Plant and Soil 101, 211–221 (1987)

PLSO 6925

Effects of intermittent waterlogging on the mineral nutrition of cotton

P.J. HOCKING[1], D.C. REICOSKY[2] and W.S. MEYER
CSIRO, Centre for Irrigation Research, Private Mail Bag, Griffith, NSW 2680, Australia
[1]CSIRO, Division of Plant Industry, GPO Box 1600, Canberra City, ACT 2601, Australia
[2]USDA-ARS, North Central Soil Conservation Research Center, Morris, MN 56267, USA

Received 30 June 1986. Revised September 1986

Key words: aeration, calcium, cotton, flooding, magnesium, manganese, phosphorus, potassium, sodium chloride, waterlogging

Abstract

A field experiment was conducted to investigate the effects of intermittent waterlogging on the nutrient status of cotton (*Gossypium hirsutum* cv. Deltapine 61). The crop was grown in a sloping plot of soil in which a gradient of water-table depth ranging from 0.04 m above to 0.60 m below the soil surface was established during two periods of waterlogging in mid summer and early autumn. The first waterlogging lasted 8 days; the second lasted 16 days.

Dry matter increases were less for severely waterlogged plants than for plants with well-aerated root systems during the first flooding, but the increases were similar during the second. Waterlogging impaired uptake of most nutrients by young plants in the first flooding, but had much less effect on nutrient uptake by older plants in the second. Waterlogging consistently reduced concentrations of P and K in the petioles and laminae of young fully-expanded leaves, and severely waterlogged plants were deficient in these nutrients by the end of the first flooding. Mn did not accumulate to toxic levels in waterlogged plants. During each flooding, waterlogged plants gained in total content of all nutrients studied, but the gains of each nutrient, except for Na, were proportionally smaller than for well-aerated plants. Fluxes of K-, Cl- and HPO_4- ions in xylem sap exuded from stumps of detopped plants which had been waterlogged were lower than those from plants with well-aerated root systems. Seed cotton yields and concentrations of nutrients in mature bolls were not affected by the two periods of waterlogging. It is concluded that although intermittent waterlogging induced nutrient stress in cotton plants, especially for P and K in young plants before flowering, they recovered with no detrimental effect upon yield.

Introduction

Irrigated summer crops are frequently subjected to periods of waterlogging and low O_2 availability in the root zone as a consequence of poor drainage, heavy rainfall following irrigation, and fluctuating shallow water-tables (Smith *et al.*, 1983). In particular, many of the fine-textured soils suitable for growing irrigated cotton in eastern Australia are characterised by poor surface drainage and low saturated hydraulic conductivity (Hodgson and Chan, 1982).

Short-term waterlogging and associated root zone anaerobiosis can injure roots and result in a variety of stress symptoms including reduced shoot growth, leaf epinasty and wilting (Drew, 1983). A major physiological effect of waterlogging is reduced uptake and transport of mineral ions by roots (Devitt and Francis, 1972; Drew and Sisworo, 1979; Slowik *et al.*, 1979). This can result in mineral nutrient stress in shoots which may be accompanied by internal redistribution of certain nutrients and premature senescense of older leaves (Drew *et al.*, 1979; Trought and Drew, 1980).

Cotton seems to be susceptible to short-term waterlogging. For example, lint yields decreased by

42% after 32 h of flooding (Hodgson, 1982), and seed + lint yields decreased by 42% after flooding for 4 days (De Bruyn, 1982). However, apart from a study using static water-tables (Meek *et al.*, 1980), there is little information on how waterlogging affects the nutritional status of cotton, especially with respect to rapidly-imposed short-term waterlogging. This paper describes nutrient responses of cotton to intermittent waterlogging using a sloping plot facility in the field which allowed several defined water-table heights to be rapidly imposed on the crop. The results reported here extend recent work on the effects of intermittent waterlogging on the water status (Reicosky *et al.*, 1985) and N nutrition (Hocking *et al.*, 1985; Schaefer *et al.*, 1987) of cotton.

Materials and methods

Sloping plot water-table facility

The sloping plot used to obtain a gradient of severity of waterlogging has been described previously (Reicosky *et al.*, 1985). In summary, it was a trench 45 m long by 5 m wide with a slope of 1.78% which was excavated in Hanwood Loam (Butler, 1979) (Typic Palexeralf) of pH 6.9–7.8 at the CSIRO Centre for Irrigation Research, Griffith, N.S.W., Australia. The sloping plot was lined with impermeable plastic sheeting, and the soil was repacked to give 0.2 m of top soil over 0.4 m of subsoil. A gravel layer 0.15 m thick beneath the repacked soil but on top of the plastic sheeting facilitated movement of water during flooding or draining. Water entered the sloping plot through a slotted PVC pipe buried in the gravel layer, and a float valve maintained the water level.

Six water-table depths were selected for plant sampling along the sloping plot: these were +0.04 (highest), −0.05, −0.17, −0.27, −0.38 and −0.60 (lowest) m with respect to the soil surface. Free surface water was visible for 4–5 m from the lower end of the sloping plot during each period of flooding. Profiles of soil matric potentials along the sloping plot as measured by tensiometers have been reported previously (Reicosky *et al.*, 1985). Roots of plants growing in the section where the water-table was 0.60 m below the soil surface were considered well aerated, and those where the water-table was 0.04 m above the soil were severely waterlogged.

Two periods of flooding were imposed on the same cotton crop in mid summer and early autumn. The first lasted 8 days from 17 to 24 January, 1983, and began when the plants were 0.6 m high and had just started flowering. The second lasted 16 days from 7 to 23 March, 1983, and began when the plants were about 1 m high and had young bolls. The duration of the first flooding was determined by the onset of visible symptoms of waterlogging (wilting). The second flooding aimed at producing similar symptoms, but was terminated after 16 days because the waterlogged plants showed no symptoms of stress, although differences in leaf growth rates were obtained between plants from the highest and lowest water-table depths in the sloping plot (Reicosky *et al.*, 1985). Water was drained from the sloping plot at the end of each flooding by pumping it from the gravel layer.

Establishment of cotton plants

Cotton (*Gossypium hirsutum* L.) cv. Deltapine 61 was sown in October 1982 in rows 0.25 m apart. Fertilizer was broadcast at the rate of 130 kg N and 44 kg P ha^{-1}, and incorporated into the top 0.1 m of soil before sowing the cotton. Seedlings were thinned to 19 plants m^{-2}; weeds were controlled by herbicides or hoeing.

To check that the cotton plants in the non-waterlogged section of the sloping plot were typical of field-grown plants, a comparison plot the same size as the sloping plot was established 15 m to one side of and parallel to the sloping plot. The soil in the comparison plot was deep-ripped to simulate the soil disturbance in the sloping plot, but there was no impermeable plastic-sheet barrier so that free soil drainage occurred. The water-table in the comparison plot was about 2.5 m below the surface, and it was not in the root zone of the cotton plants (Reicosky *et al.*, 1985).

Except for the periods of waterlogging, plants in the sloping and comparison plots received the same P fertilizer and irrigation treatments. Only half of the comparison plot, however, was given the same N fertilizer treatment as the sloping plot; the second half received no N to assess crop response to the applied N fertilizer (Hocking *et al.*, 1985). A

Table 1. Selected weather data for first and second floodings. Values are means for time intervals indicated for each flooding

Climatic parameter		Number of days from start of flooding				
First flooding		*1–2*	*3–4*	*5–6*	*7–8*	
Air temp. (°C)	max.	27.2	33.0	38.2	34.0	
	min.	12.1	12.5	16.2	17.2	
	mean	19.7	23.2	28.1	25.0	
Rel. humidity (%)	max.	66.5	67.6	76.9	76.0	
	min.	17.5	17.5	11.0	14.5	
	mean	41.0	40.9	36.5	39.1	
Solar radiation ($MJ\,m^{-2}$)		31.3	30.1	29.7	31.3	
Rainfall (mm)		0	0	0	0	
Second flooding		*1–3*	*4–6*	*7–9*	*10–12*	*13–16*
Air temp (°C)	max.	35.8	33.7	30.1	30.0	24.0
	min.	22.1	16.6	19.0	15.5	15.6
	mean	29.5	24.9	24.2	22.8	19.5
Rel. humidity (%)	max.	64.0	68.9	74.3	80.1	92.0
	min.	19.8	24.7	33.2	31.1	56.9
	mean	39.3	45.0	52.1	55.0	78.6
Solar radiation ($MJ\,m^{-2}$)		21.8	20.5	14.9	22.5	10.0
Rainfall		0	0	0	0	9.3

supplementary dressing of 75 $kg\,N\,ha^{-1}$ was applied to the sloping plot to assist plant recovery after the first flooding, and to the high-N half of the comparison plot. Only results from the high-N part of the comparison plot are presented in this paper.

Plants in the sloping plot were irrigated by sprinklers before and after each period of waterlogging. Irrigation was applied to plants in the sloping plot and in the comparison plot when tensiometers at a soil depth of 0.15 m indicated -30 kPa. The amount of water applied at each irrigation was equal to the cumulative pan evaporation measured at a meteorological station 500 m from the experimental site. Other weather data were also collected at this station, and these are given in Table 1 for the two periods of waterlogging.

Harvest of plant material

A narrow walkway was placed across the sloping plot at each of the selected water-table depths to facilitate plant sampling. The day before the floodings began and at the end of each period of waterlogging, 6 representative plants were cut at soil level from a zone 1.5 m either side of the walkway at each water-table depth for tissue analysis, and separated into stems + petioles, leaf laminae and bolls. Samples of 6 representative plants were also harvested from the high-N section of the comparison plot.

In addition, two representative samples each of 12 youngest fully-expanded leaves were collected from the main axes of plants at each water-table depth along the sloping plot and from plants in the high-N part of the comparison plot, and separated into petioles and laminae. This was done because the youngest fully-expanded leaf is often used to diagnose the nutritional status of cotton (Hearn, 1981). The leaf samples were collected daily during the first flooding and every 2 or 3 days during the second.

Collection of root exudate

Xylem sap was collected at each water-table depth from stem stumps of 3 plants cut off about 2 cm above the surface at the end of the first flooding, and at the beginning and end of the second, as described previously (Hocking *et al.*, 1985). All sap collections were made between 11.00 and 13.00 h to avoid possible diurnal fluctuations in ion concentrations.

Nutrient analyses

Plant material was dried at 80°C and ground to pass a 20 mesh (0.84 mm) screen. Concentrations of P, K, Ca, Mg, Na and Mn in the ground material were determined from diluted 1:1 nitric/perchloric acid digests by an autoanalyser (P), flame photometer (K, Na) and atomic absorption spectrophotometer (Ca, Mg and Mn). Phosphorus in xylem sap was determined on the autoanalyser or by ion chromatography. Chloride was estimated by silver ion titration after extracting plant material with a nitric/acetic acid mixture.

Analysis of data

Because the experiment was restricted to one sloping plot water-table facility, it is only possible to provide sampling errors for each water-table treatment. Data are presented for plants from the high-N section of the comparison plot, but this plot should not be regarded as a control plot because the soil was not treated in exactly the same way as that in the water-table facility. As mentioned above, its purpose was to provide a check that the growth and nutrition of plants in the non-waterlogged section of the sloping plot were typical of field-grown cotton.

Results

Plant growth

The appearance and leaf growth responses of the plants during the two flooding events have been described previously (Reicosky *et al.*, 1985). Briefly, in the first flooding leaf growth rates had decreased in waterlogged plants by 4 days after flooding began and, by day 8, about 80% of the plants from these treatments had wilted. During the second flooding, leaf growth rates decreased in waterlogged plants, but these plants did not wilt or show other symptoms of stress.

Plants from all treatments gained dry matter during both floodings (Table 2). Severely waterlogged plants accumulated proportionally less dry matter than plants with well-aerated root systems during the first flooding, but the proportional gains in dry matter were similar for waterlogged and well-aerated plants during the second flooding. Dry matter gains by young plants during the first flooding were proportionally greater than those of older

Table 2. Amounts of dry matter in whole tops of cotton plants immediately before and after short-term waterlogging. Developing bolls made up approximately 30% of the dry matter of tops from each treatment at end of second flooding. Values are means of 6 plants ± S.E.

Water-table depth (m)	Whole plant top dry wt(g)		Dry wt gain by plant top during flooding (%)
	Before flooding	End of flooding	
First flooding			
+0.04	24.8 ± 3.3	30.8 ± 3.2	24
−0.05	26.3 ± 2.9	37.2 ± 4.2	41
−0.17	29.1 ± 3.8	40.8 ± 3.9	40
−0.27	25.6 ± 2.7	41.2 ± 4.1	61
−0.38	27.4 ± 3.0	47.5 ± 5.3	73
−0.60	28.6 ± 3.1	49.5 ± 5.7	73
CP[a]	34.1 ± 3.9	57.4 ± 6.5	68
Second flooding			
+0.04	84.8 ± 9.5	109.7 ± 11.0	29
−0.05	85.5 ± 9.0	107.6 ± 10.9	26
−0.17	83.4 ± 9.1	109.9 ± 10.0	32
−0.27	89.5 ± 8.3	113.4 ± 8.6	27
−0.38	86.6 ± 8.9	117.7 ± 12.7	36
−0.60	91.2 ± 10.5	122.3 ± 10.9	34
CP	89.2 ± 8.7	124.1 ± 11.2	39

[a] CP: plants from high-N part of comparison plot.

Table 3. Effect of water-table depth on boll number and seed cotton yields at maturity. Values are means of 10 samplings of 1 m^2 ± S.E.

Water-table depth (m)	No. bolls m^{-2}	Seed cotton yield ($kg\,m^{-2}$)
+0.04	69 ± 9	0.24 ± 0.02
−0.05	96 ± 10	0.35 ± 0.02
−0.17	110 ± 14	0.41 ± 0.03
−0.27	104 ± 9	0.37 ± 0.03
−0.38	92 ± 9	0.26 ± 0.02
−0.60	84 ± 8	0.23 ± 0.02
CP[a]	110 ± 8	0.29 ± 0.02

[a] CP: plants from high-N part of comparison plot.

plants during the second flooding, with the exception of plants which were severely waterlogged.

Yield data for plants harvested at maturity are shown in Table 3. Numbers of bolls and seed cotton yields in the sloping plot were highest where the intermittent water-table was between 0.05 and 0.27 m below the surface, and did not appear to be

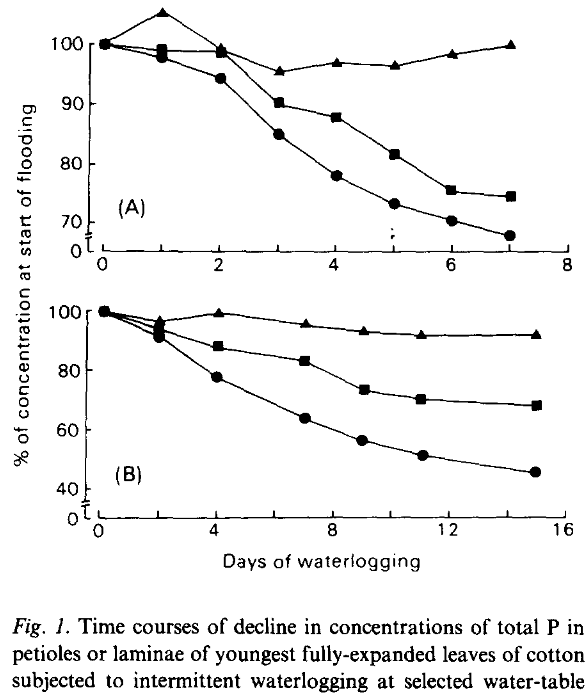

Fig. 1. Time courses of decline in concentrations of total P in petioles or laminae of youngest fully-expanded leaves of cotton subjected to intermittent waterlogging at selected water-table depths along the sloping plot water-table facility. Data have been normalised to a common percentage scale in which a rating of 100 designates the concentration of P in leaf laminae or petioles immediately before the start of each period of waterlogging. Each point is the mean of two samples each of 12 leaf laminae or petioles. (**A**) leaf laminae, first flooding (**B**) petioles, second flooding. *Symbols* for water-table depths are as follows: ●——● + 0.04 m; ■——■, −0.27 m; ▲——▲, −0.60 m.

related to the observed vegetative growth responses during the two periods of waterlogging.

Concentrations of nutrients in youngest fully-expanded leaves

First flooding. Concentrations of P, K and Mn decreased in laminae of the youngest fully-expanded leaves during the first flooding in all but the lowest water-table treatment (−0.60 m) and the comparison plot (Table 4); the decreases were usually greatest in the higher water-table treatments (Table 4 and Fig. 1A). By contrast, concentrations of Cl, Ca, Mg and Na increased in laminae, with the greatest increases usually in plants from the lower water-table treatments.

Concentrations of all nutrients except for Na decreased in petioles from waterlogged plants. Decreases in concentrations also occurred in petioles of plants from the lowest water-table treatment and the comparison plot for P, K, Ca, Mg and Mn, but not for Cl and Na. As found for laminae, decreases in petiolar nutrient concentrations were usually greatest in severely waterlogged plants.

Second flooding. Changes in concentrations of nutrients in laminae and petioles of the youngest fully-expanded leaves during the second flooding were generally consistent with those of the first flooding (Table 5). The most notable differences between the second and first floodings were the increases in Mn concentrations in petioles from waterlogged plants in contrast to decreases in the first flooding, and the decreases in concentrations of Na in laminae and petioles of all plants as opposed to the substantial increases during the first flooding. Again, decreases in nutrient concentrations in laminae and petioles during the period of flooding were usually greatest and most rapid in severely waterlogged plants (Table 5; Fig. 1B).

Concentrations of nutrients in plant tops

During the first flooding, concentrations of P, Cl, K and Mg declined in leaves and stems of plants from all water-table depths as well as the high-N comparison plot, and concentrations of Ca and Mn declined in stems but not in leaves (data not

Table 4. Effects of first flooding on concentrations of selected nutrients in the lamina and petiole of the youngest fully-expanded leaf of cotton. Values are the % increase or decrease in concentration of a particular nutrient in the leaf lamina or petiole during the 8 days of the first flooding, and are the means of two bulk samples each of 12 leaves. Range of values for both samples within ± 10% of mean value. Values in parentheses are concentrations of a particular element for plants from the highest water-table treatment at the end of the flooding expressed as $mg\,g^{-1}$ dry wt or $\mu g\,g^{-1}$ dry wt (Mn)

Water-table depth (m)	Change in concn during period of flooding (%)			
	Lamina	Petiole	Lamina	Petiole
	Phosphorus		*Chloride*	
+0.04	−32 (1.3)	−58 (1.4)	12 (4.4)	−33 (7.4)
−0.05	−31	−50	7	−30
−0.17	−35	−55	5	−16
−0.27	−24	−46	5	−12
−0.38	−20	−43	16	−13
−0.60	0	−40	26	11
CP[a]	5	−22	44	9
	Potassium		*Calcium*	
+0.04	−47 (7.3)	−37 (23.2)	16 (25.4)	−41 (15.8)
−0.05	−32	−26	5	−8
−0.17	−20	−27	13	−3
−0.27	−25	−31	11	−7
−0.38	0	−27	40	−10
−0.60	30	−19	31	−12
CP	28	−15	24	−15
	Magnesium		*Sodium*	
+0.04	5 (5.6)	−39 (5.4)	18 (1.4)	11 (1.2)
−0.05	1	−34	51	70
−0.17	10	−25	53	67
−0.27	10	−27	35	76
−0.38	5	−33	51	80
−0.60	6	−13	51	102
CP	1	−11	4	4
	Manganese			
+0.04	−14 (45.8)	−9 (34.9)		
−0.05	−8	−4		
−0.17	−11	−12		
−0.27	−15	−16		
−0.38	−12	−8		
−0.60	1	−3		
CP	6	−7		

[a] CP: plants from high-N part of comparison plot.

shown). Concentrations of Na increased in leaves and stems of all plants from the sloping plot during the first flooding, but the increases were usually proportionally greater for plants from the higher water-table treatments.

Patterns of change in concentrations of nutrients in leaves and stems during the second flooding were similar to those of the first, except for increases rather than decreases in concentrations of Ca and Mn in stems (data not shown).

Amounts of nutrients in plant tops

Within the sloping plot, plants that were not waterlogged made the greatest gains in all nutrients except for Na during the first flooding (Table 6). Severely waterlogged plants lost P and K, possibly due to leakage of HPO_4- and K-ions from damaged roots.

Although plants gained in nutrient content during the second flooding, the magnitude of the increase in content of a particular nutrient was usually proportionally less than during the first flooding (Table 6). Plants from the comparison plot made greater gains in all nutrients than plants from the lowest water-table treatment of the sloping plot during the second flooding.

At the end of the second flooding, developing bolls contained from about 5% (Na) to 45% (P) of the quantity of a specific nutrient in plant tops (Table 7). The content of most nutrients in bolls as a proportion of the content in the whole shoot was usually higher in plants which had been severely waterlogged (Table 7).

Concentrations and amounts of nutrients in mature bolls

Concentrations and amounts of nutrients in mature bolls did not show consistent patterns with respect to severity of plant waterlogging. Concentrations of P and Mg were higher in the lint + seeds than in the boll residue, but the opposite occurred for Cl, K, Ca and Na (data not shown).

Minerals in xylem sap

In the first flooding, the performance of roots of waterlogged plants was impaired because xylem sap did not exude from their stumps when they were detopped. However, xylem sap exuded from freshly-cut stumps of plants from all water-table

Table 5. Effects of second flooding on concentrations of selected nutrients in the lamina and petiole of the youngest fully-expanded leaf of cotton. Values are the % increase or decrease in concentration of a particular nutrient in the leaf lamina or petiole during the 16 days of the second flooding, and are the means of two bulk samples each of 12 leaves. Range of values for both samples within ± 10% of mean value. Values in parentheses are concentrations of each nutrient for plants from the highest water-table treatment at the end of the flooding expressed as mg g^{-1} dry wt or $\mu g\, g^{-1}$ dry wt (Mn)

Water-table depth (m)	Change in concn during period of flooding (%)			
	Lamina	Petiole	Lamina	Petiole
	Phosphorus		*Chloride*	
+0.04	−41 (2.4)	−54 (1.3)	−9 (9.2)	−39 (13.9)
−0.05	−47	−53	−14	−44
−0.17	−31	−39	−1	−28
−0.27	−28	−31	7	−13
−0.38	−20	−35	4	−6
−0.60	19	−8	9	7
CP[a]	15	−5	30	6
	Potassium		*Calcium*	
+0.04	−34 (12.4)	−45 (29.6)	−11 (30.5)	−27 (15.2)
−0.05	−39	−35	−8	−29
−0.17	−29	−24	1	6
−0.27	−33	−27	4	7
−0.38	−15	−17	1	9
−0.60	−11	−23	8	8
CP	−14	−15	4	9
	Magnesium		*Sodium*	
+0.04	−30 (5.0)	−41 (4.4)	−23 (2.0)	−26 (2.0)
−0.05	−32	−27	−23	−4
−0.17	−27	−12	−11	0
−0.27	−9	−19	−4	−13
−0.38	−9	−8	−5	−2
−0.60	−11	−5	−4	−14
CP	−4	−7	−3	−12
	Manganese			
+0.04	5 (69.3)	50 (58.7)		
−0.05	2	25		
−0.17	2	17		
−0.27	1	22		
−0.38	0	3		
−0.60	2	8		
CP	0	−10		

[a] CP: plants from high-N part of comparison plot.

depths in the sloping plot at the end of the second flooding (Table 8).

At the end of the first flooding, concentrations of K-, Cl- and HPO_4- ions were highest in sap exuded from stumps of partially waterlogged plants (Table 8), but the opposite occurred with fluxes of these ions from roots because of the low rates of sap exudation from the waterlogged plants.

Although the cotton plants had visually recovered from the first flooding by the start of the second, concentrations of K- and HPO_4- ions (Table 8) in xylem sap from plants of the highest water-table treatment were lower than in sap from plants of the other treatments or the comparison plot.

Concentrations of K- and HPO_4- ions in xylem sap decreased during the second flooding, not only in waterlogged plants but also in those from the lowest water-table treatment and the comparison plot (Table 8). Concentrations of Cl- ions, however, increased in sap from all plants in the sloping plot and the comparison plot. Fluxes of ions from roots decreased in all plants irrespective of water-table depth during the second flooding, but the decreases were greatest for plants which had been severely waterlogged.

Discussion

A major advantage of the variable water-table depth facility is that it enables study of the mineral nutrition of plants subjected to a continuum of degrees of waterlogging of their root systems, ranging from complete inundation to the absence of a water-table within the rooting zone. In our experiment, cotton plants in the non-waterlogged section of the sloping plot appeared to be typical of field-grown plants, as evidenced by their similar growth and nutrition to those from the high-N part of the comparison plot.

The results presented here indicate that uptake of P and several other nutrients was impaired in waterlogged cotton, especially in young plants just before flowering. In the second flooding, the plants showed no symptoms of stress despite over two weeks of waterlogging (Reicosky *et al.*, 1985), and plant nutrient status was not as perturbed as in the first flooding, so it is likely that the cotton root systems had become more tolerant of or had adjusted to waterlogging, as found in a study with soybean (Stanley *et al.*, 1980).

The most consistent and dramatic differences between severely waterlogged plants and those with well-aerated root systems occurred with P and K. Concentrations of these nutrients were always re-

Table 6. Amounts of selected nutrients in cotton plants at the beginning and end of two short-term periods of waterlogging. Amounts expressed as mg per plant top. Values are means of 6 plants. S.E. of means within ± 12% of mean values

Nutrient		Water-table depth (m)						
		+0.04	−0.05	-0.17	−0.27	−0.38	−0.60	CP[a]
	First flooding							
P	start	63	67	80	68	82	76	110
	finish	55	73	82	81	113	108	148
	% gain or loss	−13	9	2	19	38	42	35
Cl	start	165	155	170	163	185	183	206
	finish	166	179	192	196	253	285	288
	% gain or loss	0	15	13	20	37	56	40
K	start	532	669	687	572	616	680	881
	finish	463	707	705	714	740	838	972
	% gain or loss	−13	6	3	25	20	23	10
Ca	start	470	573	645	560	613	625	744
	finish	590	839	836	780	978	1082	1151
	% gain or loss	26	46	30	39	60	73	55
Mg	start	140	172	215	192	204	210	236
	finish	148	197	242	226	252	305	317
	% gain or loss	6	15	13	18	24	45	34
Na	start	25	22	24	23	21	22	40
	finish	44	53	52	39	42	51	89
	% gain or loss	76	141	117	70	100	132	123
Mn	start	1.26	1.50	1.55	1.61	1.77	1.71	1.80
	finish	1.32	1.73	1.83	1.75	2.13	2.31	2.39
	% gain or loss	5	15	18	9	20	35	33
	Second flooding							
P	start	235	227	223	232	246	243	261
	finish	238	238	243	254	256	291	355
	% gain or loss	1	5	9	9	4	20	36
Cl	start	660	620	578	740	663	777	648
	finish	659	653	643	761	712	813	902
	% gain or loss	0	5	10	3	7	5	39
K	start	1553	1637	1676	1934	1905	2117	1994
	finish	1604	1687	1812	2031	2064	2256	2353
	% gain or loss	3	3	8	5	8	7	18
Ca	start	1336	1405	1371	1390	1382	1375	1345
	finish	1387	1444	1421	1409	1525	1517	1642
	% gain or loss	4	3	4	2	10	10	22
Mg	start	350	367	384	371	319	380	382
	finish	349	370	378	278	348	409	434
	% gain or loss	0	0	0	2	9	8	14
Na	start	138	147	127	146	138	159	127
	finish	163	170	154	168	158	191	156
	% gain or loss	18	16	21	15	15	20	23
Mn	start	4.56	5.42	5.12	5.93	4.56	4.42	4.50
	finish	5.60	6.74	6.28	6.23	5.63	4.98	5.41
	% gain or loss	23	24	23	5	23	13	20

[a] CP: plants from high-N part of comparison plot.

duced in waterlogged plants in both floodings, whereas changes in concentrations of other nutrients such as Mg and Ca were less consistent. Of all the nutritional effects reported in studies on waterlogging and poor root-zone aeration, decreased concentrations of P and K are the most common (Devitt and Francis, 1972; Drew and Sisworo, 1979; Drew *et al.*, 1979; Trought and Drew, 1980), whereas with Ca and Mg the results range from decreased concentrations (Labanauskas *et al.*,

Table 7. Proportion (%) of amounts of nutrients in plant tops present in developing bolls at end of second flooding. Values are means of 6 plants ±S.E.

Water-table depth (m)	Nutrient						
	P	Cl	K	Ca	Mg	Na	Mn
+0.04	49 ± 4.1	29 ± 1.6	44 ± 2.8	10 ± 0.8	25 ± 2.1	8 ± 0.6	24 ± 2.9
−0.05	50 ± 4.9	22 ± 2.4	36 ± 2.7	8 ± 0.5	24 ± 1.5	6 ± 0.3	15 ± 1.8
−0.17	46 ± 3.3	22 ± 1.8	33 ± 3.5	7 ± 0.5	19 ± 1.2	5 ± 0.5	13 ± 0.6
−0.27	43 ± 4.0	20 ± 1.7	33 ± 1.9	7 ± 0.4	16 ± 1.0	4 ± 0.2	14 ± 2.5
−0.38	39 ± 3.5	20 ± 1.3	29 ± 2.3	6 ± 0.5	20 ± 1.1	6 ± 0.3	19 ± 2.1
−0.60	41 ± 2.7	16 ± 1.4	30 ± 1.5	6 ± 0.5	18 ± 2.3	3 ± 0.2	19 ± 0.9
CP[a]	36 ± 3.0	16 ± 1.2	26 ± 2.0	5 ± 0.3	17 ± 0.9	2 ± 0.1	17 ± 1.4

[a] CP: plants from high-N part of comparison plot.

Table 8. Volume of sap exuded and concentrations and fluxes of K-, Cl- and HPO_4- ions in xylem sap from detopped cotton plants subjected to intermittent waterlogging. Volumes of sap expressed as μl plant^{-1}h^{-1}; concentrations expressed as μg ml^{-1}, and fluxes as μg h^{-1}. Values are means of three plants from each water-table depth. S.E. of means within ±15% of mean values

Water-table depth (m)	Vol. sap	K		Cl		HPO_4	
		Concn	Flux	Concn	Flux	Concn	Flux
	End flooding 1						
+0.04	0	–	–	–	–	–	–
−0.05	0	–	–	–	–	–	–
−0.17	0	–	–	–	–	–	–
−0.27	0	–	–	–	–	–	–
−0.33	116	727	84	139	16	57	7
−0.38	199	718	143	133	27	66	13
−0.52	237	688	163	124	29	42	10
−0.60	1642	437	718	119	195	39	64
CP[a]	2873	409	1216	84	250	40	119
	Start flooding 2						
+0.04	273	318	87	64	17	234	64
−0.05	422	377	159	59	25	350	148
−0.17	476	402	191	83	40	365	174
−0.27	572	437	250	76	43	440	252
−0.33	–	–	–	–	–	–	–
−0.38	536	432	232	88	47	355	190
−0.52	–	–	–	–	–	–	–
−0.60	612	455	278	72	44	374	229
CP	641	490	314	68	44	360	231
	End flooding 2						
+0.04	6	194	1	105	1	142	1
−0.05	62	269	17	114	7	196	12
−0.17	113	378	43	126	14	180	20
−0.27	124	407	50	116	14	163	20
−0.33	–	–	–	–	–	–	–
−0.38	214	383	82	107	23	186	40
−0.52	–	–	–	–	–	–	–
−0.60	284	398	113	95	27	178	51
CP	372	369	137	101	38	170	63

[a] CP: plants from high-N part of comparison plot.

1972; Meek *et al.*, 1980; Trought and Drew, 1980) to no change (Letey *et al.*, 1961; Singh and Ghildyal, 1980; Stanley *et al.*, 1980). Although severely waterlogged plants usually gained in nutrient content during the floodings, total uptake of all nutrients except for Na was less than for plants which had not been waterlogged, as found in other studies (Labanauskas *et al.*, 1972; Lal and Taylor, 1970).

The decreased nutrient concentrations in waterlogged cotton plants are probably attributable to (1) aging effects, as plants from the lowest water-table treatment and the comparison plot often showed reductions in concentrations during both floodings, and (2) a greater proportional reduction in nutrient uptake by waterlogged roots and transport to the shoot than in dry matter accumulation by the shoot. The reduced uptake of nutrients by waterlogged plants may have been due to death of roots. Evidence that the first flooding was severe enough to result in some root death has been presented in a previous paper (Reicosky *et al.*, 1985). Even so, it is difficult to know the extent that root death may have contributed to reduced nutrient uptake by waterlogged cotton plants in our study. It is also possible that reduced uptake of nutrients by the waterlogged cotton plants could have been due to unavailability of these nutrients from the soil solution during both floodings. However, a number of studies (Trought and Drew, 1980; Orchard and So, 1985) have indicated that there is little change in concentrations of plant-available P, K, Ca and Mg in the soil solution during intermittent waterlogging.

There is evidence that Na uptake and its transport to shoots increase during waterlogging or anaerobiosis of the root zone, and increased Na concentrations have been reported in shoots of a wide variety of waterlogged plants (Letey *et al.*, 1961; Labanauskas *et al.*, 1972), including cotton

(Meek *et al.*, 1980). It has been suggested that this is because Na- ion extrusion pumps in roots are dependent upon aerobic respiration (Drew, 1983). Our results show that Na concentrations and contents increased in stems and leaves of waterlogged plants to a greater extent than the other nutrients in both floodings. There are reports of Cl concentrations also increasing in waterlogged plants (Labanauskas *et al.*, 1972; Meek *et al.*, 1980), but the reverse usually occurred in our study.

Waterlogging can result in the release of heavy metals such as Mn from bound forms in the soil to the plant-available pool (Bjerre and Schierup, 1985; Orchard and So, 1985), and it has been proposed that these metallic ions may injure plant roots, or shoots if taken up (Drew, 1985). However, inconsistent results have been reported for the effects of intermittent waterlogging on concentrations of Mn in the soil solution, ranging from a substantial increase (Bjerre and Schierup, 1985) to no change (Leyshon and Sheard, 1974). Equally inconsistent results have been reported for Mn concentrations in plants subjected to waterlogging or root-zone anoxia, ranging from increases (Bjerre and Schierup, 1985) to no change (Leyshon and Sheard, 1974) or decreases (Slowik *et al.*, 1979). In our study, concentrations of Mn increased in leaves but not stems of waterlogged plants in the first flooding, and increased in both leaves and stems in the second flooding. However, concentrations of Mn in leaves of waterlogged plants at the end of both floodings were well below the level of 2.0 mg g^{-1} at which toxicity occurs in cotton (Hearn, 1981).

Concentrations of P, K, Ca and Mg in laminae and petioles of the youngest full-expanded leaves were adequate at the start of each flooding, but concentrations of P and K were close to deficiency levels (Hearn, 1981) by the end of the first flooding, and P was marginally deficient at the end of the second. Concentrations of NO_3-N had also reached deficiency levels by the end of both floodings (Hocking *et al.*, 1985). Deficiencies of N, P and K are known to modify stomatal behaviour in maize (Peaslee and Moss, 1966) and cotton (Radin and Parker, 1979), and the concurrence in the experiment reported here of decreased leaf growth (Reicosky *et al.*, 1985) and incipient deficiencies of P and K indicates that nutritional stress may have been involved in regulating stomatal responses and leaf growth of the waterlogged cotton plants.

There was no effect of waterlogging on concentrations of nutrients in mature bolls, and similar results have been reported for grain from waterlogged wheat (Labanauskas *et al.*, 1975). However, the total quantity of N, P, K and Na in grain of waterlogged wheat decreased by about 50% because of yield reductions (Labanauskas *et al.*, 1975), but this did not occur in our cotton.

Waterlogging reduced the volume of xylem sap exuded from stumps of detopped plants, and decreased the fluxes of K-, Cl- and HPO_4- ions. Reported decreases in exudation rates from detopped, waterlogged plants have been attributed to decreased cell membrane permeability to the radial passage of water, and lack of active accumulation of osmotica to drive root pressure (Drew, 1983). In the first flooding of our study, the increased concentration of ions associated with low flux rates suggests decreased permeability to the radial passage of water across roots of severely waterlogged plants.

Although the waterlogged cotton plants had wilted and were deficient in some nutrients at the end of the first flooding, these stresses appear to have had beneficial effects in that they accelerated boll production (Reicosky *et al.*, 1985), so that seed cotton yields were highest for plants which had been moderately waterlogged during the two floodings (Table 2). We do not know why the moderately waterlogged plants gave the highest yields. Accelerated boll development and yield increases have been reported when cotton plants were stressed before flowering (Hearn, 1980), and in the present experiment the main flowering period occurred after the first flooding when plants had apparently recovered from the effects of waterlogging. It is unlikely that plants from the lowest water-tables (-0.38 and -0.60 m) were subjected to water deficits which would have reduced yields because sprinkler irrigation based on tensiometer readings ensured that plants in these treatments and the comparison plot were kept adequately watered during both flooding events. We can only speculate that the first flooding reduced the vegetative growth of the moderately waterlogged plants but promoted their reproductive development and boll production, and that this effect persisted through to maturity of the plants.

In conclusion, the evidence from this and other studies (Meek *et al.*, 1980; Hocking *et al.*, 1985) indicates that active uptake of key nutrients such as N, P and K is impaired in waterlogged cotton plants. This reduction in nutrient uptake occurs quite soon after cotton becomes waterlogged (see Fig. 1), and can result in the plants becoming deficient for certain nutrients such as N and P. It is clear, however, that under the conditions of our experiment, cotton can recover from intermittent waterlogging and its associated nutrient stresses with no yield penalty.

Acknowledgements

We thank Roger Sides for field assistance and for help with preparation of plant material for nutrient analyses, Leith Higgins for most of the nutrient analyses and Lina Onorato for preparing the typescript.

References

Bjerre G K and Schierup H H 1985 Influence of waterlogging on availability and uptake of heavy metals by oat grown in different soils. Plant and Soil 88, 45–56.

Butler B E 1979 A soil survey of the horticultural soils in the Murrumbidgee Irrigation Areas of New South Wales. CSIRO Div. Soils Bull. 287. Revised edition of Bull. Counc. Scient. Ind. Res., Melb. No. 118.

DeBruyn L P 1982 The effect of over-irrigation on the growth and production of *Gossypium hirsutum*. Irrig. Sci. 3, 177–184.

Devitt A C and Francis C M 1972 Effect of waterlogging on the mineral content of *Trifolium subterraneum*. Aust. J. Exp. Agric. Anim. Husb. 12, 614–617.

Drew M C 1983 Plant injury and adaptation to oxygen deficiency in the root environment: A review. Plant and Soil 75, 179–199.

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.

Drew M C, Sisworo E J and Saker L R 1979 Alleviation of waterlogging damage to young barley by application of nitrate and a synthetic cytokinin, and comparison between the effects of waterlogging, nitrogen deficiency and root excision. New Phytol. 82, 315–329.

Hearn A B 1980 Water relationships in cotton. Outlook Agric. 10, 159–166.

Hearn A B 1981 Cotton nutrition. Field Crop Abstracts 34, 11–34.

Hocking P J, Reicosky D C and Meyer W S 1985 Nitrogen status of cotton subjected to two short term periods of waterlogging of varying severity using a sloping plot water-table facility. Plant and Soil 87, 375–391.

Hodgson A S 1982 The effects of duration, timing and chemical amelioration of short-term waterlogging during furrow irrigation of cotton in a cracking grey clay. Aust. J. Agric. Res. 33, 1019-1028.

Hodgson A S and Chan K Y 1982 The effect of short term waterlogging during furrow irrigation of cotton in a cracking grey clay. Aust. J. Agric. Res. 33, 109–116.

Labanauskas C K, Stolzy L H and Handy M F 1972 Concentrations and total amount of nutrients in citrus seedlings (*Citrus sinensis*) and in soil as influenced by different soil oxygen treatments. Soil. Sci. Soc. Am. Proc. 36, 454–457.

Labanauskas C K, Stolzy L H and Luxmoore R J 1975 Soil temperature and soil aeration effects on concentrations and total amounts of nutrients in 'Yecora' wheat grain. Soil Sci. 120, 450–454.

Lal R and Taylor G S 1970 Drainage and nutrient effects in a field lysimeter study. II. Mineral uptake by corn plants. Soil Sci. Soc. Am. Proc. 34, 245–248.

Letey J, Lunt O R, Stolzy L H and Szuszkiewicz T E 1961 Plant growth, water use and nutritional response to rhizosphere differential oxygen concentration. Soil Sci. Soc. Am. Proc. 25, 183–186.

Leyshon A J and Sheard R W 1974 Influence of short-term flooding on the growth and plant nutrient composition of barley. Can. J. Soil Sci. 54, 463–473.

Meek B D, Owen-Bartlett E C, Stolzy L H and Labanauskas C K 1980 Cotton yield and nutrient uptake in relation to water table depth. Soil Sci. Soc. Am. J. 44, 301–305.

Orchard P W and So H B 1985 The response of sorghum and sunflower to short-term waterlogging. II. Changes in the soil environment under waterlogged conditions. Plant and Soil 88, 407–419.

Peaslee D E and Moss D N 1966 Stomatal conductivities in K-deficient leaves of maize (*Zea mays* L.) Crop Sci. 8, 427–430.

Radin J W and Parker L L 1979 Water relations of cotton plants under nitrogen deficiency. II. Environmental interactions on stomata. Plant Physiol. 64, 499–501.

Reicosky D C, Meyer W S, Schaefer N L and Sides R D 1985 Cotton response to short-term waterlogging imposed with a water-table gradient facility. Agric. Water Manag. 10, 127–143.

Schaefer N L, Melhuish F M, Reicosky D C and Meyer W S 1987 The effect of an intermittent water-table gradient on soil and xylem nitrate in cotton. Plant and Soil. (*In press*).

Singh R and Ghildyal B P 1980 Soil submergence effects on nutrient uptake, growth, and yield of five corn cultivars. Agron. J. 72, 737–741.

Slowik K, Labanauskas C K, Stolzy L H and Zentmyer G A 1979 Influence of rootstocks, soil oxygen, and soil moisture on the uptake and translocation of nutrients in young avocado plants. J. Am. Soc. Hort. Sci. 104, 172–175.

Smith R C G, Mason W K, Meyer W S and Barrs H D 1983 Irrigation in Australia: development and prospects. Adv. Irrig. 2, 99–153.

Stanley C D, Kaspar T C and Taylor H M 1980 Soybean top and root response to temporary water tables imposed at three different stages of growth. Agron. J. 72, 341–346.

Trought M C T and Drew M C 1980 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.