging was examined at two soil temperatures kept constant throughout

Table 4. Effect of waterlogging on the concentrations of inorganic nutrients in the shoots of young wheat plants grown at different soil temperatures. Values are in μmole g$^{-1}$ dry weight of main shoot and tillers.

| Nutrient | Treatment | Soil temperature (°C) | | | |
|---|---|---|---|---|---|
| | | 6 | 10 | 14 | 18 |
| Nitrogen | Control | 1290 | 1980 | 2360 | 2380 |
| | Waterlogged | 1010 | 760 | 1020 | 970 |
| | Waterlogged as per cent control | 78 | 38 | 43 | 41 |
| Phosphorus | Control | 38 | 57 | 67 | 67 |
| | Waterlogged | 34 | 27 | 28 | 27 |
| | Waterlogged as per cent control | 88 | 48 | 42 | 41 |
| Potassium | Control | 510 | 837 | 942 | 983 |
| | Waterlogged | 279 | 234 | 273 | 313 |
| | Waterlogged as per cent control | 55 | 28 | 29 | 32 |
| Calcium | Control | 70 | 99 | 119 | 128 |
| | Waterlogged | 64 | 70 | 101 | 99 |
| | Waterlogged as per cent control | 91 | 70 | 85 | 77 |

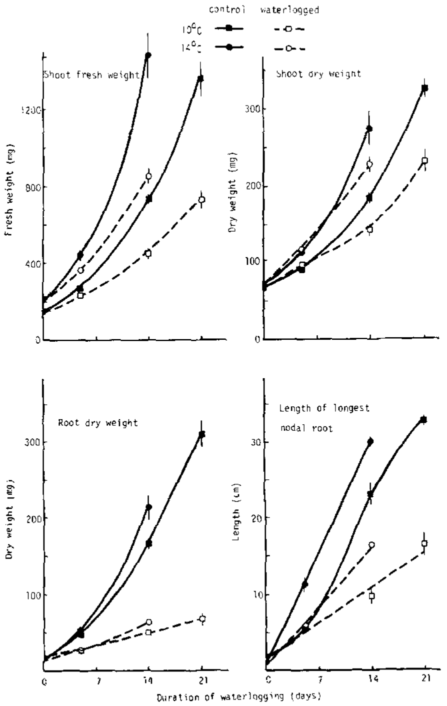

Fig. 5. The response of wheat to the duration of waterlogging at two soil temperatures. Plants were maintained at the stated temperature throughout the experiment. Values are means per plant. Bars indicate ± S.E. where these exceed symbol size.

the growth of the plants to find whether the apparent tolerance to waterlogging at lower temperatures seen in the preceding experiment was simply a reflection of the slower rates of growth and senescence. Although growth was slower at 10°C, the decrease in shoot and root weight, and nodal root length, relative to controls was similar to that in plants at 14°C (Fig. 5). By the time plants at 10°C had reached the same growth stage as those at 14°C (after 21 and 14 d, respectively) the two sets of plants were of similar weight and size (Fig. 5). This was true both of the controls and of the plants in waterlogged soil. Similar relations were found for the content of inorganic nutrients accumulated in the shoots as a result of uptake by the roots (Fig. 6). With waterlogging the amounts of nitrogen, phosphorus and potassium accumulated at 10°C lagged behind those at 14°C, but at the same growth stage, values were approximately equal in the two sets of plants. In terms of the final concentration of a nutrient in the shoot (Table 5), waterlogging caused similar declines relative to controls at both temperatures. The effect resembled that recorded in Table 4 for plants brought to their new temperatures only two days before the onset of waterlogging.

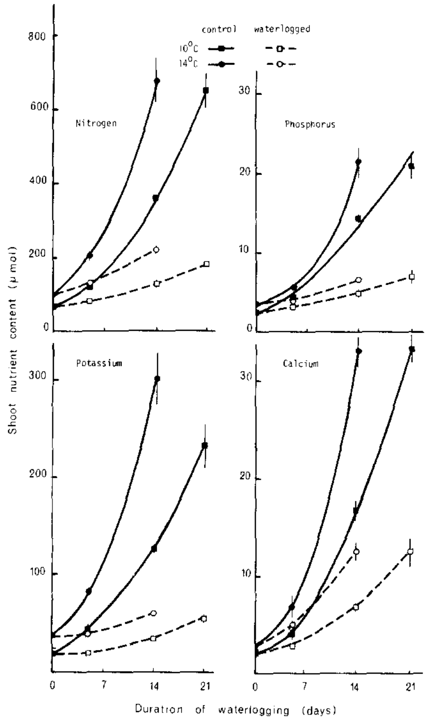

Fig. 6. Shoot nutrient content in wheat with duration of waterlogging at two soil temperatures. Conditions were as in Fig. 5. Values are means per plant ± S.E. where this exceeds symbol size.

Table 5. Effect of waterlogging on the concentrations of inorganic nutrients in the shoots of young wheat plants grown at two constant soil temperatures. Values are in µmole g$^{-1}$ dry weight of main shoot and tillers. Plants, grown at the two temperatures, were sampled at the same growth stage, after 21 and 14 d treatment.

| Nutrient treatment | | Soil temperature and duration of waterlogging | |
|---|---|---|---|
| | | 10°C, 21 days | 14°C, 14 days |
| Nitrogen | Control | 420 | 519 |
| | Waterlogged | 152 | 195 |
| | Waterlogged as per cent control | 36 | 38 |
| Phosphorus | Control | 64 | 79 |
| | Waterlogged | 28 | 28 |
| | Waterlogged as per cent control | 45 | 36 |
| Potassium | Control | 1120 | 1720 |
| | Waterlogged | 358 | 425 |
| | Waterlogged as per cent control | 32 | 25 |
| Calcium | Control | 164 | 193 |
| | Waterlogged | 83 | 87 |
| | Waterlogged as per cent control | 51 | 45 |

All differences between control (non-waterlogged soil) and waterlogged treatments were statistically significant ($P$ 0.05).

## Discussion

### *Effect of soil temperature on changes in the composition of the soil solution during waterlogging*

When a soil becomes waterlogging, the rate of oxygen depletion depends on the respiration rate of roots and soil micro-organisms, the solubility of oxygen in the water and the rate of oxygen diffusion through the soil to respiring roots. Luxmore and Stolzy[18], describing the relative effects of temperature changes on these factors, identify respiration rate, which will approximately double for a rise of 10°C, as the major influence. Likewise, carbon dioxide accumulation as a result of respiration will be affected by temperature in a parallel way. In the present study the depletion of oxygen from the *bulk* soil was nearly complete within 36 h (Fig. 1) even at the lowest temperature (6°C). The concentration of oxygen at the surface of respiring roots would have declined more rapidly than this because of the slow diffusion of oxygen through the soil water. Although the soil was quickly depleted of oxygen at all temperatures, the loss of nitrate was much retarded in the coolest soil suggesting perhaps that respiratory oxygen consumption was less sensitive to temperature than were denitrification and microbiological immobilization. Concurrent with the decline in oxygen, concentrations of nitrous oxide and nitrite increased, indicating the onset of denitrification. However, our results cannot be used reliably to estimate *rates* of denitrification *i.e.* the flux of nitrogen gases from the soil, because:

1) The sequence of reduction, $NO_3 \rightarrow NO_2 \rightarrow N_2O \rightarrow N_2$ (Cooper and Smith[7]) means that the concentrations of intermediates in the soil solution will depend on the rates of production and utilization in each step in the denitrification process. Thus the concentrations of nitrite and nitrous oxide in the soil water will not necessarily reflect the rate of denitrification. In our experiments nitrate disappeared from the soil solution much more slowly at temperatures of 14°C and below compared with 18°C. The greatest accumulation of nitrous oxide and nitrate occurred at 6°C, when the disappearance of nitrate was slow.

2) Part of the flux of nitrogen gases from the soil is as $N_2$, which we did not measure. The ratio $N_2O$:$N_2$ in the denitrification gas varies with temperature, being greatest at lower temperatures[4], and also with the concentration of nitrate remaining in solution[2,21].

3) Part of the nitrate-nitrogen lost from solution may be immobilized in organic compounds in the soil[8,28]. Thus, nitrate disappearance is not necessarily equivalent to denitrification. Furthermore, the relative rates of immobilization and denitrification can vary with the temperature[8].

Ethylene accumulated in the soil water most rapidly at higher temperatures, consistent with earlier work[26], but the concentration reflects the relative rates of production and consumption. The decline in concentration with time at 18°C (Fig. 2) may thus be regulated either by a fall in production perhaps due to scarcity of substrates, or by a more intense utilization by micro-organisms[19].

The gradual decline in the nitrate concentration in the waterlogged soil was associated with a decline in calcium, and to a lesser extent potassium. The fall in cation concentrations presumably served to maintain ionic equilibria between the soil solution and exchange surfaces[22].

### *Plant response to waterlogging at different soil temperatures*

In both types of experiment, the symptoms of waterlogging damage were least conspicuous at the lower soil temperatures. The onset of injury followed closely on the initial fall in the soil oxygen concentration[31]. However, the rates of oxygen depletion were relatively little affected by soil temperature, and the concentrations measured in the bulk soil probably over-estimated those at the root surface. It seems unlikely, therefore that a lower rate of oxygen depletion from the soil water explains the greater tolerance to waterlogging at lower temperatures in our experiments (see Introduction, mechanism 1).

The significance, in relation to waterlogging damage to plants, of changes in the nature and concentrations of organic and inorganic solutes in the soil solution has been reviewed[11,14]. There is extensive evidence that it is the rapid fall in the oxygen concentration around the roots that acts as the trigger for damage (for further discussions see Cannell and Jackson[6], Drew and Lynch[11], Grable[14]). Many of the symptoms of waterlogging damage to wheat can be reproduced simply by deoxygenation of nutrient solution cultures, the concentrations of all other dissolved solutes being maintained[33], although such observations do not rule out the possibility of toxic concentrations of solutes sometimes accumulating in soils under anaerobic conditions.

In the present study, temperature modified the accumulation in the soil water of carbon dioxide, ethylene, nitrous oxide and nitrite and also altered the loss of nitrate, calcium and potassium. However, the apparently improved tolerance of wheat to waterlogging at low temperatures is not readily explained in terms of any of these soil components. Concentrations of carbon dioxide were smaller than those that induce plant damage[11], while nitrous oxide and nitrite, also at concentrations that are not damaging to roots[6,11], accumulated most at temperatures where plants were least affected by waterlogging. The concentrations of the major nutrient ions were always in the range conducive to healthy plant growth during at least the initial 10 days. In the longer term the loss of nitrate from solution could be detrimental. Ethylene was present at physiologically active concentrations in the soil water at the higher temperatures. Its presence in the rooting medium can retard shoot and root growth in maize[17], but the stimulatory role of ethylene in adventitious rooting and aerenchyma formation[10] would be expected to confer an improved tolerance to waterlogging. We did not monitor iron, manganese, hydrogen sulphide and the volatile fatty acids in these experiments, but earlier experiments in the series under essentially the same conditions[31] at temperatures of 14°C indicated that none was likely to attain harmful concentrations in the soil we used during the period of the experiment.

We therefore conclude that under our conditions, temperature modified the waterlogging response of wheat mainly by its direct effect on the plant (see Introduction, mechanisms 3–5).

The greater tolerance to waterlogging at the lower temperatures may have reflected the plants' improved ability to adapt in some way to oxygen shortage, or the diminished growth rate of the plant or the slowing of root metabolism, (see Introduction, mechanisms 3–5), or some combination. In the experiments where soil temperatures were altered shortly before the onset of waterlogging, the seminal roots appeared less severely damaged by waterlogging at the lower temperatures, but nutrient accumulation by the shoot was greatly impaired, and further seminal root growth was restricted. This suggests that the roots at low temperatures could survive oxygen deficiency but were not functioning effectively. Likewise, the decrease (relative to the controls) in the length of the nodal roots extending into the waterlogged soil was similar at all temperatures. Thus root respiration was probably too fast even at low soil temperatures to allow oxygen diffusion through intercellular spaces (diffusion rates would be little affected by these temperature differences) to maintain a concentration at the apex that was sufficient for normal elongation (see Armstrong[1] for a theoretical discussion). The fraction of the lower leaves senescing prematurely was generally greater at the lower temperatures. If senescence and nitrogen retranslocation from the lower leaves to the younger leaves are closely linked, as we reported elsewhere[32], our result would indicate that at low temperatures plants are better able to retranslocate nitrogen from the lower leaves to the young leaves, relative to the rate of production of new leaves and tillers.

However, in part, the apparently greater tolerance to waterlogging at low temperatures may simply reflect the slower growth rate (see Introduction, mechanism 4). The extent of waterlogging damage to shoots clearly is closely related to the amount of growth made during the waterlogging period, which is greatest at the higher temperature. Our experiment in which soil temperatures were maintained constant revealed that the extent of damage caused by waterlogging at 14° and 10°C was similar when plants were compared at the same growth stage rather than at the same chronological age.

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