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The response of sorghum and sunflower to short-term waterlogging

I. Effects of stage of development and duration of waterlogging on growth and yield

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Summary The effect of waterlogging on sunflower and sorghum was investigated in relation to stage of development (sunflower–6–leaf, buds-visible, anthesis; sorghum–5–leaf, initiation, anthesis) and duration of waterlogging (3, 6 and 9 days) under glasshouse conditions. Additionally, the potential adaptation of the two crops was observed by waterlogging some plants at all three growth stages. With sunflower, leaf expansion and stem extension were inhibited by waterlogging at the 6–leaf and buds-visible stage although these effects did not always persist until maturity while, with anthesis waterlogging, rapid desiccation of leaves was observed. Yield was most affected by the anthesis waterlogging but no consistent effect on seed number or 1000 seed weight was recorded.

Waterlogging sorghum plants suppressed normal tillering but had little effect on dry weight of the main stem. Late tillering was stimulated by waterlogging. Reductions in leaf area occurred at all stages of development in response to waterlogging with these effects being more marked at initiation. Similarly, yield was most reduced by the initiation waterlogging largely as a result of reduced seed number.

In neither species was there a clear relationship between duration of waterlogging and subsequent reduction in growth and yield. With respect to yield, stage of development seemed to be of greater importance than the duration of waterlogging. The growth and yield of multiple-waterlogged sunflowers was less affected by the anthesis treatment than that in plants experiencing a single waterlogging, suggesting that some form of adaptation was induced. In contrast, no such response was seen in sorghum.

Introduction

The response of plants to waterlogging is usually considered to be dependent on genotype, environmental conditions, stage of development and the duration of the waterlogging period[2,17]. It is well documented that considerable variation in waterlogging tolerance exists both between and within species[6,7,8]. Further, under conditions of short-term waterlogging (*i.e.* up to 10 days), numerous authors have shown that the greater the duration of waterlogging, the more damaging the effect[8,10,14] although this is not true for all species or all environments[9]. With respect to stage of development, no consistent pattern of plant damage can be discerned from the literature and this is suggested to be due to variations in experimental technique, environmental conditions and definitions of growth stages[2].

There is considerable fragmentation of information relating plant response to waterlogging. A wide range of effects have been reported but few attempts have been made to establish the relative contribution that each makes to waterlogging damage or to place them in a specific time-scale. Again, many observations have been limited to plants waterlogged only during the seedling stage of growth.

In the following experiment, the interaction between stage of development and the duration of waterlogging was investigated in relation to growth and yield of sunflower and sorghum. These species were selected since they are both important summer crops and provide contrasting plant types (dicotyledonous and monocotyledonous, respectively). Further, the potential adaptation of the two species was also examined by imposing waterlogging at several growth stages. The differences and similarities between the applied treatments were documented to provide a basis for the later investigation of changes in the soil environment, the physiological response of the two species and factors contributing to waterlogging damage.

Materials and methods

The experiment was performed using the 2–10 cm layer of a grey lateritic podzolic soil (Plinthustalf) which had been air-dried and passed through a 2 mm sieve. The moisture characteristic of disturbed samples of this soil, together with chemical and physical properties, have previously been described[4]. The drainage holes of 23 cm diameter pots were sealed by pressing silastic-covered corks over each hole and 5 kg of soil was added. Three seeds of sunflower (*Helianthus annuus* var. Suncross 52) or sorghum (*Sorghum bicolor* var. E57) were sown and pots were watered to 90% field capacity. The soil was maintained at approximately this level by weighing 10 pots at frequent intervals with due additions of water to the soil surface. Allowance was also made for the increase in plant weight with time from previously reported work with these species under similar cultural conditions[15, 19]. Plants were thinned to 1 per pot at the 2–leaf stage to give a uniform population.

Waterlogging treatments were imposed for 3, 6 or 9 days by slowly adding sufficient water to raise the water table to the soil surface where it was maintained for the required period. Treatments were released by breaking the silastic seals and allowing free drainage. Sunflowers were waterlogged at 6–leaf (V), buds-visible (I) or anthesis (A) growth stages. For sorghum, these coincided with the 5–leaf (V), initiation (I) and anthesis (A) stages of development, respectively. A further series of treatments consisted of waterlogging at all three growth stages for 3, 6 and 9 days. These treatments are designated as VIA 3, VIA 6 and VIA 9. In such cases, pots were resealed with silastic prior to the imposition of waterlogging. All treatments were replicated three times.

The experiment was conducted under glasshouse conditions between August and December 1979, under a temperature regime of 27°C (± 2°C) maximum and 18°C (± 2°C) minimum.

Leaf area and plant height were measured frequently throughout the experiment as indices of plant growth. The former was measured non-destructively using the relationship leaf area = max. leaf length × max. leaf width × 0.7 for sunflower[5] and max. leaf length × max. leaf

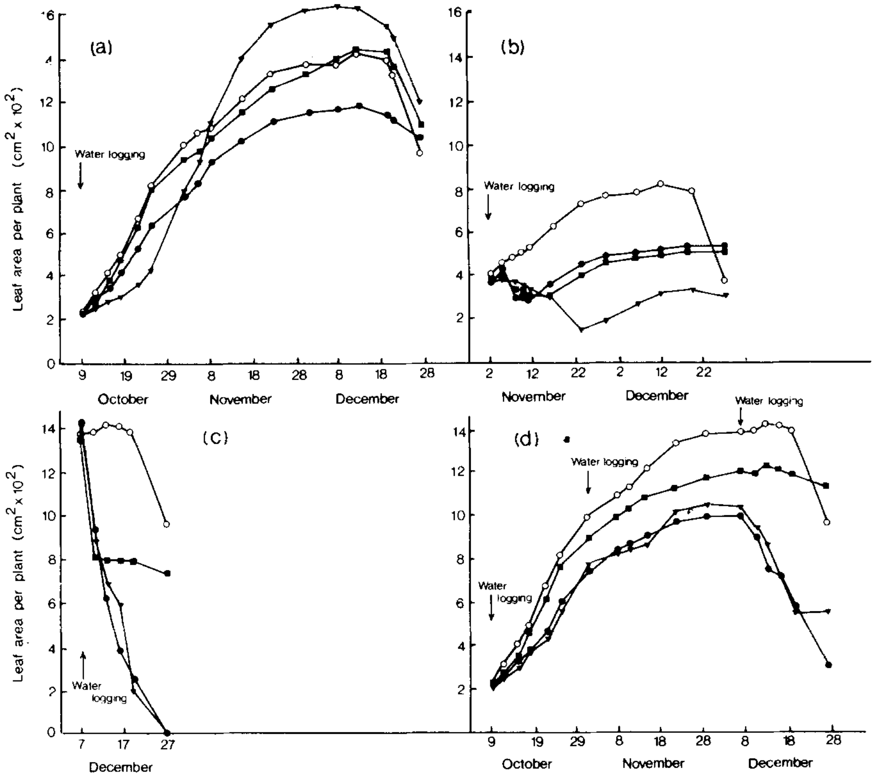

Fig. 1. Green leaf area development patterns of sunflower waterlogged during (a) vegetative, (b) buds-visible, (c) anthesis and (d) all three growth stages.

○ – control • – waterlogged for 6 days

▪ – waterlogged for 3 days ▾ – waterlogged for 9 days

width X 0.76 for sorghum[19]. Where leaves had commenced yellowing, a visual estimation of the per cent green leaf area remaining was made. Any leaf with less than 10 per cent green area was categorised as senescent. Plant height was measured from the soil surface to the apex for sunflowers. With sorghum, measurements were taken from the soil surface to the uppermost internode during the initial stages and to the base of the head following panicle emergence.

At maturity, sunflowers were separated into head and stem plus leaf components prior to drying to a constant weight at 80°C. Sorghum was separated into main stem and tillers and these further divided into head and stem/leaf components. Following drying, all fractions were weighed prior to removing the seed for yield and yield component determinations. All waterlogging treatments in sorghum resulted in the suppression of 'normal' tillering patterns or tiller death but, subsequently, stimulated the production of late tillers which were immature at the time of harvest. Thus, for comparisons between sorghum treatments, these were not included.

Results

Leaf area development

Waterlogging sunflower for 3 days at the 6–leaf stage (vegetative, V) had no apparent effect on leaf area development patterns (Fig. 1a).

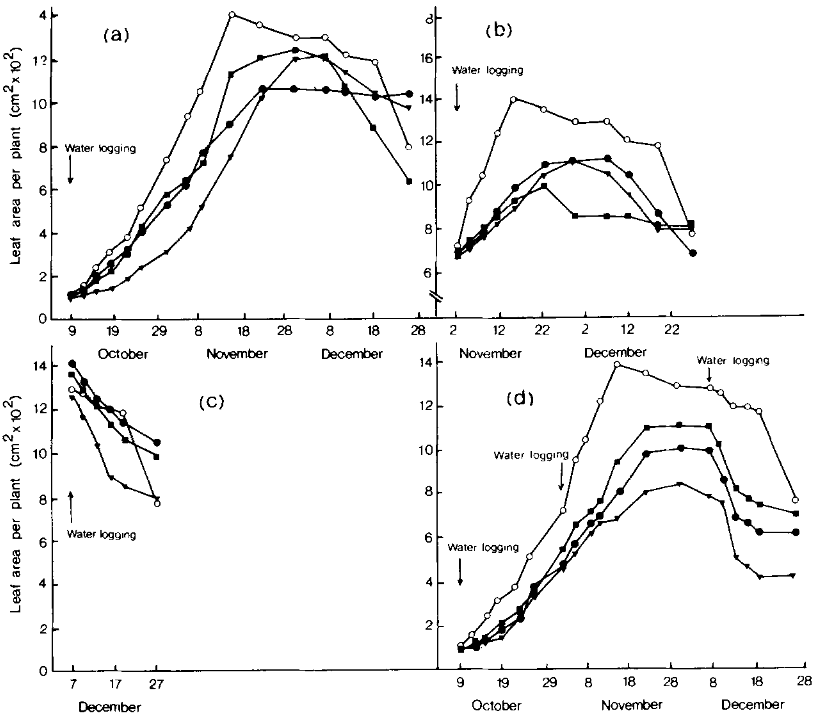

Fig. 2. Green leaf area development patterns of sorghum waterlogged during (a) vegetative, (b) buds-visible, (c) anthesis and (d) all three growth stages.
○ – control ● – waterlogged for 6 days
■ – waterlogged for 3 days ▼ – waterlogged for 9 days

Significant reductions for most of the growth cycle resulted from 6 days waterlogging while 9 days waterlogging at the vegetative stage caused an initial reduction which was compensated for by a larger leaf area at later growth stages. More marked effects were noted by waterlogging at buds-visible (Fig. 1b) and anthesis (Fig. 1c) where large reductions in green leaf occurred in all waterlogged plants. With anthesis waterlogging for 6 and 9 days (A6 and A9) leaf areas declined rapidly to zero. Plants waterlogged at all three growth stages (VIA 3) developed smaller leaf areas than controls although differences were not significant until 3 weeks after the buds-visible treatment (Fig. 1d). Reductions in leaf area resulted from VIA 6 and VIA 9 treatments with both developing smaller leaf areas than VIA 3 and control plants. However, waterlogging at buds-visible and anthesis had a relatively smaller effect on VIA plants than those experiencing a single waterlogging.

All sorghum plants waterlogged at the 5–leaf stage possessed smaller leaf areas than non waterlogged plants for much of the experiment (Fig. 2a) while waterlogging at initiation resulted in significant reductions which persisted to maturity (Fig. 2b). Plants waterlogged at either of these stages showed both a reduction and a delay in reaching maximum leaf area. In contrast, waterlogging at anthesis had little effect with only A9 plants exhibiting a significant reduction in leaf area (Fig. 1c). As with the V and I plants, the VIA treatments resulted in a reduction and delay in reaching maximum leaf area (Fig. 1d). Further, waterlogging at anthesis had a greater effect on VIA than A plants.

Leaf expansion

Increase in leaf area (at the V and I stages of growth) were calculated after adjusting for the area of senesced leaves, thus enabling the effects of waterlogging on leaf expansion rates to be determined. Leaf expansion was complete at anthesis and, hence, A data are not presented.

At the 6–leaf stage (V), leaf expansion of sunflowers was retarded during the waterlogging period although V3 and V6 plants rapidly recovered (Table 1). With V9 plants, reduced expansion rates persisted for 7 days after the release of waterlogging but this was followed by expansion at a greater rate than non-waterlogged plants. At the buds–visible stage (I), a significant depression in leaf expansion resulted from waterlogging and, while the I3 and I6 plants recovered, I9 plants had a lower leaf expansion rate than controls throughout the period of measurement. The rapid increase in leaf area noted in V9 plants during the post–waterlogging period was curtailed in the VIA 9 treatment by the second period of waterlogging.

Waterlogging sorghum at the 5–leaf stage resulted in a marked reduction in leaf expansion, particularly in the 6- and 9-day treatment (Table 2). At initiation plant response was less clear. Reductions in leaf expansion were quite marked during the actual waterlogging period but, in the I6 and I9 plants, significant increases were observed shortly after the release of waterlogging although these were of short duration. The response of VIA plants was similar to that observed in plants treated to a single waterlogging event at only one of the growth stages.

Leaf senescence

Patterns of leaf senescence of sunflower were unaffected by waterlogging at the 6–leaf stage (Fig. 3a). In contrast, marked increases in leaf mortality were noted at both the buds-visible (Fig. 3b) and anthesis (Fig. 3c) waterlogging, with complete senescence occurring in the A6 and A9 plants. At both stages, leaf death was preceded by wilting suggesting and interruption of water uptake. The VIA plants

Table 1. Sunflower leaf expansion rates (cm^2 plant day^{-1})

Days	0–3	3–6	6–9	9–13	13–16	16–23	23–27	27–30	30–37	37–44			
Control	32.6a	28.8a	30.7a	42.2a	49.1ab	24.1a	17.4a	19.0a	18.2a	16.8a			
V3*	**17.5b**	25.6ab	42.7a	37.2a	56.8a	19.2a	15.4a	19.5ab	17.7a	15.4a			
V6	**17.3b**	**15.8bc**	29.7a	28.9a	35.7b	16.8a	21.3a	30.8b	14.2a	12.6a			
V9	**16.5b**	**9.2c**	**5.1b**	14.2b	23.9c	46.3b	43.5b	58.6c	42.9b	22.3a			
	0–3	3–6	6–9	9–13	13–20								
Control	23.2a	19.0a	13.4a	21.8a	16.8a								
I3**	**15.2b**	16.9a	12.3a	12.4b	13.6a								
I6	**17.4b**	**8.9b**	4.9b	12.2b	16.4a								
I9	**13.2b**	**8.2b**	**3.5b**	6.4c	4.0b								
	0–3	3–6	6–9	9–13	13–16	16–24	24–27	27–30	30–33	33–37	37–44	44–52	52–60
Control	32.6a	28.8a	30.7a	42.2a	49.1a	24.2a	23.2a	19.0a	13.4a	21.8a	16.8b	6.1a	2.4a
VIA3***	**16.1b**	28.1a	35.0a	37.4a	40.6a	19.3a	**11.9b**	15.1ab	12.3a	15.1b	10.1c	5.7a	4.5a
VIA6	**15.3b**	**15.0b**	24.2a	29.6b	49.1a	22.4a	**10.3b**	**13.1b**	10.4a	10.5bc	22.0a	5.7a	3.5a
VIA9	**14.3b**	**16.7b**	**11.6b**	17.8c	30.4b	33.9b	**10.3b**	7.5c	**10.9a**	7.7c	10.7c	1.5a	0a

Numbers in bold indicate waterlogging period.
Plants waterlogged at the * vegetative, ** buds-visible or *** both stages for 3, 6 or 9 days.
Data were analysed within each time period. Means without a common subscript differ significantly (Duncan's Multiple Range Test 5%).

Table 2. Sorghum leaf expansion rates (cm^2 plant day^{-1})

Days	0–3	3–6	6–9	9–13	13–16	16–23	23–27	27–30	30–37	37–44	
Control	18.7a	27.4a	24.6a	25.7a	45.6a	30.1a	51.9a	38.9a	52.4a	11.0a	
V3*	**15.0ab**	11.0b	10.1b	24.2a	31.6b	23.9b	20.9b	36.9a	61.0a	19.4a	
V6	**12.6b**	**15.1b**	10.3b	13.3b	36.6b	16.2c	25.1b	35.9a	35.2b	20.0a	
V9	**11.2b**	**15.2b**	**3.1c**	11.0b	16.9c	15.1c	**24.5b**	31.9a	39.1b	39.2b	
	0–3	3–6	6–9	9–13	13–20	20–27					
Control	69.2a	48.9a	58.8a	47.9b	11.0a	9.3a					
I3**	**17.9b**	47.8a	34.2b	51.2a	10.8a	8.4a					
I6	**23.0b**	**28.9b**	37.0b	64.0a	15.3a	8.9a					
I9	**25.5b**	**16.1c**	**45.3b**	32.9c	24.2b	12.7a					
	0–3	3–6	6–9	9–13	13–16	16–24	24–27	27–30	30–33	33–37	37–44
Control	18.7a	27.4a	24.7a	15.7a	45.6a	30.6a	69.2a	38.9a	58.8a	47.9ab	11.0c
VIA3***	**14.8a**	13.3b	14.6b	14.9a	21.7b	30.2a	**32.5b**	20.3b	20.2b	56.2a	22.7ab
VIA6	**16.8a**	**16.4b**	6.1c	5.1b	49.6a	16.8b	**34.9b**	**26.7b**	20.1b	42.7b	27.0a
VIA9	**15.8a**	**17.3b**	**6.9c**	5.3b	20.4b	18.7b	**25.2c**	**25.3b**	**25.3b**	28.3c	17.6bc

Figures in bold indicate waterlogging period.
Plants waterlogged at the * vegetative, ** initiation or *** both stages for 3, 6 or 9 days.
Data were analysed within each time period. Means without a common subscript differ significantly (Duncan's Multiple Range Test 5%).

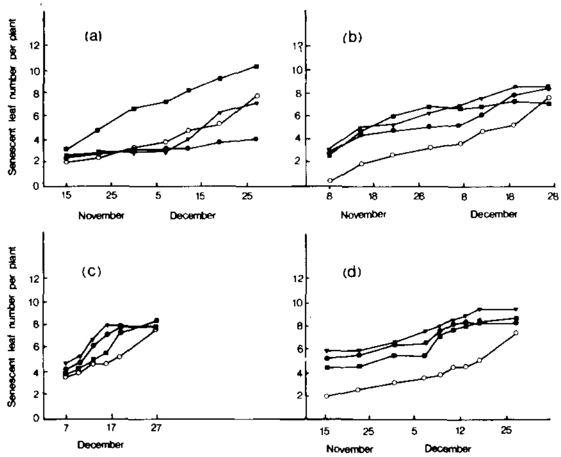

Fig. 3. Senescent leaf number of sunflower waterlogged during (a) vegetative, (b) buds-visible, (c) anthesis and (d) all three growth stages.

○ – control ● – waterlogged for 6 days
■ – waterlogged for 3 days ▼ – waterlogged for 9 days

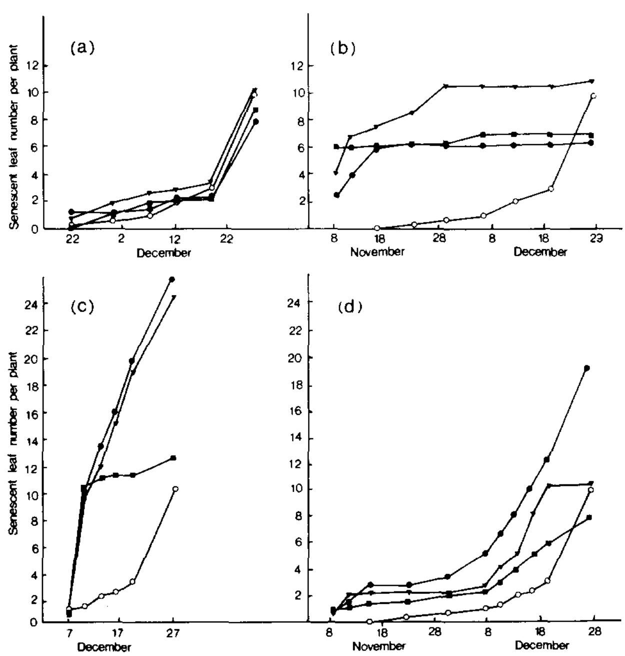

Fig. 4. Senescent leaf number of sorghum waterlogged during (a) vegetative, (b) buds-visible, (c) anthesis and (d) all three growth stages.

○ – control ● – waterlogged for 6 days
■ – waterlogged for 3 days ▼ – waterlogged for 9 days

Table 3. Effect of stage of development and duration of waterlogging on mature plant height (cm) of sunflower and sorghum

	Days	V	I	A	
Sunflower	0	114b	114a	114a	114ab
	3	126a	98b	116a	118a
	6	114b	97b	115a	99bc
	9	101c	92b	115a	90c
Sorghum	0	82a	82a	82a	82a
	3	94ab	86a	84a	98c
	6	102bc	96b	84a	89b
	9	117c	98b	85a	89b

Data were analysed within each species and treatment.
Means without a common subscript within each column differ significantly (Duncan's Multiple Range Test 5%).

were less affected at buds-visible and anthesis than plants waterlogged solely at these stages (Fig. 3d).

Leaf senescence of sorghum showed no consistent trend following waterlogging at the 5–leaf stage (Fig. 4a). Although no effect was observed during the waterlogging period, V3 plants exhibited significantly greater rates of leaf senescence at later stages of growth. A marked increase in senescent leaves resulted from waterlogging at initiation, with all three durations eliciting similar effects (Fig. 4b), while, at anthesis, waterlogging led to only slight increases in leaf mortality (Fig. 4c). With VIA plants, waterlogging at both initiation and anthesis resulted in significant increases in leaf mortality (Fig. 4d).

Plant height

At the 6–leaf stage all waterlogging treatments tended to reduce stem extension of sunflowers but, at maturity, this was only evident in the plants waterlogged for 9 days (Table 3). In contrast, V3 plants grew faster at later stages of growth such that final plant height was increased relative to non-waterlogged controls. At the buds–visible stage, plant height was significantly reduced in all plants subjected to waterlogging, an effect which persisted to maturity. Stem extension was complete at anthesis, and hence, waterlogging had no effect on plant height. Plants subjected to several waterlogging periods were less affected at buds–visible than the I plants and only the VIA 9 treatment resulted in a significant reduction in plant height.

Increasing the duration of waterlogging at the 5–leaf stage resulted in an increase in mature plant height of sorghum. A similar trend was observed in I plants although significant reductions in height occurred

Table 4. Sunflower dry matter production, yield and yield components

Treatment	Stem + Leaves (g)	Head (g)	Total Plant (g)	Seed (g)	Seed Number	1000 Seed (g)
Control	24.0 e	21.70 f	45.67 d	10.17 bcd	230	43.87
V3	18.93 cde	21.23 ef	40.17 cd	10.77 cd	305	38.17
V6	17.93 bcd	19.60 def	37.53 bc	7.83 abcd	195	40.70
V9	17.70 bcd	20.23 ef	37.93 bcd	8.80 abcd	217	42.30
I3	14.23 abc	16.17 bcde	30.40 ab	7.80 abcd	287	31.23
I6	12.43 a	13.90 abcd	26.33 a	8.73 abcd	344	24.77
I9	13.43 ab	12.93 abc	26.37 a	6.90 abcd	218	37.70
A3	20.37 de	12.37 ab	32.73 abc	2.43 a	37	44.37
A6	21.83 de	9.00 a	30.83 ab	2.33 a	151	26.93
A9	18.23 bcd	9.17 ab	27.40 a	3.10 ab	135	21.67
VIA 3	18.23 bcd	18.43 cdef	36.67 bc	11.80 d	400	29.07
VIA 6	14.83 abc	9.73 ab	24.57 a	3.97 abc	130	23.07
VIA 9	14.57 abc	13.07 abc	27.63 a	7.23 abcd	243	30.43

Data were analysed between treatments. Means without a common subscript within each column differ significantly (Duncan's Multiple Range Test 5%).

Table 5. Sorghum dry matter production, yield and yield components

Treatment	Total stem + leaves (g)	Total head (g)	Total Seed (g)	Seed Number	1000 seed weight (g)
Control	28.93 b	60.10 e	49.90 e	1855 d	28.10
V3	21.73 a	48.07 cde	40.60 cde	1360 abcd	29.90
V6	18.23 a	43.07 bcd	37.13 bcd	1057 abc	35.70
V9	19.23 a	43.20 bcd	37.00 bcd	1127 abc	32.27
I3	17.20 a	31.90 ab	27.23 ab	873 ab	32.07
I6	17.00 a	36.53 abc	31.23 abc	1018 abc	30.77
I9	16.16 a	32.77 ab	28.20 ab	852 a	33.77
A3	20.67 a	54.70 de	45.90 de	1583 cd	29.13
A6	21.57 a	49.93 cde	42.50 cde	1447 bcd	30.37
A9	19.07 a	41.43 abcd	35.00 abcd	1171 abc	30.00
VIA 3	15.37 a	31.33 ab	26.87 ab	831 a	33.37
VIA 6	16.40 a	29.77 ab	25.47 a	897 ab	29.60
VIA 9	15.37 a	27.73 a	23.67 a	779 a	30.60

Data were analysed between treatments. Means without a common subscript within each column differ significantly (Duncan's Multiple Range Test 5%).

shortly after the imposition of waterlogging. Stem extension was also reduced in VIA plants shortly after the initiation waterlogging but, again, a greater rate of elongation at later stages of growth led to all treatments being taller than non-waterlogged plants by maturity. As with sunflowers, stem extension was complete at anthesis and waterlogging was without effect.

Dry matter production, yield and yield components

Most waterlogged treatments caused a reduction in stem plus leaf weights of sunflower although this was most evident in the buds–visible and VIA plants (Table 4). In contrast, the anthesis water-logging caused the greatest reduction in head dry weight and this appeared largely related to marked reductions in seed yield. With respect to this latter parameter, there was generally a high degree of variability within and between treatments, with some plants producing a large number of small seeds and others producing small amounts of larger seed. In the former case, yield was undoubtedly over-estimated since some of the seed would have been discarded under commercial conditions. Generally, there was no relationship evident between the duration of waterlogging and subsequent effects for any of the yield or yield component parameters.

With sorghum, waterlogging disrupted 'normal' tillering patterns and stimulated the production of late tillers. Since these were green at the time of harvest, they were not included in dry matter and yield data (Table 5). Stem plus leaf dry weights were unaffected by water-logging but marked reductions in head weight and seed yield of most I and VIA plants occurred. The reductions were largely a result of reduced seed numbers with individual seed weights remaining stable. Waterlogging at the 5–leaf and anthesis stages of growth had little effect on either dry matter production or yield.

Discussion

This experiment illustrated that stage of development, species and duration of waterlogging are important factors determining plant response. Visual observations indicated marked differences between the two species with sunflower, for example, experiencing rapid wilting of leaves at the buds–visible and anthesis stages of growth while signs of water stress in sorghum (*i.e.* leaf rolling) developed much more slowly and were preceded by leaf yellowing. The latter suggests that nutrient uptake may have been restricted in sorghum and, hence, contributed to waterlogging damage.

The waterlogging treatments generally affected sunflower to a greater degree than sorghum. The anthesis waterlogging, in particular, severely reduced both leaf area (with concurrent increases in senescent leaf number) and grain yield with relatively little effect on sorghum. Variations between species and stages of development may arise as a result of differences in growth and developmental processes which occur at the time of waterlogging. During the vegetative stage, leaf expansion was inhibited in both species but plant height was reduced only in sunflower since stem elongation occurs slowly in sorghum at this stage. In contrast, waterlogging at initiation and the buds–visible stage resulted not only in reduced leaf expansion, but also in reduced stem extension and increased leaf senescence in both species.

The aerial environment was similar at all periods of waterlogging but differences in the soil environment between species and stages of development may also contribute to the observed variations. A greater root mass at later stages of growth could lead to a more rapid depletion of oxygen, thus hastening the onset of reduced conditions. This situation may be further aggravated by the depletion of soil nitrogen with time (through plant uptake), thereby decreasing nitrate available to poise the soil redox potential[12]. Such a relationship implies that (a) the longer the duration of waterlogging, the greater the reduction in soil redox (and possible plant damage), and (b) plants should experience greater waterlogging damage at later stages of growth. In relation to (a), no clear trends could be discerned in the present experiment although generally three days waterlogging had less effect than waterlogging for nine days. Similarly for (b), while such a relationship may be proposed for sunflower, sorghum appeared less affected by waterlogging at anthesis than at initiation.

The absence of clear relationships between the duration of waterlogging, stage of development and waterlogging damage may be due to the ability of both species to display a variety of compensatory growth mechanisms such as increases in leaf area, leaf area duration and plant height. In sorghum, this could be related to the suppression of tillering which leads to more assimilate being available for growth of the main stem. It may also be the result of a hormonal imbalance since numerous authors[13,16] have recorded changes in hormonal levels following waterlogging, particularly in those supplied by the root. In this experiment, the observations of wilting and yellowing of leaves suggest an impairment of root function and, therefore, a possible reduction in root hormone synthesis leading to alterations in 'normal' growth patterns.

It is evident that sunflowers possess the ability to adapt to waterlogging. A comparison of Figures 1c and 1d indicates that VIA plants were much less affected by the waterlogging at anthesis than plants waterlogged solely at this stage. In contrast, a similar comparison for sorghum (Figures 2c and 2d) shows no such effect. The nature of the adaptation was not investigated but the results of Kawase[13] indicate that sunflowers possess the ability to form aerenchyma when subjected to waterlogging, resulting in improved root aeration via the shoot. Hence, the formation of aerenchyma during waterlogging at the vegetative and/or buds–visible stage may ameliorate the effects of waterlogging at anthesis. Another potential adaptation may be the ability of sunflower to develop adventitious roots during prior waterlogging periods which would act to reduce damage at later stages through their ability to maintain a better oxygen supply[15]. The development of a smaller leaf area by VIA sunflowers may also be seen as an adaptation since this would reduce water use and delay the onset of stress conditions.

Yields of sunflower were most reduced by waterlogging at anthesis. Problems arose in assessing yield since, in many instances, waterlogged plants produced a large number of small seeds which, under commercial conditions, would be discarded. Thus, in general, yield from all waterlogging treatments with the exception of the V plants, tends to be overestimated. With sorghum, seed size was much more stable and the results clearly show a marked depression in yield of both I and VIA plants, again suggesting that in the latter prior waterlogging induced little or no adaptation. These results are consistent with those previously reported[11].

The results of this experiment demonstrate that differences exist between species and stages of development in relation to plant response to waterlogging. By investigating the changes which occur in the soil environment and the physiological and morphological response of the two species, the major factors operating to cause waterlogging damage may be determined.

Further studies have been carried out to document the changes which occur in the soil following waterlogging and the resultant effects on plant-water relations, nutrient uptake and changes in root morphology. These will be the subject of later papers.

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