

## Nutrient accumulation and translocation in maturing wheat plants grown on waterlogged soil

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### Abstract

Wheat plants (*Triticum aestivum* L., cv. Arina) growing in large pots (perforated at the bottom for controls, intact for flooding) were embedded in the field in spring. Waterlogging was initiated at anthesis and was maintained throughout the maturation period. Grain yield as well as potassium, phosphorus and magnesium contents in the shoot were decreased on flooded soil, while manganese and iron contents increased considerably. Total calcium and zinc contents per shoot remained comparable to those in controls. The reduction of potassium, phosphorus and magnesium contents by waterlogging was greatest in the grains, while manganese and iron accumulated mostly in the vegetative parts and the glumes. Zinc contents were also lowered in the grains during waterlogging due to an inhibited redistribution from the vegetative parts to the grains. Our results indicate that flooding caused not only an accumulation of manganese and iron in the shoot, but also affected the redistribution of macro- and micronutrients to the maturing gains.

### Introduction

In flooded soils water enters the gas spaces and displaces oxygen and other gases. The remaining oxygen dissolved in water is rapidly depleted by the respiration of plant roots, microorganisms and fungi (Scott and Evans, 1955; Ponnampereuma, 1984). When the oxygen supply is very low, some microorganisms make use of electron acceptors other than oxygen for their respiratory oxidations. The reviews by Armstrong (1982) and Ponnampereuma (1984) show that numerous compounds such as nitrate, iron, manganese and sulfate are reduced. Iron and manganese are solubilised and may become toxic for crop plants. The oxidation-reduction potential is an indirect measure for these changes (Pearsall, 1938). Thus, there is a rapid decrease of oxygen availability at 330 mV, of nitrate at 220 mV, the

appearance of soluble and reduced manganese at 200 mV, of soluble and reduced iron at 120 mV, and the disappearance of sulfate at -150 mV (Gambrell and Patrick, 1978).

Growth and metabolism of plants not adapted to wetland conditions are inhibited in waterlogged soil. Oxygen deficiency in the root environment causes an earlier senescence of the oldest leaves (Drew and Sisworo, 1979; Trought and Drew, 1980b). There are reductions of root and shoot growth as well as of nutrient accumulation in young wheat plants grown on nutrient solution with a limited oxygen supply (Barret-Lennard et al., 1988; Buwalda et al., 1988; Trought and Drew, 1980a). Similar results were reported for young barley and wheat plants on waterlogged soil (Cannell et al. 1980; Drew and Sisworo, 1979; Trought and Drew, 1980b,c; Belford 1981). In the reports mentioned above nitrogen,

phosphorus and potassium contents in the shoot were always more affected by oxygen deficiency than magnesium and calcium contents. Waterlogging can also affect the pattern of sinks and sources in the plant partly due to the limited oxygen availability in the root environment, which reduces root respiration. Thus, the carbohydrate transport in the phloem to the roots and subsequent phloem unloading were found to be reduced in maize and wheat seedlings under hypoxic conditions (Saglio, 1985; Waters et al., 1991). Luxmoore et al. (1973) reported a reduced yield of wheat when the plants were flooded 20 to 30 days during the grain filling period. Short term flooding did not influence yield. The yield reduction in wheat is influenced by the duration of waterlogging as well as by the developmental stage of the plants at the beginning of this treatment (Belford, 1981; Cannell et al. 1980; Watson et al. 1976). The number of grains per ear and the average dry weight per grain are relevant in this context, but the relative importance of these two yield components depends on the timing of waterlogging.

The aim of the work reported here was to determine the effects of long-term waterlogging after anthesis on the accumulation and redistribution of nutrients in wheat plants. Our experiments focus on the translocation of macro- and micronutrients from vegetative plant parts to the ear and within the ear to the maturing grains.

## Materials and methods

### *Plant material and waterlogging*

Winter wheat (*Triticum aestivum* L., cv. Arina) was grown in a field near Bern. Intact polyethylene pots (36 cm diameter, 38 cm high) were embedded in the soil for flooding. Pots of the same size were perforated at the bottom and used for controls. Soil and young plants were transferred to the pots on April 10. Waterlogging with tap water started at anthesis (June 28) and was maintained throughout the maturing period, while control pots only received water by rain. The redox potentials in the soil were monitored during the experiment 5 cm, 10 cm and 15 cm

below the soil surface with redox electrodes according to Armstrong (1982).

### *Analyses of nutrients in soil samples*

Soil samples were taken twice (July 23 and August 5) 10–20 cm below the soil surface. For pH measurements 5 g humid soil was mixed with 10 mL H<sub>2</sub>O. After 12 h the soil was resuspended and 1 min later the pH was determined with an electrode. Nitrate was measured colorimetrically by nitration of salicylic acid (Cataldo et al. 1975) in a water extract (5 g humid soil and 20 mL H<sub>2</sub>O incubated 30 min on a shaker prior to centrifugation for 10 min at 2000 g). Supernatant (500 µL) was mixed with 50 µL sodium salicylate (5 g L<sup>-1</sup>). After drying at 95°C the tubes were cooled to ambient temperature and 25 µL H<sub>2</sub>SO<sub>4</sub> were added and allowed to react for 10 min with the samples. Afterwards 2.3 mL H<sub>2</sub>O and 125 µL 177 mM sodium potassium tartrate in 10 N NaOH were mixed with the samples and 10 min later the extinctions were read at 420 nm. For standards NaNO<sub>3</sub> (0–4 µg N) was used.

Ammonium was quantified in a KCl extract (5 g humid soil and 20 mL 1 M KCl incubated 30 min on a shaker prior to centrifugation for 10 min at 2000 g) with the phenol-hypochlorite reaction described by Weatherburn (1967). Supernatant (1 mL) was mixed with 0.1 mL 205 mM Na<sub>2</sub>-EDTA (pH 7) and 1 min later with 0.2 mL phenolate solution (744 mM phenol, 1.14 mM sodium nitroprusside), 0.4 mL freshly prepared hypochlorite solution (22.7 mM dichloroisocyanuric acid in 342 mM sodium phosphate buffer, pH 11.8) and 0.8 mL H<sub>2</sub>O. The tubes were incubated for 30 min and the extinction was read at 628 nm. Standards with 0–3 µg N were prepared with (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> in 1 M KCl.

Ammonium acetate (1 M pH 4.8) was used to extract potassium, manganese and iron by shaking 5 g humid soil and 20 mL solution for 30 min followed by centrifugation for 10 min at 2000 g. These elements were quantified by atomic absorption spectrometry after appropriate dilution of the supernatant with 1.267 g L<sup>-1</sup> CsCl suprapur in 0.1 N HCl (for potassium) or with 0.1 N HCl (for manganese and iron).

The dry matter contents of the soil samples

were determined separately. All contents of extractable nutrients were expressed per g dry soil.

#### Analyses of nutrients in plant material

Plants from 4 different pots for each treatment were collected weekly from anthesis to harvest and separated into leaves, stem segments, grains and glumes. From the middle of each ear 4 spikelets were divided into grains and glumes (containing glumes, lemmas and paleas). These samples, the rest of the ear, the leaf blades and the stem sections were analysed separately. The plant parts were dried at 105°C, weighed and heated in glass tubes for 8 h at 550°C. After cooling 0.2 mL HCl (10 N) and 7.8 mL H<sub>2</sub>O were added to each tube. The solutions were mixed and diluted with 1.267 g L<sup>-1</sup> CsCl suprapur in 0.1 N HCl (for potassium), with 13.37 g L<sup>-1</sup> LaCl<sub>3</sub> · 7H<sub>2</sub>O in 0.1 N HCl (for calcium and magnesium) and with 0.1 N HCl (for iron, manganese and zinc) prior to measuring the elements by atomic absorption spectrometry. Phosphate was quantified colorimetrically with a vanadate-molybdate-reagent (Merck Darmstadt).

#### Results

Decreases in the redox potential of non-perforated pots were observed before artificial flooding. These changes were caused by partial waterlogging after rain. In such pots wheat roots may already have been suffering to some extent from hypoxia and the mineral composition of the shoots may have been influenced before the onset of flooding. The total period of waterlogging was actually longer than designed and this fact should be taken into consideration when comparing the results presented here with those from other experiments. After waterlogging the redox potential of the soil became more negative in a similar manner at 5, 10 and 15 cm below the soil surface and remained in a negative range until harvest (Fig. 1). In control pots the redox potential was always above +350 mV. These data indicate that the plants in control pots were under normoxia. As a control, soil extracts were analysed 25 and 38 days after the start of

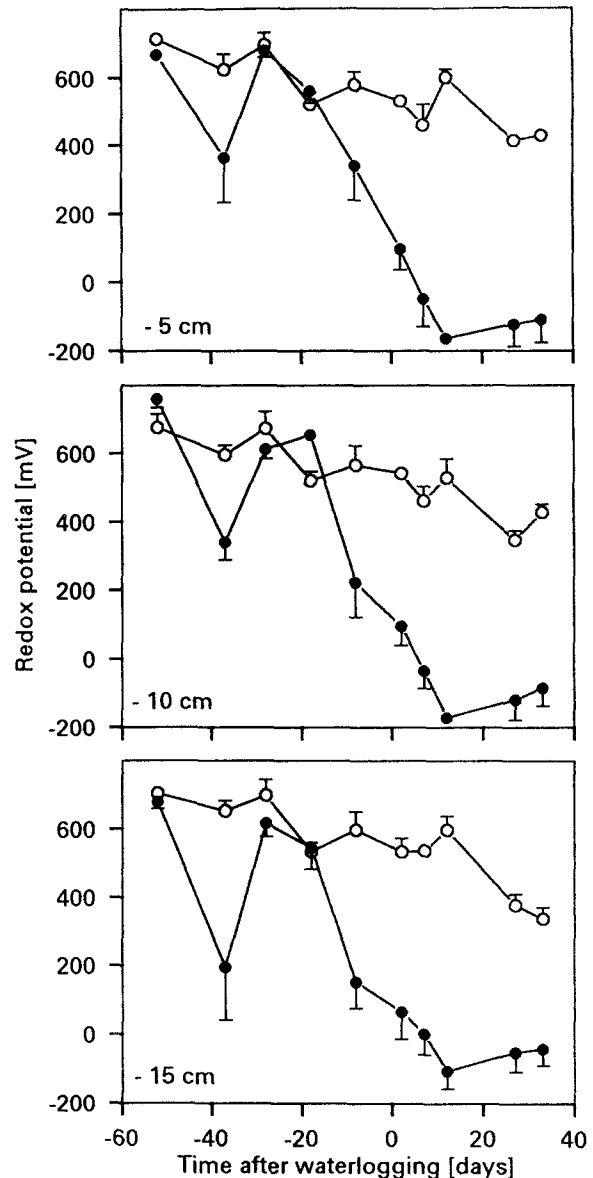


Fig. 1. Effect of waterlogging on redox potentials at different levels below the soil surface (-5, -10 and -15 cm). Waterlogging started June 28 (day 0) and continued until harvest (day 38). Redox potentials at pH 7 with a standard hydrogen electrode as a reference were computed from the measured values (platinum electrodes, Ag/AgCl reference electrode). Means of 4 replicates are shown for control pots (○) and waterlogged pots (●). Standard errors are shown when exceeding the size of the symbol (on one side only for clarity).

continuous flooding (Table 1). A large increase in the sum of dissolved and exchangeable manganese and iron was observed after waterlogging.

Table 1. Effect of waterlogging on pH and nutrient availability in the soil. Means of 6 independent pots are shown for soil samples collected 25 and 38 days after waterlogging. Least significant differences were computed at the 5% ( $LSD_{.05}$ ) and 1% ( $LSD_{.01}$ ) level

Analysis	Waterlogged		Control		$LSD_{.05}$	$LSD_{.01}$
	Day 25	Day 38	Day 25	Day 38		
pH	6.37	6.63	6.18	6.10	0.26	0.36
Nitrate ( $\mu\text{g N g}^{-1}$ )	1.05	1.21	4.95	3.76	1.24	1.69
Ammonium ( $\mu\text{N g}^{-1}$ )	7.44	15.75	3.18	1.52	6.62	9.03
Potassium ( $\mu\text{g K g}^{-1}$ )	173.4	148.6	163.1	141.6	61.7	84.1
Iron ( $\mu\text{g Fe g}^{-1}$ )	192.5	534.0	9.4	9.1	219.0	298.7
Manganese ( $\mu\text{g Mn g}^{-1}$ )	197.1	255.8	1.8	0.6	86.4	117.8

Ammonium concentrations increased, while nitrate concentrations decreased in waterlogged pots. The availability of potassium, which is not subjected to redox reactions in the soil, remained comparable in control and flooded pots.

A major net accumulation of dry matter occurred after anthesis (day 0) only in the grains (Fig. 2). Waterlogging reduced the dry matter accumulation in the ear by reducing both the number of grains per ear and the dry matter per grain (Table 2). The reduced grain yield was mainly caused by a premature cessation of grain growth after day 17 and only to a minor extent by a slowed dry matter accumulation before day 17 (Fig. 2). Senescence and desiccation were observed earlier on waterlogged than on control pots.

The contents of iron and manganese in the shoot were higher on waterlogged soil (Fig. 3). The iron content in the grains was higher on flooded soil than on control pots, while no major influence on the accumulation of manganese in the grains was detected. A marked increase of the iron content in vegetative parts and glumes was observed between day 24 and day 31. The increased availability in the soil (Table 1) affected the delivery of this micronutrient to all shoot parts, including the grains (Fig. 3). The net increase in manganese contents in the grains was very similar for control and treated plants (Fig. 3), although dry matter accumulation in the grains was negatively affected by waterlogging (Fig. 2). The manganese contents in the glumes at the end of the season remained higher on waterlogged pots, but this quantity was in both cases far below that of the grains (Fig. 3). Manganese was lost from vegetative parts of control plants during maturation, while on

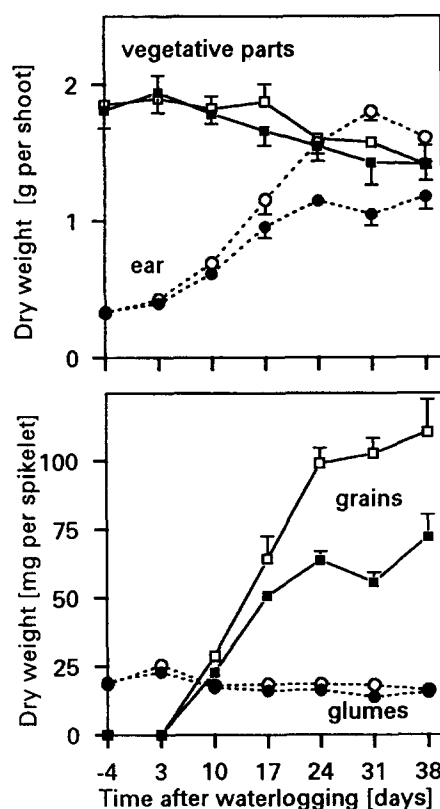


Fig. 2. Effect of waterlogging on dry weight of different plant parts during grain filling. Waterlogging started June 28 (day 0) and continued until harvest (day 38). Means of 4 replicates are shown for control pots ( $\circ$ ,  $\square$ ) and waterlogged pots ( $\bullet$ ,  $\blacksquare$ ). Standard errors are shown when exceeding the size of the symbol (on one side only for clarity).

flooded soil the manganese level remained high until harvest. The availability of zinc in the soil is not sensitive to changes in the redox potential and the behaviour of this micronutrient in the plant differed from that of manganese and iron. During the first two weeks after anthesis a

Table 2. Effect of waterlogging on the development of wheat grains. The numbers of grains per ear and per spikelet are based on samples collected 24 days (4 replicates), 31 days (4 replicates) and 38 days (8 replicates) after waterlogging. The dry weights refer to the final harvest 38 days after waterlogging (8 replicates). Means  $\pm$  SE and significances (t-test) at the 5%(\*), 1%(\*\*) and 0.1%(\*\*\*) level are shown

	Waterlogged	Control	Significance
<b>Whole ear</b>			
Number of grains [grains per ear]	28.69 $\pm$ 1.35	33.06 $\pm$ 1.14	*
Dry weight of grains [mg per grain]	27.38 $\pm$ 3.19	39.06 $\pm$ 1.33	**
<b>Spikelets from the middle of the ear:</b>			
Number of grains [grains per spikelet]	2.20 $\pm$ 0.09	2.55 $\pm$ 0.08	**
Dry weight of grains [mg per spikelet]	64.28 $\pm$ 6.08	103.85 $\pm$ 6.22	***

decrease of zinc contents was observed in vegetative parts of all plants regardless of the soil status. Afterwards control plants continued to lose zinc from the vegetative parts, whereas in waterlogged plants the zinc contents increased again. The higher zinc contents in vegetative parts were paralleled by lower contents in the ear and were most likely caused by diminished remobilisation. Within the ear zinc levels in the glumes were low and decreased during grain maturation, while in the maturing grains zinc was accumulated in a manner similar to the dry matter.

The contents of calcium in the vegetative parts and in the glumes were hardly influenced by waterlogging, while the calcium contents in the grains of waterlogged plants were lower (Fig. 4). This macronutrient is characterised by a poor mobility in the phloem and the rather small quantity of calcium in the ear was most likely translocated via the xylem from the roots to the top of the plant (Marschner, 1986). The phloem-mobile elements potassium, phosphorus and magnesium can be translocated from vegetative parts to the ear. The total contents of these macronutrients in the shoots were already reduced before flooding. These differences can be explained by partial waterlogging in intact pots after rain periods before the onset of artificial flooding. Potassium, phosphorus and magnesium were lost from vegetative parts on waterlogged soil and on control pots. Their accumulation as well as that of the immobile calcium in the maturing grains was reduced in a manner similar to the dry matter yield when plants were flooded. The loss of mobile nutrients from vegetative parts exceeding the simultaneous ac-

cumulation in the ear can be explained by leakage in the rain (Schenk and Feller, 1990; Tukey, 1970), although a translocation via the phloem to the roots cannot be completely ruled out. In the glumes the time courses for the macronutrients mentioned were not affected by hypoxia in the root environment.

## Discussion

The heavy rainfalls around day -40 and day -10 caused already partial waterlogging in non-perforated pots. The total duration of waterlogging was actually longer than designed (especially at the bottom of these pots) with consequences for the redox potential, the availability of nutrients in the soil and the nutrient uptake by the wheat plants. After the beginning of permanent flooding at day 0 the redox potential decreased similarly at -5, -10 and -15 cm. At day 2 it was at all positions below 100 mV, a value at which roots suffer from oxygen deficiency and the reduction of manganese and iron becomes significant. After day 10 the redox potential remained throughout the grain filling period below 0 mV. As a consequence of the changes in the soil, root and shoot growth and nutrient acquisition may be affected (Drew and Sisworo, 1979; Gambrell et al. 1991; Trought and Drew, 1980c). The nutrient uptake into wheat roots can be influenced by altered nutrient concentrations in the soil solution or by altered root properties (Good and Muench, 1993; Kramer, 1951; Kramer and Jackson, 1954).

Our data show that waterlogging caused increased ammonium and decreased nitrate con-

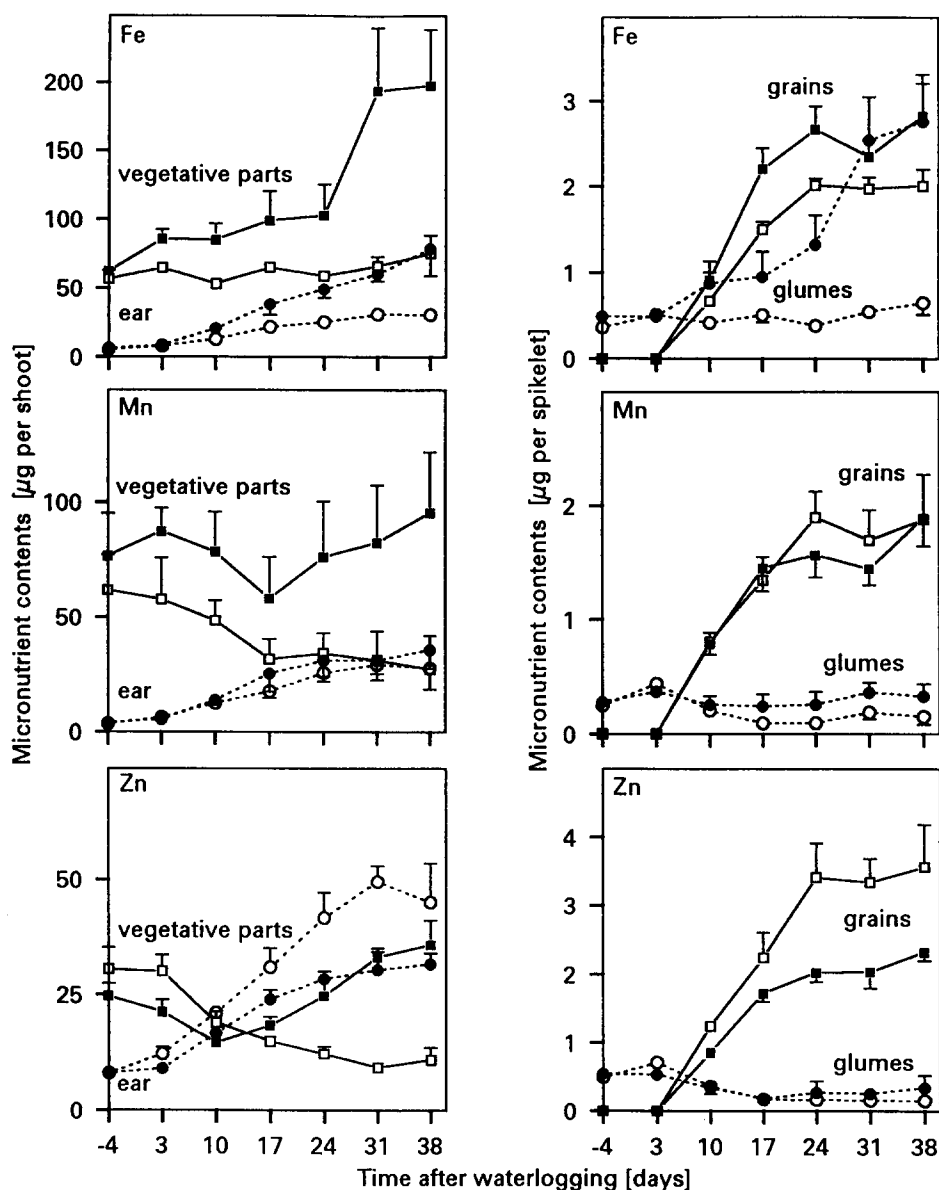


Fig. 3. Effect of waterlogging on the distribution of the micronutrients Fe, Mn and Zn in wheat shoots during grain filling. Waterlogging started June 28 (day 0) and continued until harvest (day 38). Means of 4 replicates are shown for control pots (○, □) and waterlogged pots (●, ■). Standard errors are shown when exceeding the size of the symbol (on one side only for clarity).

tents in the soil, and solubilised manganese and iron as expected. Other micronutrients (e.g. zinc) or macronutrients (calcium, potassium, magnesium, phosphorus) are not subject to reduction and solubilisation. The effects of nitrogen availability on plants are complex, since the relative abundance of nitrate and ammonium influences the acquisition of other ions and the

long-distance transport between the roots and the shoot in both directions (Lindt and Feller, 1987; Van Beusichem et al. 1988). Nitrate can be translocated as such via the transpiration stream, while ammonium is generally assimilated in the roots. Organic substrates delivered from the shoot to the roots are required during ammonium utilisation to fuel assimilatory processes

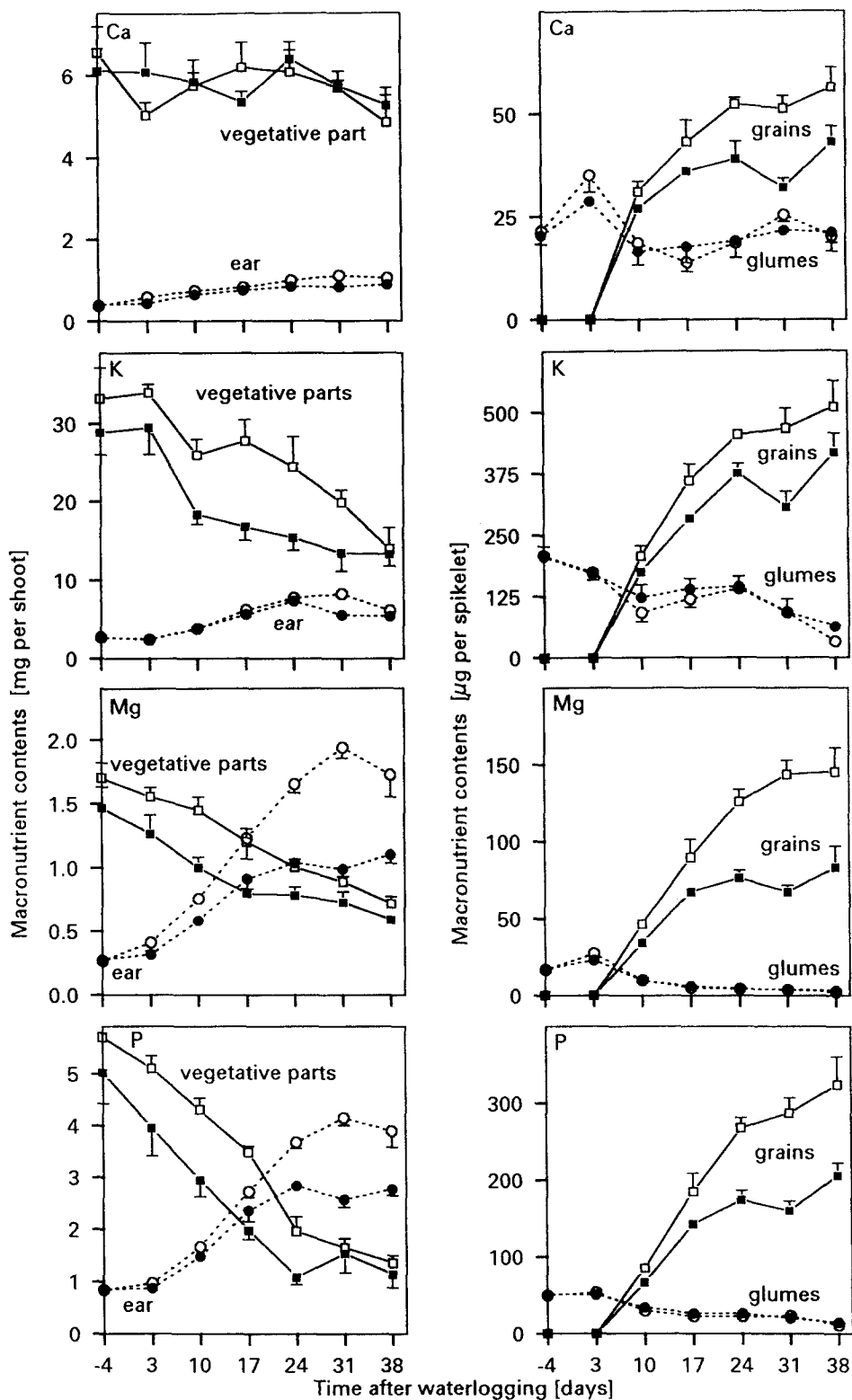


Fig. 4. Effect of waterlogging on the distribution of the macronutrients Ca, K, Mg and P in wheat shoots during grain filling. Waterlogging started June 28 (day 0) and continued until harvest (day 38). Means of 4 replicates are shown for control pots (○, □) and waterlogged pots (●, ■). Standard errors are shown when exceeding the size of the symbol (on one side only for clarity).

and to provide the C-skeletons for the synthesis of organic compounds transported via the xylem to the shoot (Lindt and Feller, 1987).

In the experiments reported here, permanent flooding started at anthesis and reduced grain filling (Fig. 2). The earlier senescence of leaves and the earlier cessation of grain growth may result from a limiting supply of a nutrient (e.g. nitrogen). The importance of nitrogen availability for yield formation in cereals on waterlogged soil has been emphasised previously by a number of authors (Belford, 1981; Cannell et al., 1980; Watson et al., 1976). Phloem-mobile nutrients (e.g. nitrogen, potassium, phosphorus) are easily redistributed within the shoot during grain maturation. If one of these elements becomes limiting, it can be remobilised and leaf senescence (accompanied by a loss of photosynthetic capacity) can be initiated. The metabolism and senescence properties of leaves may also be affected by altered phytohormone concentrations in the xylem sap transported from the roots to the shoot (Jackson, 1991; Voesenek et al., 1990). The earlier leaf senescence reduces photosynthesis and, as a consequence, the source capacity for phloem-mobile assimilates and inorganic solutes. The accumulation of nutrients with a poor phloem mobility (e.g. calcium) may be indirectly influenced by a reduced cumulative transpiration (Schenk and Feller, 1990). Two yield components were considered in this study. Both the average number of grains per ear and the average dry matter per grain were reduced by waterlogging (Table 2). These findings are consistent with results reported previously by other investigators (Belford, 1981; Watson et al., 1976). It must be borne in mind that the relative importance of these two yield components may depend on the time and duration of flooding and on the nutrient status of the wheat plants (Cannell et al., 1980).

The increased manganese and iron contents in the whole shoot may be explained by the reduction and solubilisation of these two elements in the flooded soil, and their different distribution within the shoot may result mainly from their different mobility in the plant. However, the accumulation of iron in the grains was less and that of manganese far less influenced than the contents in the vegetative parts and the glumes.

The micronutrient zinc represents an interesting element in this context. Its availability in the soil is not influenced by hypoxic conditions and the total contents in the shoot were very similar in flooded and control plants, but the distribution within the shoot differed considerably. Since zinc and dry matter accumulation in the grains were similarly decreased after flooding, zinc concentrations in the harvested grains were comparable for treated plants and controls. In contrast, zinc contents in vegetative parts were strongly increased after flooding. A major accumulation of this element was observed in the flag leaf sheath (data not shown). The regulatory mechanisms involved in this zinc redistribution are not yet satisfactorily known.

Waterlogging and oxygen deficiency can directly influence nutrient uptake by affecting the availability of nutrients in the soil or by affecting root activities. Furthermore, indirectly altered source-to-sink relations within the shoot can influence the redistribution of phloem-mobile nutrients from senescing shoot parts to the grains. All the possibilities mentioned may be relevant for yield formation and for the composition of grains and straw at harvest.

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### References

- Armstrong W 1982 Waterlogged soils. *In* Environment and Plant Ecology. Second Edition. Ed. J R Etherington. pp 290–330. John Wiley & Sons Publishers, Chichester, UK.
- Barrett-Lennard E G, Leighton P D, Buwalda F, Gibbs J, Armstrong W, Thomson C H and Greenway H 1988 Effects of growing wheat in hypoxic nutrient solutions and of subsequent transfer to aerated solutions. I. Growth and carbohydrate status of shoots and roots. *Aust. J. Plant Physiol.* 15, 585–598.
- Belford R K 1981 Response of winter wheat to prolonged



- waterlogging under outdoor conditions. *J. Agric. Sci. Camb.* 97, 557–568.
- Buwalda F, Barrett-Lennard E G, Greenway H and Davies B A 1988 Effects of growing wheat in hypoxic nutrient solution and of subsequent transfer to aerated solutions. II. Concentrations and uptake of nutrients and sodium in shoots and roots. *Aust. J. Plant Physiol.* 15, 599–612.
- Cannell R Q, Belford R K, Gales K, Dennis C W and 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, 117–132.
- Cataldo D A, Haroon M, Schrader L E and Youngs V L 1975 Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. *Commun. Soil Sci. Plant Anal.* 6, 71–80.
- Drew M C and Sisworo E J 1979 The development of waterlogging damage in young barley plants in relation to plant nutrient status and changes in soil properties. *New Phytol.* 82, 301–314.
- Gambrell R P, Delaune R D and Patrick W H 1991 Redox processes in soils following oxygen depletion. *In Plant Life under Oxygen Deprivation: Ecology, Physiology and Biochemistry*. Eds. M B Jackson, D D Davies and H Lambers. pp 101–117. SPB Academic Publishing, The Hague.
- Gambrell R P and Patrick W H 1978 Chemical and microbiological properties of anaerobic soils and sediments. *In Plant Life in Anaerobic Environments*. Eds. D D Hook and R M M Crawford. pp. 375–423. Ann Arbor Science Publications, Ann Arbor, Michigan, USA.
- Good A G and Muech D G 1993 Long-term anaerobic metabolism in root tissue: Metabolic products of pyruvate metabolism. *Plant Physiol.* 101, 1163–1168.
- Jackson M B 1991 Regulation of water relationships in flooded plants by ABA from leaves, roots and xylem sap. *In Abscisic Acid: Physiology and Biochemistry*. Eds. W J Davies and H G Jones. pp. 217–226. Bios Scientific Publishers, Oxford, UK.
- Kramer P J 1951 Causes of injury to plants resulting from flooding of the soil. *Plant Physiol.* 26, 722–736.
- Kramer P J and Jackson W T 1954 Causes of injury to flooded tobacco plants. *Plant Physiol.* 29, 241–245.
- Lindt T and Feller U 1987 Effect of nitrate and ammonium on long distance transport in cucumber plants. *Bot. Helv.* 97, 45–52.
- Luxmoore R J, Fischer R A and Stolzy L H 1973 Flooding and soil temperature effects on wheat during grain filling. *Agron. J.* 65, 361–365.
- Marschner H 1986 *Mineral Nutrition of Higher Plants*. Academic Press, London, 674 p.
- Pearsall W H 1938 The soil complex in relation to plant communities. *J. Ecol.* 26, 180–193.
- Ponnamperuma F N 1984 Effects of Flooding on Soil. *In Flooding and Plant Growth*. Ed. T T Kozlowski. pp. 9–45. Academic Press, London, UK.
- Saglio P H 1985 Effect of path or sink anoxia on sugar translocation in roots of maize seedlings. *Plant Physiol.* 77, 285–290.
- Schenk D and Feller U 1990 Effect of phloem interruption on leaf senescence and nutrient redistribution in wheat (*Triticum aestivum*). *In Plant Nutrition – Physiology and Applications*. Ed. M L van Beusichem. pp. 121–125. Kluwer Academic Publishers, Dordrecht.
- Scott A D and Evans D D 1955 Dissolved oxygen in saturated soil. *Soil Sci. Soc. Am. Proc.* 19, 7–12.
- Trought M C T and Drew M C 1980a The development of waterlogging damage in young wheat plants in anaerobic solution cultures. *J. Exp. Bot.* 31, 1573–1585.
- Trought M C T and Drew M C 1980b The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.). I. Shoot and root growth in relation to changes in the concentration of dissolved gases and solutes in the soil solution. *Plant and Soil* 54, 77–94.
- Trought M C T and Drew M C 1980c The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) II. Accumulation and redistribution of nutrients by the shoot. *Plant and Soil* 56, 187–199.
- Tukey H B 1970 The leaching of substrates from plants. *Annu. Rev. Plant Physiol.* 21, 305–324.
- Van Beusichem M L, Kirkby E A and Baas R 1988 Influence of nitrate and ammonium nutrition on the uptake, assimilation, and distribution of nutrients in *Ricinus communis*. *Plant Physiol.* 86, 914–921.
- Voesenek L A C J, Harren F J M, Bögemann G M, Blom C W P M and Reuss J 1990 Ethylene production and petiole growth in *Rumex* plants induced by soil waterlogging: The application of a continuous flow system and a laser driven intracavity photoacoustic detection system. *Plant Physiol.* 94, 1071–1077.
- Waters I, Kuiper P J C, Watkin E and Greenway H 1991 Effects of anoxia on wheat seedlings. I. Interaction between anoxia and other environmental factors. *J. Exp. Bot.* 42, 1427–1435.
- Watson E R, Lapins P and Barron R J W 1976 Effect of waterlogging on the growth, grain and straw yield of wheat, barley and oats. *Aust. J. Exp. Agric. Animal. Husb.* 16, 114–122.
- Weatherburn M W 1967 Phenol-hypochlorite reaction for determination of ammonia. *Anal. Chem.* 39, 971–974.

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