

Water logging may inhibit plant growth primarily by nutrient deficiency rather than nutrient toxicity

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ABSTRACT

The aim of our experiments was to investigate whether nutrient deficiency or toxicity is the cause for growth inhibition of wheat and barley in waterlogged soils. Experiments using two soils (top and subsoil) differing largely in various characteristics revealed a growth inhibition of wheat and barley in the case of subsoil due to water logging, without Fe or Mn toxicity. Water culture experiments with anaerobic (N₂) and aerobic aeration confirmed that oxygen deficiency did not induce nutrient toxicity (Fe, Mn) but caused sub-optimum nutrient supply (N, P, K, Mn, Cu, Zn) of wheat and barley plants. In a split-root water culture experiment with barley, cultivating half of the root system in varying combinations of aerobic/anaerobic and with/without K supply, it was shown that sufficient K uptake occurred only when K and oxygen were applied in the same root compartment. We suggest that due to O₂ deficiency in the root medium, synthesis of ATP may be inhibited leading thus to a decrease in nutrient uptake. Nutrient deficiency rather than toxicity appears to be the major cause for the poor plant growth in waterlogged soils.

Keywords: water logging; growth; nutrients; toxicity; deficiency

In last decades the weight of agricultural machines has increased and consequently the soil compaction has increased due to the use of such machines under wet soil conditions (Abu-Hamdeh 2003). In wet and cold springs, such compacted soils may be waterlogged and plants show visual symptoms of water logging. On waterlogged sites, plants show chlorosis and necrotic spots on older leaves. Both Mn toxicity and N deficiency may be induced by the low redox potential in waterlogged soils that produces plant-available Mn²⁺ and promotes denitrification of NO₃⁻. Under these anaerobic conditions, root metabolism and root growth are inhibited, since the lack of O₂ affects the energy status of the plant (Drew 1988). Water logging reduces leaf superoxide dismutase activity, leaf catalase activity, and root oxidizability of *Brassica napus* L. (Zhou and Lin 1995). Gutierrez Boem et al. (1996) reported that water logging resulted in a decrease of N, P, K and Ca uptake by *Brassica napus* L. On the other hand, water logging changes the available ion concentration of the soil solution. Due to electron excess, Fe^{III} and Mn^{IV} are reduced to Fe^{II} and Mn^{II}, respectively. Rice roots can avoid uptake of the accumulated Fe^{II} and Mn^{II} ions by a release of oxygen into the rhizosphere for Fe and Mn oxidation (Mengel and Kirkby 2001). Plants such as wheat and barley are not able to oxidize Fe and Mn so that a toxicity of

Mn and Fe may occur under waterlogged conditions (Drew 1988).

The objective of this study was to analyse whether water logging and oxygen deficiency inhibit the growth of spring barley and spring wheat primarily by a deficiency or by a toxicity of nutrients.

MATERIAL AND METHODS

Three experiments were conducted with spring barley (*Hordeum vulgare* L. cv. Ingrid) and spring wheat (*Triticum aestivum* L. cv. Thassos).

Effect of water logging on mineral nutrition (soil experiment)

A completely randomized two-factorial experiment was carried out under natural conditions over a four-week period with topsoil (0–0.30 m depth) from an alluvial soil and subsoil (0.40–0.60 m depth) from a brown soil derived from loess. The topsoil is characterized by a higher amount of available nutrients and by higher concentrations of total organic carbon and of nitrogen (Table 1).

The soils were filled into Ahr pots (12 kg topsoil and 13 kg subsoil per pot) and were fertilized with 20 g/pot (subsoil) and 15 g/pot (topsoil) of a com-

Table 1. Soil characteristics

Soil characteristics	Topsoil	Subsoil
pH (0.01M CaCl ₂)	7.4	6.3
N _t (g/kg)	4.3	0.3
NO ₃ -N ¹⁾ (mg/kg)	37.4	0.6
NH ₄ -N ¹⁾ (mg/kg)	3.0	0.0
N _{org} ¹⁾ (mg/kg)	22.8	1.3
Total organic carbon (g/kg)	31.4	2.3
Carbonate (g/kg)	17.2	0.0
Clay (g/kg)	446	199
Silt (g/kg)	436	398
Sand (g/kg)	118	403
K ²⁾ (mg/kg)	254.0	44.8
P ²⁾ (mg/kg)	208.9	8.8
Mg ³⁾ (mg/kg)	227.0	203.0
Cu ⁴⁾ (mg/kg)	4.9	0.9
Mn ⁴⁾ (mg/kg)	27.3	15.5
Fe ⁴⁾ (mg/kg)	48.8	24.7
Zn ⁴⁾ (mg/kg)	2.9	0.5

¹0.01M CaCl₂-extractable according to Houba et al. (1986)²CAL-extractable according to Schüller (1969)³extractable Mg according to Schachtschabel (1954)⁴DTPA-extractable according to Lindsay and Norvell (1978)

pound fertilizer (12% N, 5% P, 14% K as sulphate, 6% S, 2% Mg). After emergence, seedlings were thinned to 25 plants/pot. 13 days after sowing, the soils were irrigated to 70% of maximum water-holding capacity in one treatment and to 110% of the maximum water-holding capacity in the treatment

of water logging. For each soil and plant species, all treatments were replicated four times. Plants were harvested when the first symptoms of yellowing of older leaves occurred. These symptoms were visible 15 days after water logging treatment. In this experiment, it was not possible to separate the roots from the soil by washing because in the water logging treatment a part of the root system was degraded and roots were destroyed by the washing procedure.

Effect of aerobic and anaerobic aeration on mineral nutrition (nutrient solution experiment)

A completely randomized two-factorial water culture experiment was conducted under natural conditions. Seven days old wheat and barley seedlings cultivated in quartz sand were transplanted into pots (four plants/pot) that contained 5 l of nutrient solution [2mM Ca(NO₃)₂, 0.5mM K₂SO₄, 0.2mM KH₂PO₄, 0.6mM MgSO₄, 5mM CaCl₂, 0.2mM Fe-EDTA, 1μM H₃BO₃, 0.5μM MnSO₄, 0.5μM ZnSO₄, 0.3μM CuSO₄, 0.005μM (NH₄)₆Mo₇O₂₄]. The nutrient solution was renewed twice a week. After 9 days of cultivation in an aerated nutrient solution the plants (barley and wheat) of four pots were harvested and the rest of the plants was grown for another 11 days. The nutrient solution was aerated either with air (control) or with N₂ (anaerobic). Air or N₂ aeration was applied to the nutrient solutions with the same pressure. For each plant species the treatments were replicated five times.

Split-root experiment

In this experiment, the effects of K supply in combination with aerobic or anaerobic conditions in nutrient solutions on growth and K uptake of

Table 2. Experimental design of the split-root experiment

Treatment	Split-root compartment			
	1		2	
	aeration	potassium ¹⁾	aeration	potassium
1	aerobic (A)	+	aerobic (A)	+
2	anaerobic (An)	+	anaerobic (An)	+
3	anaerobic (An)	+	aerobic (A)	0
4	anaerobic (An)	0	aerobic (A)	+
5	anaerobic (An)	+	aerobic (A)	+

¹4mM K as K₂SO₄ (+) was added; 0 = no K was supplied

barley were investigated. Therefore, six 16 days old barley seedlings cultivated in nutrient solution (mineral concentration already described) were carefully transferred into split-root pots so that the root system was equally divided into two halves. Each compartment was filled with 10.5 l of nutrient solution. Plants were cultivated for 15 days in split-root containers in a growth chamber (day: 16 hrs light, 80 W/m², 25°C; night: 8 hrs dark, 18°C). The experiment comprised five treatments, which were replicated three times (Table 2).

During the growth of barley, the nutrient solution was changed twice a week and the K concentration of the solutions in the split-root compartments was determined daily. After 15 days shoots were harvested and roots were separately harvested from each split-root compartment.

Analyses

Shoots and roots of plants were dried at 80°C. Total N in plants was analysed by means of the Kjeldahl method. Cations were determined after dry-ashing at 450°C for 20 hrs and solubilization of the ash in 5M HNO₃ using an atomic adsorption spectrometer (Spectra 220 FS, Varian Co. Australia). The P concentration was measured in the ash solution using the vanadate-molybdate method (Gericke and Kurmies 1952). The alkalinity of shoots and roots was measured with the method of Jungk (1968). Water-soluble glucose, fructose, and sucrose (extraction at 60°C) were enzymatically analysed using an enzymatic test kit (Fortmeier and Schubert 1995). The root length was measured using the line-intersection method (Tennant 1975). The results were statistically evaluated (mean value, standard error of mean) with a one- or two-factor analysis of variance at the 5% probability level of significance using the software program Statgrafics Plus Version 3 for Windows.

RESULTS

Effect of water logging on growth and plant nutrient concentrations (soil experiment)

Water logging resulted in a significant decrease of shoot dry weight production of both plant species on the subsoil. The relative effect was stronger in barley than in wheat although it is known that water logging in humic soils can produce organic substances that may inhibit plant growth. In contrast, on the topsoil no significant reduction of shoot dry weight production due to water logging was observed. There was even a higher shoot dry weight of wheat in the waterlogged treatment compared to the control treatment (Table 3).

The determination of the nutrient concentrations in barley and wheat shoots indicates that the N, P, K, Mg, Cu, Zn, and Mn concentrations decreased significantly in the water logging treatment. The concentrations of Fe and Ca were not affected by water logging (Table 4). Especially in the water logging treatment of the subsoil, the K concentrations in the shoots of spring barley and spring wheat were significantly below the sufficient K concentration range according to Bergmann (1992), although the subsoil was sufficiently supplied with K. On the topsoil, the K concentrations in the shoots of spring barley and spring wheat were decreased by water logging but to a lesser degree compared to the subsoil.

Effect of aerobic and anaerobic aeration on shoot and root biomass and nutrient concentrations (nutrient solution experiment)

Since we observed different effects of soil water logging on growth and nutrient concentrations of wheat and barley using the two soils, we conducted a further experiment in water culture to investi-

Table 3. Shoot dry matter of spring barley and spring wheat grown on subsoil and topsoil as related to a 15 days waterlogging period

Plant	Subsoil		Topsoil	
	control	waterlogging	control	waterlogging
g dry matter/pot				
Barley	25.8 (± 1.5) ¹⁾ 100%	9.7* ²⁾ (± 0.6) 38%	17.4 (± 0.3) 100%	16.0* (± 1.1) 92%
Wheat	23.7 (± 0.8) 100%	10.5* (± 0.3) 44%	15.8 (± 1.0) 100%	17.5* (± 0.8) 110%

¹⁾standard error of mean, ²⁾significant difference at the < 5% probability level

Table 4. Mineral concentrations of spring barley and spring wheat shoots as related to a 15 days period of waterlogging on topsoil and subsoil

Nutrients	Wheat			Barley			
	control	waterlogging	SC	control	waterlogging	SC	
Topsoil	mg/g dry matter						
	N	47.1	38.1* ²⁾	30–45	49.9	34.8*	20–40
	P	6.2	4.9*	3.5–6.0	5.1	3.9*	3.5–6.0
	K	57.4	48.6*	33–45	63.2	45.1*	30–55
	Ca	6.3	5.8	4–10	8.3	6.9*	5–10
	Mg	1.9	1.4*	2–3.5	2.3	1.9*	1.5–3.0
	mg/kg dry matter						
	Mn	41.8	27.5*	35–100	37.9	21.9*	30–100
	Cu	12.2	10.0*	7–15	10.5	7.2*	6–12
	Fe	92.8	89.7	–	89.9	69.1	–
	Zn	39.6	28.5*	25 – 70	38.4	26.5*	20–60
Subsoil	mg/g dry matter						
	N	49.1	29.0*	30–45	48.9	34.5*	20–40
	P	4.6	3.3*	3.5–6	4.4	3.6*	3.5–6.0
	K	50.5	28.0*	33–45	54.5	28.1*	30–55
	Ca	4.9	6.2	4–10	8.1	12.2*	5–10
	Mg	3.2	2.0*	2–3.5	3.0	2.8*	1.5–3.0
	mg/kg dry matter						
	Mn	53.9	35.1*	35–100	63.9	47.7*	30–100
	Cu	10.7	7.9*	7–15	10.1	9.4*	6–12
	Fe	72.1	70.0	–	69.5	71.0	–
	Zn	38.6	21.4*	25–70	40.5	34.1*	20–60

SC – sufficient concentration according to Bergmann (1992), ²⁾significant difference at the < 5% probability level

gate the effects of O₂ deficiency on growth and on concentrations of nutrients and carbohydrates. The shoot and root growth of wheat and barley was significantly inhibited by the anaerobic aeration during the 11 days of application (Table 5).

The mineral concentrations in the shoots of barley and wheat are presented in Table 6. Anaerobic aeration induced a strong decrease of the mineral nutrient concentrations of barley and wheat relative to control plants. In barley, the Fe concentration was slightly higher in the anaerobic treatment, but the concentration of 163.2 mg Fe/kg dry matter was not at a toxic level. It is evident that in the anaerobic treatment most of the mineral elements in wheat and barley are below the sufficient concentration documented by Bergmann (1992). Although the mineral element concentrations were decreased

by anoxia, the concentrations of sucrose, glucose, and fructose were enhanced in the shoots of wheat and barley due to N₂ aeration of the nutrient solution (Table 7).

The alkalinity was higher in roots than in shoots; it was decreased in the shoots and roots by N₂ aeration (Table 8). The increase of the carbohydrate concentration in the shoots and the decrease of alkalinity in roots and shoots by the anaerobic root media indicate a change of the inorganic cation/anion balance of the plants.

Split-root experiment

In this experiment the effects of aerobic and anaerobic aeration of the root medium and of

Table 5. Shoot dry weight, root dry weight and root length of spring barley and spring wheat as related to an 11 days period of different aeration of the nutrient solution

	Wheat		Barley	
	aerobic	anaerobic	aerobic	anaerobic
Shoot (g dry matter/pot)	2.98 (\pm 0.62) ¹⁾	2.07* ²⁾ (\pm 0.10)	2.93 (\pm 0.12)	2.26* (\pm 0.13)
Root (g dry matter/pot)	0.82 (\pm 0.04)	0.32* (\pm 0.01)	1.08 (\pm 0.07)	0.49* (\pm 0.03)
Root length (m/pot)	10.6 (\pm 0.43)	7.7* (\pm 0.31)	9.2 (\pm 0.6)	7.7* (\pm 0.3)

¹⁾standard error of mean, ²⁾significant difference at the < 5% probability level

K application to the different root compartments were investigated for barley. The fresh and dry weights of shoots were significantly higher in the treatment with K application and air aeration in both root compartments compared to the other treatments (data not presented). The root fresh weight, as related to K application and different aeration, is presented in Figure 1. It is evident that the kind of aeration had a stronger effect on the root fresh weight than K application. The highest root fresh weight was observed in the compartments that were continuously aerobic. The effect of K application on the root fresh weight was less than that of the anaerobic treatment (Figure 1).

The lowest K concentration and the lowest K uptake of barley were determined in the treatment An+/A–, although in this treatment barley was supplied separately in one compartment with oxygen and in the other compartment with K (Figures 2 and 3).

DISCUSSION

Anaerobic soil conditions increase oxalate-soluble P and Fe in soils (Zhang et al. 2003). Also, soil flooding improves the bioavailability of P, Fe, and Mn to rice, which is adapted to water logging (Drew 1988). Plants that are not tolerant to water logging, may suffer from Fe or Mn toxicity (Horst 1988). On acid flooded soils, even rice may suffer from Fe toxicity (DeDatta et al. 1990). Graven et al. (1965) reported that the Mn concentration increased in alfalfa shoots by soil flooding and that the Mn concentration reached a toxic level. Also Drew (1988) found that water logging often induces an increase of Mn and Fe in shoots of wheat and barley. In contrast, our results obtained in soils differing in a number of characteristics (Table 1) showed a significant decrease of the N, P, K, Mg, Zn and Mn concentrations in wheat and barley shoots (Table 4). Our findings agree with those of Morad

Table 6. Mineral concentrations of spring barley and spring wheat shoots as related to an 11 days period of different aeration of the nutrient solution

Nutrients	Wheat			Barley		
	aerobic	anaerobic	SC	aerobic	anaerobic	SC
mg/g dry matter						
N	49.6	30.3* ¹⁾	40–50	49.2	34.7*	28–50
P	7.3	3.4*	3.5–6.0	6.9	4.4*	3.5–6.0
K	53.9	28.2*	33–45	66.4	39.4*	30–55
mg/kg dry matter						
Mn	116.8	24.3*	35–100	69.6	16.3*	30–100
Cu	12.5	4.8*	7–15	9.1	6.7*	6–12
Fe	139.1	112.1	–	137.2	163.2	–
Zn	65.0	26.1*	25–70	56.9	29.3*	20–60

SC – sufficient concentration according to Bergmann (1992), ¹⁾significant difference at the < 5% probability level

Table 7. Carbohydrate concentrations (mg/g dry matter) of spring barley and spring wheat shoots as related to an 11 days period of different aeration of the nutrient solution

Carbohydrate	Wheat		Barley	
	aerobic	anaerobic	aerobic	anaerobic
Sucrose	21.6 (\pm 1.7) ¹⁾	44.4* ²⁾ (\pm 3.6)	12.8 (\pm 0.8)	18.7* (\pm 1.7)
Glucose	4.5 (\pm 0.7)	17.8* (\pm 1.1)	3.3 (\pm 0.3)	15.9* (\pm 0.7)
Fructose	4.7 (\pm 0.6)	18.9* (\pm 0.9)	5.5 (\pm 0.2)	17.3* (\pm 1.3)

¹⁾standard error of mean, ²⁾significant difference at the < 5% probability level

Table 8. Alkalinity of shoots and roots of spring barley and spring wheat as related to an 11 days period of different aeration of the nutrient solution (in mmol NaOH/100 g dry weight)

	Wheat		Barley	
	aerobic	anaerobic	aerobic	anaerobic
Shoot	118.2 (\pm 1.0) ¹⁾	70.1* ²⁾ (\pm 2.8)	138.7 (\pm 1.4)	95.6* (\pm 1.7)
Root	143.3 (\pm 3.2)	74.2* (\pm 4.8)	149.5 (\pm 3.8)	102.8* (\pm 5.3)

¹⁾standard error of mean, ²⁾significant difference at the < 5% probability level

and Silvestre (1996) who observed a decrease of mineral element concentration in various plants due to anoxia.

The question arises why the nutrient uptake may be inhibited by oxygen deficiency. Under anaerobic conditions the concentration of soluble carbohydrates (glucose, fructose, sucrose) increased in shoots (Table 7) indicating that photosynthates did not limit nutrient uptake. Carbohydrate accumulation generally occurs when the growth is inhibited due to various stress conditions or nutrient deficiency (Schubert 1995). Morad and Silvestre (1996) reported that under oxygen-deficient conditions the root cell energy pool greatly decreased. It is likely that ATP concentrations in

roots decreased because of inhibition of respiration by anoxia (Drew 1988). Low ATP concentrations in roots affect the activity of the plasma membrane H⁺ ATPase (Schubert and Yan 1999). The low concentration of most of the analysed nutrients may be, due to anoxia, a direct consequence of the low H⁺ ATPase activity. The decreased alkalinity due to anoxia (Table 8) indicates, that inorganic cation uptake was more sensitive than inorganic anion uptake, which is a consequence of partial depolarization of the membrane potential at low H⁺ ATPase activity (Schubert and Lauchli 1988).

The data of the split-root water culture experiment with barley indicate that anoxia in a root compartment inhibited K uptake (Figure 2), al-

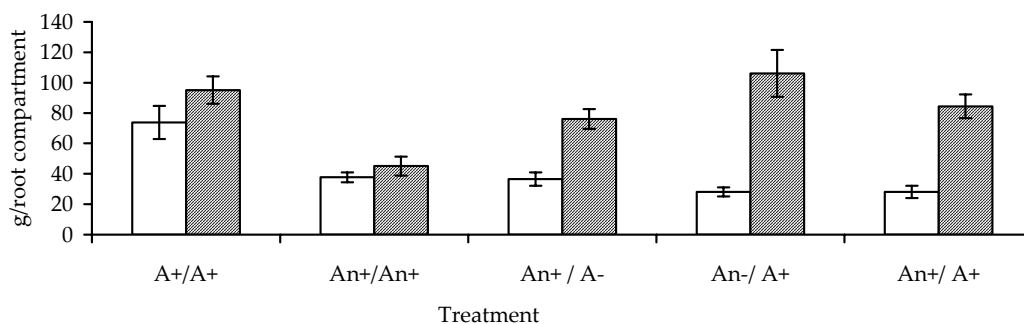


Figure 1. The effect of K application on the root fresh weight of barley in a split-root experiment
A = aerobic, An = anaerobic, + = K supply, - = no K supply

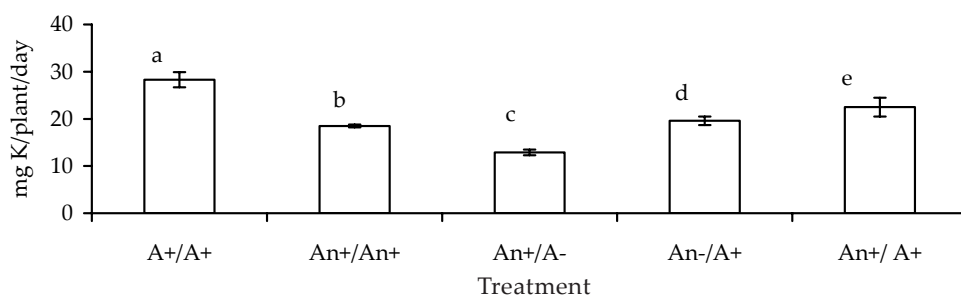


Figure 2. K uptake of barley plants in a split-root experiment
A = aerobic, An = anaerobic, + = K supply, - = no K supply

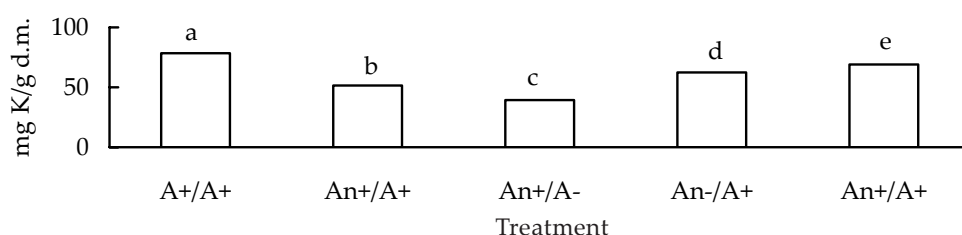


Figure 3. K concentration of barley plants in a split-root experiment
A = aerobic, An = anaerobic, + = K supply, - = no K supply

though the other half of the root system was supplied with oxygen (Table 2). Sufficient K uptake only occurred when K and oxygen were applied in the same root compartment. This result indicates that neither energy nor oxygen was translocated from one root segment to the other, and that K uptake of barley occurs if both K and oxygen are available.

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ABSTRAKT

Zamokření může inhibovat růst rostlin spíše deficiencí živin než jejich toxicitou

Cílem pokusů bylo zjistit, zda je nedostatek či toxicita živin příčinou inhibice růstu pšenice a ječmene na zamokřených půdách. Pokusy se dvěma zeminami výrazně odlišných vlastností (ornice a podorniči) vykazovaly omezení růstu pšenice a ječmene v případě pěstování na podorniční vrstvě v důsledku zamokření, ovšem bez vystupující toxicity Fe a Mn. Pokusy v živných roztocích v anaerobních (N₂) a aerobních podmínkách potvrdily, že nedostatek kyslíku nevyvolává toxicitu živin (Fe, Mn), vzniká však suboptimální zásobenost živinami (N, P, K, Mn, Cu, Zn) u rostlin pšenice a ječmene. V pokusu s rozdělenými kořeny rostliny ječmene na dvě poloviny do dvou kompartmentů živného roztoku (split – root) byly zvoleny kombinace aerobních a anaerobních podmínek za přítomnosti i absence draslíku v roztoku. Dostatečný příjem K rostlinou byl pouze za přítomnosti kyslíku a draslíku v daném kořenovém kompartmentu. Lze předpokládat, že nedostatek kyslíku v kořenovém médiu mohl omezovat syntézu ATP, což vedlo ke snížení příjmu živin. Hlavní příčinou inhibice růstu rostlin na zamokřených půdách je spíše deficeience živin než jejich toxicita.

Klíčová slova: zamokření; růst; živiny; toxicita; deficeience

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