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A drought experiment using mobile shelters: the effect of drought on barley yield, water use and nutrient uptake

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SUMMARY

Automatic mobile shelters were used to keep rain off a barley crop in a drought experiment. The treatments ranged from no water during the growing season to regular weekly irrigation. This paper reports the effect of drought on the harvest yield and its components, on water use and nutrient uptake.

Drought caused large decreases in yield, and affected each component of the grain yield. The magnitude of each component varied by up to 25% between treatments, and much of the variation could be accounted for by linear regression against the mean soil water deficit in one of three periods. For the number of grains per ear, the relevant period included tillering and ear formation; for the number of ears per unit ground area, the period included stem extension and tiller death; for grain mass, the period included grain filling.

The harvest yields were linearly related to water use, with no indication of a critical period of drought sensitivity. The relation of grain yield to the maximum potential soil water deficit did show that a prolonged early drought had an exceptionally large effect on both yield and water use.

Two unsheltered irrigation experiments, also on barley, were made in the same year on a nearby site. The effects of drought on yield in these experiments were in good agreement with the effects observed on the mobile shelter site.

When fully irrigated, the small plots under the mobile shelters used water 11% faster than larger areas of crop, because of advection. The maximum depth from which water was extracted was unaffected by the drought treatment. When 50% of the available soil water had been used the uptake rate decreased, but the maximum depth of uptake continued to increase.

Measurements of crop nutrients at harvest showed that nitrogen uptake was large, because of site history, and that phosphate uptake was decreased by drought to such an extent that phosphate shortage may have limited yield.

INTRODUCTION

Throughout this century there have been many experimental investigations of the sensitivity of cereal crops to periods of drought (Salter & Goode, 1967). In the field, experiments are subject to the vagaries of weather, so that the water supply to the crop cannot be fully controlled except in climates with very low rainfall in the growing season. This limits the detail of field investigations, particularly in attempts to establish whether there are critical stages in the crop's development, stages at which even small droughts have a large effect on yield. As a result, it is often necessary to consider the results of many years' experiments before reaching conclusions, even though this may involve averaging over other factors such as soil fertility, sowing dates, weather conditions and amounts of disease. Because the timing of morphological changes will depend on weather conditions, it is also necessary to follow crop development in detail. The problems inherent in detailed field investigations can be appreciated from the discussion of Russian work in Salter & Goodes' (1967) review of the effect of drought and its timing on crop growth.

Barley may be more sensitive to drought at specific stages in its development, or it may be affected by shortage of water equally at any time in its growing season. Skazkin (1961) concluded that cereals, including barley, are particularly sensitive from the time of meiotic cell division until fertilization of the flowers; this 'critical stage' includes ear emergence and anthesis. His conclusion, however, is not always supported by other work. Penman (1971) concluded from irrigation experiments over a number of years that 'barley behaves as a grass crop up to the time of ear emergence . . . what happens after has little detectable effect'. A technique that allows the crop to be subjected to a range of predetermined and quantifiable drought treatments in a single year would facilitate the identification of critical stages.

In experiments on plants in pots or lysimeters, growing in glasshouses or other controlled environments (e.g. Aspinall, Nicholls & May, 1964), it is possible to control the water supply, and to distinguish the response of a crop to a drought at any stage in its development. Further, the periods of water stress can be timed to coincide with particular development stages, because the soil volume is limited and its available water exhausted more rapidly than occurs in the field. However, the pattern of stress build-up differs in the two environments, and for this and other reasons, the quantitative response to water stress in laboratory experiments is often not repeated in the field.

A number of workers have protected field experiments from rain. Shelters moved by hand have often been used (Spratt & Gasser, 1970; Johnson & Moss, 1976), though the crop microclimate must be affected by prolonged covering (Legg *et al.* 1978). Wells & Dubetz (1970) used an automatic shelter over lysimeters in a comparison of the response of two barley cultivars to drought. An alternative approach was taken by Rackham (1972), who used gutters between crop rows to intercept rain. Gutters are readily available and easy to use in experiments on a variety of soils. However, only 30–60% of the total rainfall is intercepted, and the presence of the gutters has an independent effect on crop growth.

There is therefore a need for experiments under field conditions but with complete control over the water supply, so that detailed measurements of crop response can be made for a wide range of drought treatments applied in a single season. The crop must be grown in the field and be covered during rainfall, but otherwise left open to natural atmospheric conditions. To this end, a pair of mobile shelters has been installed at Rothamsted (Legg *et al.* 1978): they move automatically, at the onset of rain, to cover the growing crop.

In 1976, barley (cv. Julia) was grown under a range of drought treatments on small plots, and measurements were made of the crop's physical environment and physiological response. The results for harvest yield and its components, and for nutrient uptake are given in this paper and are interpreted in relation to crop water use. In order to assess the effect of the small plot size, the results are compared with the yield and water use of

Table 1. *The experimental treatments on the mobile shelter site*

			Treatment											
			1	2	3	4	5	6	7	8	9	10	11	12
	Drilling	31 March	—	—	—	—	—	—	—	—	—	—	—	—
		7 April	—	—	—	—	—	—	—	—	—	—	—	—
	Emergence	14 April	—	—	—	—	—	—	—	—	—	—	—	—
		21 April	—	—	—	—	—	—	—	—	—	—	—	—
Period 1	1st spikelet	28 April	—	—	—	25	25	25	25	25	25	25	25	25
		5 May	—	—	—	20	20	20	20	20	20	20	20	20
		12 May	—	—	—	20	20	20	20	20	20	20	20	20
		19 May	—	—	—	—	—	—	—	14	14	14	14	14
		26 May	—	—	—	—	—	—	—	19	19	19	19	19
Period 2	Max. no. of spikelets	2, 3 June	30	—	—	30	—	—	—	—	—	20	20	20
		9, 10 June	30	—	—	30	—	—	—	—	—	35	35	35
		16, 17 June	35	—	—	35	40	—	—	—	—	35	35	35
	Anthesis	23, 24 June	20	40	—	20	20	—	—	40	—	20	20	20
Period 3		30 June	60	60	—	60	60	60	—	60	—	—	60	60
		1, 2 July												
		7, 8, 9 July	55	40	—	55	55	55	—	55	—	—	55	55
		14, 15 July	40	30	—	40	40	30	—	40	—	—	—	40
		21 July												
	Harvest	28 July												

The numbers in the body of the table are the irrigation totals (mm) applied each week on dates given. The periods 1, 2 and 3 refer to those used in the analysis of components of yield later in the paper.

barley on two larger but unsheltered irrigation experiments on a nearby field in the same season.

EXPERIMENTAL PROCEDURE

The mobile shelter experiments

The mobile shelters, ancillary equipment, soil type and size of discards needed to eliminate nearly all interactions between plots have been described by Legg *et al.* (1978). The land covered by the shelters was divided into 24 plots, 3·0 × 4·5 m, each having a set of trickle irrigation lines. A plank 0·20 m wide bisecting each plot (half plot area 3·0 × 2·15 m) allowed access to the centre of the plot. There were access tubes for neutron probe measurement of soil water content (Long & French, 1967) to 1·5 m depth in 17 of the 24 plots, and measurements were made at 0·05 m intervals to 0·3 m depth and then at 0·1 m intervals to 1·5 m depth.

Irrigation treatments. Each drought treatment consisted of a single period during which irrigation was withheld. The length of drought periods varied (Table 1) but each period was selected so that the drought ended at a time related to the crop's development (Gallagher, Biscoe & Scott, 1976). Two stages of development were chosen as being of special interest: ear initiation and anthesis. Treatments 1 and 4 were re-watered when the number of spikelets initiated in the developing ear should have reached its maximum. Treatments 2, 5, 6 and 8 were re-watered at or about anthesis. For treatments 3, 7, 9, 10 and 11, the drought continued till harvest. For each group of treatments, the first named treatment had the longest period of drought and subsequent treatments had shorter periods.

The treatments may also be grouped by starting date of the drought: treatments 1, 2 and 3, starting after emergence; treatments 4, 5, 6 and 7, four weeks after emergence; treatments 8 and 9, six weeks after emergence. Treatment 12, the fully watered treatment, may be regarded as a 'control' treatment for all of these groups.

There were three replicates each of treatments 2, 3, 5, 7 and 12 to allow destructive measurement on the crop. Two of the six half plots of these treatments were reserved for final harvest, two used for growth analysis sampling and two for other measurements. There were two replicates each of treatments 1 and 6, and one each of treatments 4, 8, 9, 10 and 11. The neutron probe measurements of soil water content were made in two replicates of treatments 2, 3, 5, 7 and 12 and one replicate of the other seven treatments.

Soil water content was measured on Monday each week, by which time the movement of water from the previous irrigation should have ceased. Irrigation was then applied on Wednesday to return the soil water content to within about 20 mm of 'field capacity'. When a plot was re-watered after a drought, the water content was not returned to field capacity immediately, to avoid drainage.

Because the crop was irrigated only weekly, drought treatments, for the first 7 days after their last irrigation, were the same as fully irrigated treatments. The effect on yield of the resulting deficit is likely to be small, as previous experiments on a similar soil have shown that yield is not reduced until the deficit exceeds 50 mm (B. K. French & B. J. Legg, unpublished).

Crop management. A tine cultivator was used for primary soil cultivation to about 20 cm depth. Seed-bed preparation followed, 376 kg/ha of a compound fertilizer ($N:P_2O_5:K_2O::20:14:14$) was applied, and ethirimol dressed seed was drilled at 168 kg/ha on 31 March 1976. A tractor with 2·65 m wheel spacing was used for the drilling operations so that any effect of the tractor wheelings would be restricted to the discard at the edge of each plot (Legg *et al.* 1978). The crop was not protected from rain till after emergence, because it was intended that the soil on all plots should be near field capacity at emergence, and that drought treatments should then be applied to a uniformly emerged crop. Emergence began on 14 April, and on 3 May there were 290 ± 17 plants/m^2 over the whole site. The crop was sprayed, using a hand sprayer, with Calixin and with Aphox to minimize mildew and aphid-transmitted diseases. From ear emergence to harvest, 0·15 m mesh netting was fixed at a height of 0·5 m on all plots to prevent lodging, and the crop was enclosed in a bird net to protect the filling grains.

The crop was harvested by hand at the end of July, and grain yield, straw yield and thousand grain mass were measured. The number of ears per unit ground area was estimated from counts of the number of fully formed stems. These counts correlated closely with the numbers of ears in the final growth analysis samples. The concentrations of N, P, K, Ca, Mg and Na were measured in the grain and straw. Similar measurements made on crop samples taken at fortnightly intervals during the growing season will be reported in a subsequent paper.

The Great Field experiments

Julia barley was also grown in two irrigation experiments using much larger plots on Great Field at Rothamsted in 1976 (Table 2). Results from both are given later in this paper, to compare with results from the mobile shelter experiment. For a micrometeorological experiment, barley was grown on an irrigated plot, M_I, and a non-irrigated

Table 2. *Summary of the mobile shelter (small plot) and Great Field (large plot) experimental conditions*

	Mobile shelter site (Little Knott field)	Great Field *M* plots	Great Field *X* plots
Area per plot	3·0 × 4·5 m	100 × 100 m	15 × 32 m
No. of plots	24	2	16
Maximum total irrigation (mm)	363	130	125
Rainfall, emergence to maturity (mm)	8·2	58·0	58·0
Sowing date	31 March	8 March	

plot, M_0, each of area 100 × 100 m and containing four neutron probe access tubes. There was also an irrigation experiment with non-irrigated, early irrigated, late irrigated and fully irrigated treatments X_0, X_E, X_L and X_F respectively. There were four replicate plots for each treatment, of area 32 × 15 m, and two non-irrigated and two fully irrigated plots contained one neutron probe access tube each.

On both experiments seed was drilled on 8 March at a rate of 160 kg/ha and with a compound fertilizer application of 310 kg/ha ($N:P_2O_5:K_2O$:: 0:20:20) and a nitrogen application of 50 kg/ha. The crop emerged on 1 April, some 2 weeks earlier than that in the mobile shelter experiment, but by early June its development was only about 1 week ahead.

Irrigation, via oscillating spray lines, was not applied on a regular weekly basis, but deficits on irrigated plots were kept below about 60 mm. The early-irrigated plots X_E were last irrigated on 12 June, and the late-irrigated plots X_L first irrigated on 21 June. Plots M_I, X_L and X_F received their last irrigation on 24 June, 9 July and 2 July respectively.

RESULTS

Water use

The measurements of soil water content were used during the course of the experiment to estimate the amount of irrigation required, and are used in this paper in the interpretation of the effects of different drought treatments on grain yield.

In this section, water use under different treatments is presented, showing how water uptake and depth of rooting were affected by drought. The measured evaporation from each treatment is compared with the potential evaporation, E_T, calculated from meteorological data (Smith, 1967, based on Penman, 1948). E_T has been shown to equal the evaporation from large areas of well watered short grass completely covering the ground (French, Long & Penman, 1973*c*). Treatment 12 in the mobile shelter experiment was never short of water, but the evaporation rate from this crop, E_{12}, is likely to exceed E_T for two reasons. First the aerodynamic resistance to evaporation is smaller for a tall crop, and, secondly, the small irrigated plots in this experiment received advected energy from adjacent non-irrigated plots (Legg *et al.* 1978). Results from the Great Field experiments are used to show to what extent advection of energy to the small plots in the mobile shelter experiment caused E_{12} to be significantly greater than the evaporation rate from large irrigated areas.

The evaporation estimate obtained from changes in soil water content is the sum of soil evaporation and crop transpiration. When crop cover is nearly complete, evaporation from the soil surface is negligible, but early in the growing season the evaporation from irrigated crops includes a large contribution from the soil surface. The values given in this section for total water use in the season will therefore be somewhat greater than the total transpiration.

Field capacity and site uniformity

The concept of field capacity has been severely criticized by many soil physicists (e.g. Sykes & Loomis, 1967; Baver, Gardner & Gardner, 1972). But Russell (1973, p. 437) recognized its usefulness for many agricultural purposes, provided the soil drains freely so that the water content is stable within a few days of wetting, and provided the water content returns to the same value after the soil has been dried and re-wetted. Field capacity is particularly useful in Britain where there is an excess of rain in the winter, and soils are close to field capacity at the beginning of each growing season. French, Long & Penman (1973*a*) showed that even where field capacity varies widely from one position to another in a field, any soil water deficits (the different between field capacity and the actual soil water content) produced by a uniform crop will vary only slightly across the field.

The first measurements of soil water content on the mobile shelter site were made on 3 May. By this date the barley had fully emerged, and the first irrigation of 25 mm had been applied on 28 April to all treatments except 1, 2 and 3 (see Table 1). The total soil water content from the surface to 1·5 m depth on the irrigated plots (averaging 12 profiles) was 554 mm, standard deviation 13 mm, and on the non-irrigated plots (averaging five profiles) was 547, S.D. 8 mm. By 3 May there had been some evaporation from all of the plots, and the soil moisture deficits of the irrigated and non-irrigated plots were estimated to be 11 and 18 mm respectively giving an initial estimate of field capacity of 565, S.D. 12 mm.

During May four of the profiles showed considerable drainage from below 1·2 m, indicative of a perched water table. The other 13 profiles showed an average loss of only 4 ± 1 mm from below 0·7 m in 3 weeks, and there was no significant difference between the plots that were receiving irrigation and those that were not. This shows that the first condition for using the field capacity concept was satisfied: the water content of the profile was very stable.

After allowing for this drainage the mean value for field capacity from all 17 water-content profiles was 559, S.D. 12 mm. The variation is remarkably small compared with that found by French *et al.* (1973*a*) or Kirby (1970); this might be expected for such a small experimental area, and confirms that the site was very uniform.

To test whether the soil had the same field capacity at the end of the drought experiment as at the beginning, four of the driest plots were re-wetted after harvest. The four plots had deficits in the range 156–186 mm and they were re-wetted by applying 25 mm of water every 3 or 4 days. When each plot had received an amount of water equal to the deficit after harvest, the mean soil moisture deficit was 18 ± 1 mm: therefore 18 mm of the applied water had drained through the soil profile. All the plots were given a further two applications of 50 mm irrigation, and a week after the second of these irrigations the mean soil moisture deficit was still found to be 18 mm. No doubt a long wet period is needed for the soil to swell and fully regain its original water holding capacity. For an irrigated plot, however, which never dries as deeply nor to such a low water content, field capacity should provide a datum that varies by less than 18 mm.

Evaporation from fully irrigated crops

The weekly evaporation can be calculated from the balance of water inputs and outputs, that is

$$\int_{\text{week}} E dt = I + R - \Delta W - d,$$

where I is the irrigation and R the rainfall in the week, ΔW the change in the total water content of the soil profile, measured with a neutron meter, and d is the drainage from the measured profile. It is probable that all plots irrigated on 28 April, 5 May and 12 May were over watered, and the estimates of E are too large by a few millimetres. After 12 May the plots were never re-watered to within less than 20 mm of field capacity, so drainage was unlikely.

The evaporation rate from the fully irrigated treatment under the mobile shelter, E_{12}, may be compared with that from the irrigated treatments in Great Field, and with the potential rate, E_T (Fig. 1*a*). The evaporation rates from plots X_F and M_I were not significantly different from each other, but were less than E_{12}, principally early and late in the season when Great Field was not being irrigated. In early May E_{12} is probably an overestimate because of drainage, but the weekly irrigation would have kept the soil surface wet and caused more evaporation from the soil than occurred at Great Field. In July the Great Field experiments were not irrigated because the crop began to lodge: under the mobile shelters irrigation continued and the crop was supported with 0·15 m mesh netting. Hence the crop in Great Field ripened earlier and the evaporation rate decreased.

In June the irrigated crops under the mobile shelters and on M_I and X_F all completely covered the ground and had not started to ripen. The evaporation totals for June were 163 ± 4, 148 ± 6, and 144 ± 8 mm respectively, and $\int E_T$ was 116 mm. Hence the ratios of E/E_T were $1{\cdot}26 \pm 0{\cdot}04$ for large field experiments and $1{\cdot}41 \pm 0{\cdot}04$ for the small plots under the mobile shelters. The ratio of 1·26 for irrigated barley is greater than the value of 1·15 given by French, Long & Penman (1973*b*), and closer to 1·3, which they found for several other crops including spring wheat. The ratio of 1·41 for the irrigated plots under the mobile shelters is significantly higher than the ratio on Great Field, and the increase was probably caused by the advection of warm dry air from the surrounding non-irrigated plots (Legg *et al.* 1978).

Grant (1975) found the ratio of E/E_T for barley to be approximately 1·0 for long periods, but this was for 'control' plots that did not receive any irrigation. The probable explanation is that the small aerodynamic resistance to be expected for the tall crop was balanced by an increase in stomatal resistance caused by shortage of water.

Evaporation from non-irrigated crops

Figure 1(*b*) shows the evaporation from plots whose drought periods extended to harvest. When irrigation was stopped early in the season (treatments 3 and 7) the evaporation rate immediately fell below E_{12}. This was because the crop had not completely covered the ground, and the soil surface soon

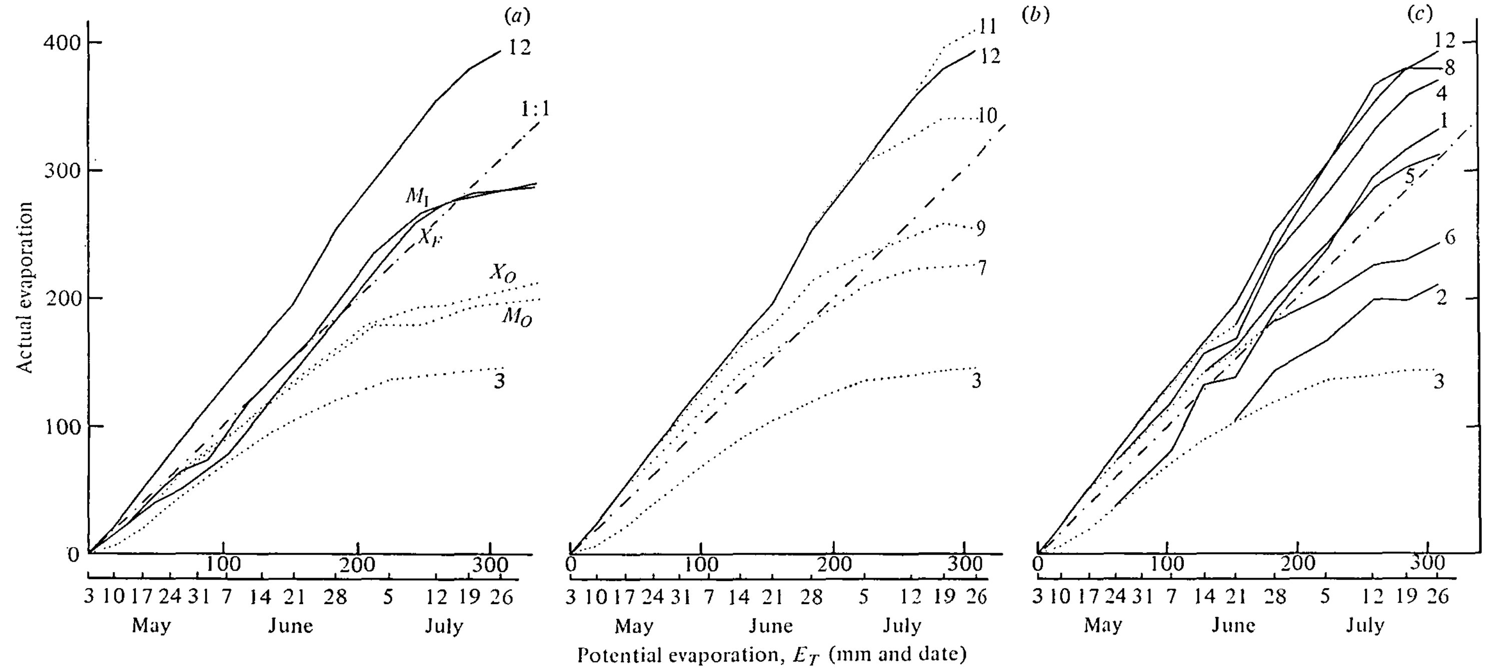

Fig. 1. Actual evaporation, $\int E\,dt$, calculated from neutron probe measurements of soil water content, against potential evaporation, $\int E_T\,dt$, from 3 May (*a*) for the fully irrigated treatments, 12 (mobile shelter site) and X_F and M_I (Great Field), and for the unirrigated treatments, 3 (mobile shelter site), X_0 and M_0 (Great Field); (*b*) for treatments with drought periods starting at various times but continuing until harvest; (*c*) for treatments that were re-watered after a drought period. A dashed line indicates evaporation during a drought period (see Table 1 for definition of the treatments).

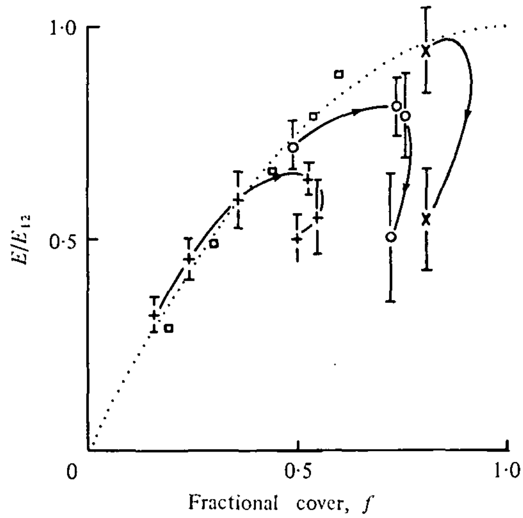

Fig. 2. The ratio of the evaporation rate, E, for various treatments during their drought period, to the rate E_{12} for the fully irrigated treatment, against the estimated fractional ground cover, f. The arrows show the direction of progression with time, for treatments 3 (+), 7 (○) and 9 (×). The dashed line represents the relationship $E/E_{12} = 1-(1-f)^2$; the points (□) are from the relationship $E/E_{12} = 0{\cdot}7$ $\text{LAI}^{\frac{1}{2}} - 0{\cdot}21$ (Ritchie & Burnett, 1971), using a relationship between leaf area index (LAI) and f obtained in the present experiment.

dried; the evaporation measured was mainly transpiration. After a time, however, the evaporation decreased sharply when the plants were stressed.

Early in the season the ratio E/E_{12} for non-irrigated plots depended on ground cover, f (Fig. 2). For treatments 3 and 7 E/E_{12}, initially increased as f increased, but then decreased as the crop became short of water. The first few values of E/E_{12} for each of these treatments fall on the line $E/E_{12} = 1-(1-f)^2$, and this gives an empirical relationship between actual transpiration, potential evaporation and fractional cover similar to that found by Ritchie & Burnett (1971). However, uncertainties in the values of E/E_{12} are large, and f was assessed by eye only.

When irrigation was stopped later in the season, on treatments 9 and 10, the evaporation rate was unchecked initially, because ground cover was large and therefore soil evaporation was unimportant. The rate decreased after 1 or 2 weeks when the plants had used all the readily available water. For treatments 7, 9 and 10, the sharp decline in evaporation started when the soil moisture deficit reached 100 mm (Fig. 3*a*). For treatment 3, the evaporation rate started to decline when the deficit was only 80 mm, though, at this time, roots were less deep. For the non-irrigated plots on Great Field, X_0 and M_0, the evaporation rate started to decline when the deficit exceeded 100 mm. (Fig. 3*b*). The results from Great Field are close to those from treatments 7 and 9 because there was some early rain.

The evaporation from unirrigated plots under the mobile shelters may be compared with that measured by Denmead & Shaw (1962) for maize growing in pots of Colo silty clay loam. They found that the volumetric water content of the soil decreased from 0·36 to 0·21 when the pots were not watered, and the proportion of water that was transpired at the potential rate depended on the magnitude of the potential rate. When the transpiration rate from pots with adequate water was 6, 4 or 1 mm/day, approximately 12, 50 or 88% respectively of the available water was transpired at the full rate. The water holding capacity of the soil under the mobile shelters is similar to that of the soil used by Denmead & Shaw. E_{12} was in the range 4–5 mm/day when the evaporation rate from treatments 3, 7 and 9 decreased, and the decrease occurred when about half of the available water had been used. The value of E_{12} was 7 mm/day when the evaporation rate for treatment 10 declined, but there was no evidence that a smaller fraction of the available water had been used.

The measured soil water deficits under treatments 3, 7, 9 and 10 (Table 3) reached their maxima as the crop ripened. Though treatment 3 had the longest drought period, its maximum deficit was 30 ± 9 mm less than treatments 7 and 9.

Treatments 7 and 9 respectively received 65 and 98 mm of irrigation early in the season but none later. This early irrigation on treatments 7 and 9 allowed the roots to develop more extensively so that they could extract more water later in the season. The maximum deficit under treatment 10 was less because the drought was late in the season and the crop ripened before all the available water had been extracted. The unirrigated plots in Great Field had the same maximum deficit as treatments 7 and 9 because there was enough rain early in the season to allow the roots to grow well.

Evaporation from rewatered crops

Some plots were rewatered after a drought (Fig. 1*c*: treatments 1, 2, 4, 5, 6 and 8). Table 4 shows that the evaporation rate, after rewatering, from plots receiving treatments 1, 4 and 8 recovered to

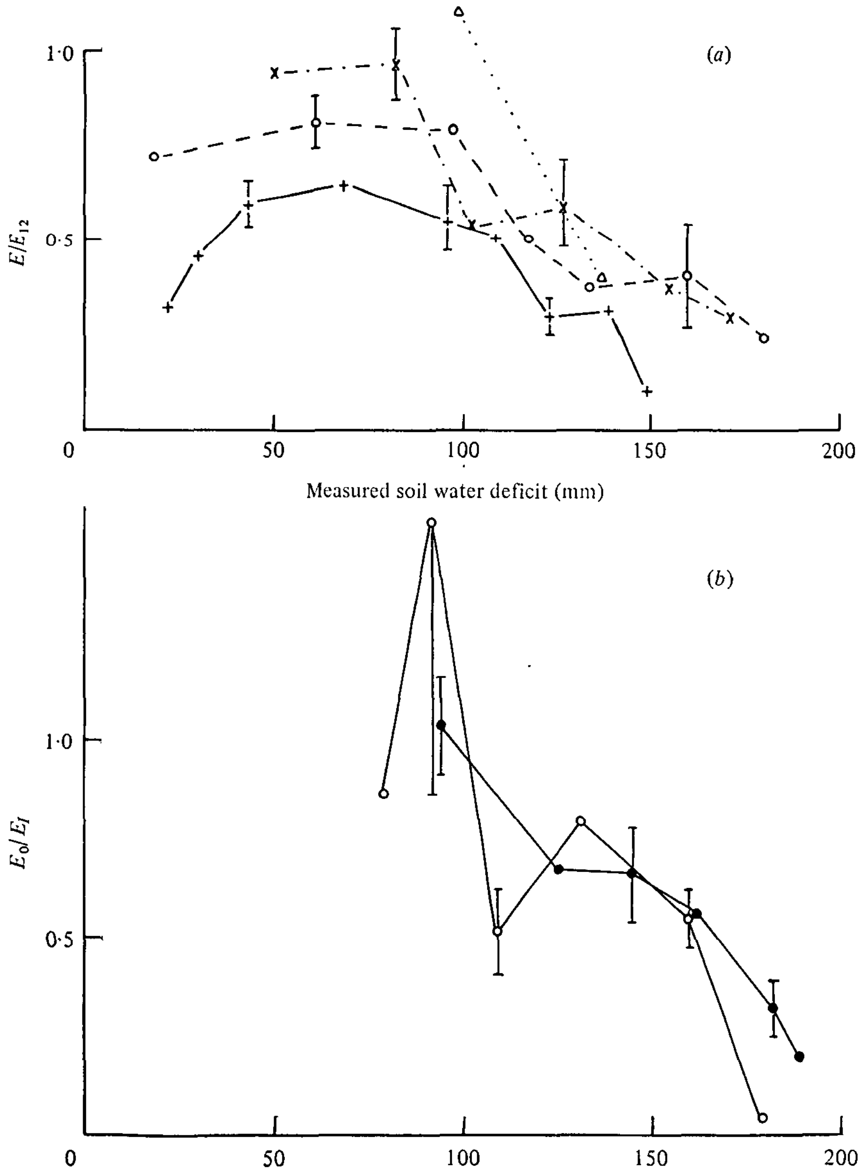

Fig. 3. (*a*) The ratio E/E_{12} against the measured soil water deficit, for treatments 3 (+), 7 (○), 9 (×) and 10 (△), during drought periods. (*b*) The ratio of the evaporation rate from unirrigated plots, E_0, to that from irrigated plots, E_I, against the measured soil water deficit for Great Field *M* plot (○) and *X* plots (●). The error bars indicate ±standard error; those shown are typical.

equal E_{12}, whereas the evaporation rate under treatments 2 and 6, and to a lesser extent treatment 5, did not. The recovery under treatments 4 and 8 is not surprising, as the drought period was short and the evaporation rate was not checked appreciably during the drought (Fig. 1*c*). Treatment 1 recovered well despite a large decrease in evaporation during the drought because this decrease was largely in evaporation from the soil surface.

The plots whose evaporation did not fully recover when rewatered (treatments 2, 5 and 6) had all received severe droughts, and water use was greatly decreased during the drought. The non-recovery of evaporation is probably due to the small ground cover, and early leaf senescence for these treatments.

Depth of water extraction

In a period with no rainfall or irrigation the depths from which water is extracted can be calculated from the soil water content measurements. Results from the mobile shelter experiment showed that roots under the irrigated treatments were active to the same depth as in the non-irrigated treatments (Fig. 4), and when irrigation was withheld they were able to extract water from the full rooting depth. This is illustrated by comparing the water uptake for treatment 7 in its first month without irrigation, with that for treatment 3 during the same period (Fig. 5). In each interval more water was used on treatment 7 than on treatment 3, but the maximum depth from which water was extracted was the same for both treatments in each interval. The same was true later in the season, when comparing treatment 10 in its first week without water with treatment 9 which by that time had had 4 weeks of drought.

As the maximum depths from which water was extracted were the same for all treatments, it is possible to draw a single graph of maximum depth of extraction against time (Fig. 6); presumably the maximum depth of root would be a few centimetres greater (McGowan, 1974). The period of most rapid extension of the zone of water uptake was from mid-May to mid-June, but the maximum depth of water extraction did continue to increase until the crop was ripe.

The maximum soil water deficits for treatments 3 and 7 differed by 35 mm (Table 3), and this difference was associated with differences between the final water content profiles at depths below 0·5 m (Fig. 4). Thus the minimum soil water content for treatment 7 was about 0·14 (volumetric) less than field capacity for all depths between 0·5 and 1·0 m, whereas under treatment 3 the difference was 0·14 at 0·5 m but only 0·07 by 1·0 m. Hence the water applied early to treatment 7 allowed the roots to be more active at depth, although not, apparently, to grow to a greater maximum depth.

Table 3. *Maximum soil water deficits for four treatments under the mobile shelters, and for two unirrigated treatments in Great Field*

Treatment	3	7	9	10	M_0	X_0
Maximum deficit (mm)	152	187	178	149	179	189
S.E.	6	6	9	9	10	7

Crop growth and yield in the mobile shelter experiment

On the mobile shelter site there were visible differences in crop growth under irrigated and non-irrigated treatments within 1 week of the first irrigation, and there were significant differences in dry weight and leaf area in the first growth analysis sample on 10 May. Ear emergence, beginning on about 8 June, and anthesis, beginning on 15 June, occurred at the same time within a few days for all the experimental treatments. Anthesis was earlier than usual, probably as a result of the warm summer. Crop maturity was also earlier, but, unlike anthesis, was markedly affected by treatment. Crops without water after 23 June matured up to 2 weeks earlier than those given water after this date, but at about the same time as crops on the rest of Rothamsted farm (the summer of 1976 was exceptionally hot and dry, and the barley harvest was earlier than usual). Some 'late' tillers were

Table 4. *Water use of re-watered plots during the drought period and after re-watering*

Treatment	1	2	4	5	6	8
Drought period	Emergence–2. vi	Emergence–23. vi	12. v–2. vi	12. v–16. vi	12. v–30. vi	26. v–23. vi
E during drought (mm)	74	120	76	118	157	97
E after drought/ E_{12} after drought	0·94 ± 0·03	0·52 ± 0·02	0·96 ± 0·03	0·77 ± 0·02	0·51 ± 0·06	1·00 ± 0·02

E_{12} is the evaporation from the fully irrigated plots.

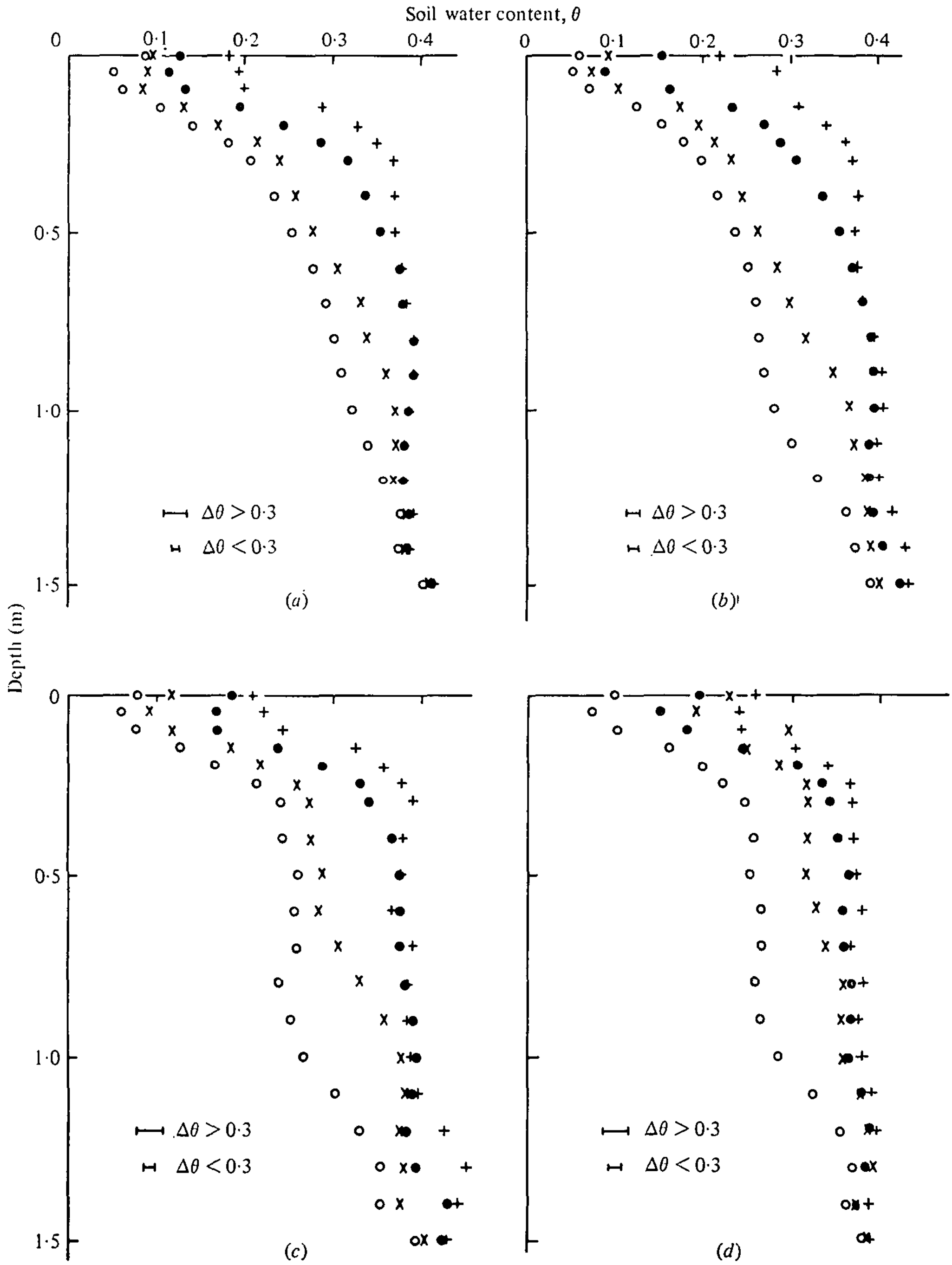

Fig. 4. Soil water content profiles on 3 May (+), 24 May (●), 15 May (×) and 12 July (○) for (*a*) treatment 3, (*b*) treatment 7, (*c*) treatment 9, (*d*) treatment 10. The error bars indicate L.S.D. ($P = 0·05$).

produced on the fully watered plots, and on those rewatered after an early drought, but they contributed little to the final yield.

Drought treatments had significant effects on yield and all its components (Table 5). Grain dry-matter yield ranged from 2·75 t/ha under treatment 3 to 5·71 t/ha under treatment 4, and straw dry matter from 3·13 t/ha under treatment 3 to 7·58 t/ha under treatment 12. The three components of grain yield may be identified through the equation, grain yield equals number of ears per unit ground area times number of grains per ear times mean grain mass. Number of ears per unit ground area ranged from $5{\cdot}5 \times 10^6$ to $7{\cdot}9 \times 10^6$/ha, number of grains per ear from 15 to 21, and mean grain mass from 29 to 38 mg.

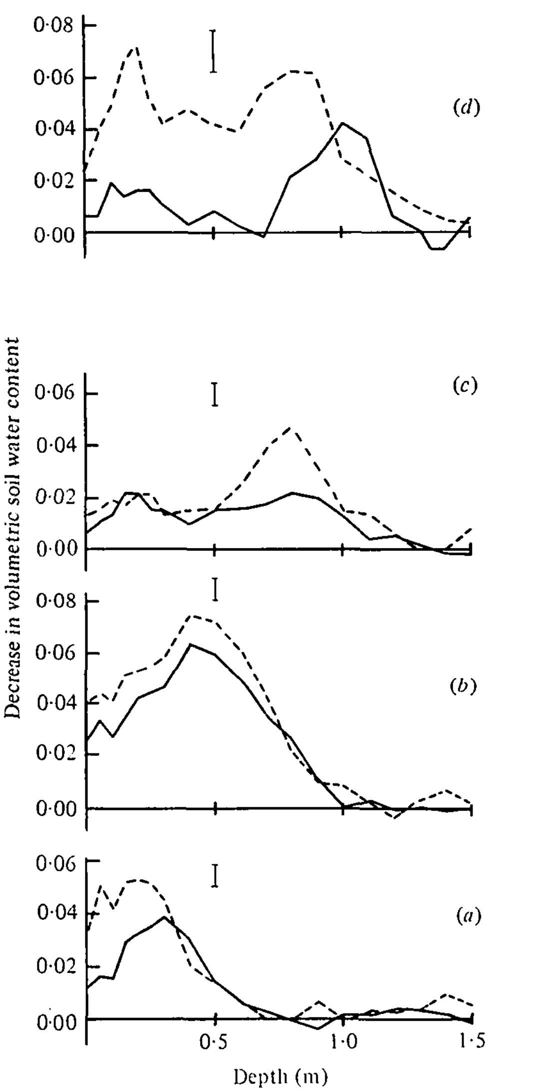

Fig. 5. The amount of water taken up from different depths for intervals through a drought. For treatments 3 (——) and treatment 7 (– – – –) for the intervals (*a*) 18–24 May, (*b*) 25 May–8 June, (*c*) 9–15 June; for treatment 9 (——) and treatment 10 (– – – –) for the interval (*d*) 29 June–5 July. The error bars show ± standard error, based on pooled variance.

To relate these components, and the total yield, to the imposed droughts and their timing it was necessary to have a quantity (or quantities) to represent the intensity of the drought. In the present experiment soil water content was measured, so an analysis based on actual soil water deficits was adopted. This analysis was used to distingush the effect of drought and its timing on the components of yield. When comparing the effect of different treatments on the final yield, a single quantity representing the total season's drought is required; Penman (1971) used the 'maximum potential soil water deficit', the difference between the potential evaporation, integrated over the season, and the water input, as rainfall and irrigation. This approach is used later in this section.

Yield components and actual deficits

The drought treatments were arranged to coincide with particular stages in crop development. The grain yield and its components, and the straw yield were analysed for their response to the mean deficit in three periods: period 1, 27 April to

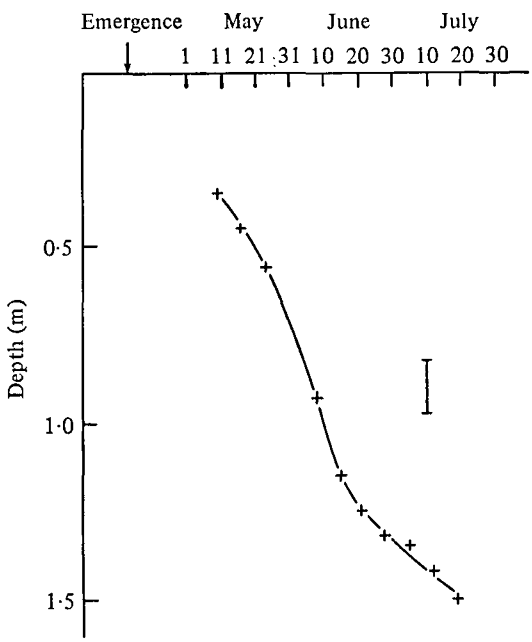

Fig. 6. The maximum depth of water extraction through the growing season (mean over all treatments). The error bar shows 2 × standard error.

Table 5. *Crop dry-matter yields and yield components for the mobile shelter experiment*

Treatment no.	1	2	3	4	5	6	7	8	9	10	11	12	S.D.
No. of replicates	2	2	2	1	2	2	2	1	1	1	1	2	—
Total dry matter (t/ha)	9·21	6·43	5·88	11·38	9·77	8·71	7·48	11·37	8·52	10·27	12·26	13·13	0·43
Grain yield (t/ha)	4·73	3·15	2·75	5·71	4·76	3·93	3·37	5·01	3·55	4·56	5·64	5·55	0·20
Straw yield (t/ha)	4·48	3·28	3·13	5·67	5·01	4·78	4·11	6·36	4·97	5·71	6·62	7·58	0·35
Mean grain mass (mg)	35·9	37·2	30·2	38·5	37·8	34·1	29·1	35·5	28·7	31·4	35·9	35·5	1·2
No. of ears $\times 10^{-6}$/ha	7·67	5·80	5·50	7·60	7·13	6·43	6·47	7·07	6·73	7·87	7·73	7·57	0·64
No. of grains per ear	17·2	14·6	16·6	19·5	17·6	17·9	17·8	20·0	18·4	18·5	20·3	20·9	1·3
No. of grains $\times 10^{-6}$/ha	132	85	91	148	126	115	115	141	124	145	157	156	5

The standard deviations (S.D.) are pooled estimates based on the seven replicated treatments.

1 June, including tiller production and spikelet initiation; period 2, 2 June to 22 June, including tiller and spikelet death, and anthesis; period 3, 23 June to 13 July, including grain filling.

The actual deficits were obtained from the weekly neutron probe measurements of soil water content, and mean values for each week were calculated. For non-irrigated treatments a simple average of the deficit at the beginning and end of each week was used. For the treatments receiving irrigation during the week, a more complicated procedure was necessary to take into account the irrigation applied during the week.

Table 6 gives the percentage of the total variation of each of the components of grain yield that was accounted for by linear regression against D_1, D_2 and D_3 (mean deficits in periods 1, 2 and 3 respectively) separately and together. The variation in each component is largely explained by the deficit in one of the three periods alone. The number of ears per unit ground area, and the number of grains per ear are closely correlated with D_2 and D_1 respectively ($P < 0{\cdot}001$) but further regressions for these components are not significant. The mean grain mass is closely correlated with D_3 ($P < 0{\cdot}001$) and subsequent regression against D_2 is also significant ($P < 0{\cdot}05$). All the significant correlations in Table 6 are negative (i.e. a small value for the component when the deficit is large) except for the correlation of mean grain mass with D_2 after regression against D_3.

Number of grains per ear. The mean number of grains per ear responded to soil water deficit in period 1 (Fig. 7*a*), when the spikelets were initiated, but not in period 2 when the number of viable spikelets per ear was decreasing. Gallagher *et al.* (1976) showed that the maximum number of spikelets initiated can be up to twice the final number of grains. It would seem therefore that the process of spikelet initiation was sensitive to drought (as observed by Husain & Aspinall (1970) in pot experiments), but that spikelet death was not. Interpretation is, however, complicated by differences between treatments in the number of tillers that survive to harvest. Tiller ears generally have less grains than main stem ears, so that a decrease in the number of ear-bearing tillers by drought in period 2 would tend to increase the mean number of grains per ear. Therefore any tendency for spikelet death to be drought sensitive may have been masked in the present analysis, and would only be revealed by measurements on main stems and tillers separately.

Number of ears per unit ground area. The number of ear-bearing stems was decreased by drought in period 2 (Fig. 7*b*), when the total number of stems is declining, but not by drought during the tillering phase itself. Aspinall *et al.* (1964) showed

Table 6. *Percentage of the variance in yield and yield components accounted for by regression against the mean soil water deficits*

		No. of ears per unit ground area	No. of grains per ear	Mean grain mass	No. of grains per unit ground area	Grain yield	Straw yield
	D_1	25*	63***	−7 NS	60***	41**	67***
Extra variance accounted for by	D_1+D_2	+36**	+3 NS	+11 NS	+27***	+35***	+15**
	D_1+D_3	+14 NS	−2 NS	+89***	+8*	+37***	+14**
	D_2	62***	38**	6 NS	75***	73***	61***
Extra variance accounted for by	D_2+D_1	−2 NS	+28**	−2 NS	+13**	+3 NS	+21***
	D_2+D_3	−3 NS	+4 NS	+81***	+0 NS	+4 NS	−3 NS
	D_3	18 NS	−4 NS	82***	12 NS	44**	19*
Extra variance accounted for by	D_3+D_1	+21*	+64***	+0 NS	+57***	+34***	+63***
	D_3+D_2	+42**	+46**	+5*	+63***	+33***	+40**
	$D_1+D_2+D_3$	58**	65***	86***	87***	85***	85***

D_1, D_2 and D_3 are the mean deficits in periods 1, 2 and 3 (see Table 1). The values given are the percentage variance accounted for (percentage reduction in the residual mean square) by the regressions against a single deficit, and the extra variance accounted for when a second deficit is included in the regression. The percentage variance accounted for by regression against all three deficits is also given. NS, $P > 0{\cdot}05$; *, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$; ***, $P < 0{\cdot}001$.

that tiller production and growth are sensitive to drought, and in this experiment the number of stems per unit ground area at the end of period 1 was only $930 \pm 150/\text{m}^2$ in stressed treatments (1, 2 and 3) compared with $1530 \pm 100/\text{m}^2$ in treatment 12. However, at harvest no treatment had more than 780 ± 70 ears/m² (Table 5) so that even the treatment most stressed in the tillering phase produced sufficient tillers for maximum number of ears per unit area when given adequate water in periods 2 and 3 (for example, treatment 1, Table 5).

Mean grain mass. The mean grain mass was most affected by drought in the grain-filling period (Fig. 7*c*), and this agrees with the observations of Aspinall *et al.* (1964). The range of grain masses for different treatments was similar to that found for Julia barley by Gallagher, Biscoe & Scott (1975) in data from National Institute of Agricultural Botany trials. They hypothesized that grain mass varied much less than the other components of grain yield, and that when assimilation after anthesis was small, compensatory translocation from the stems provided a large part of the grain dry matter. The present experiment shows that when yield is limited by drought, the percentage decrease in mean grain mass can be as great as the decrease in the other components of grain yield (Fig. 7*a*–*c*). Drought in the grain-filling period led to a small mean grain mass, though there was still evidence of compensatory translocation of dry matter from the stems (see section on straw yields below).

Regression of mean grain mass against the deficits in periods 2 and 3 shows a significant positive correlation with deficit in period 2, the fitted equation being

$$\text{mean grain mass} = 38{\cdot}4 + 0{\cdot}030\ D_2 - 0{\cdot}077\ D_3\ \text{mg}$$

with deficits in mm. Thus drought in period 2 tended to increase the mean grain mass, and this may reflect the decreased competition for assimilate in the grain filling period after drought in period 2 has decreased the total number of grains. However, the change in the ratio of tillers to main stems will also contribute to the increase, as the mean grain mass on tillers is generally smaller than on main stems (Gallagher *et al.* 1976).

The positive and negative effects of water deficits on mean grain mass observed in this experiment explain why the response of grain mass to drought has often been indeterminate (Rackham, 1972). In field irrigation experiments with rainfall late in the season it is possible for the non-irrigated treatment to have a larger mean grain mass than the irrigated (Kirby, 1968).

Grains per unit ground area. The total number of grains was determined more precisely than the number of ears per unit ground area, and hence the number of grains per ear (Table 5). For treatments

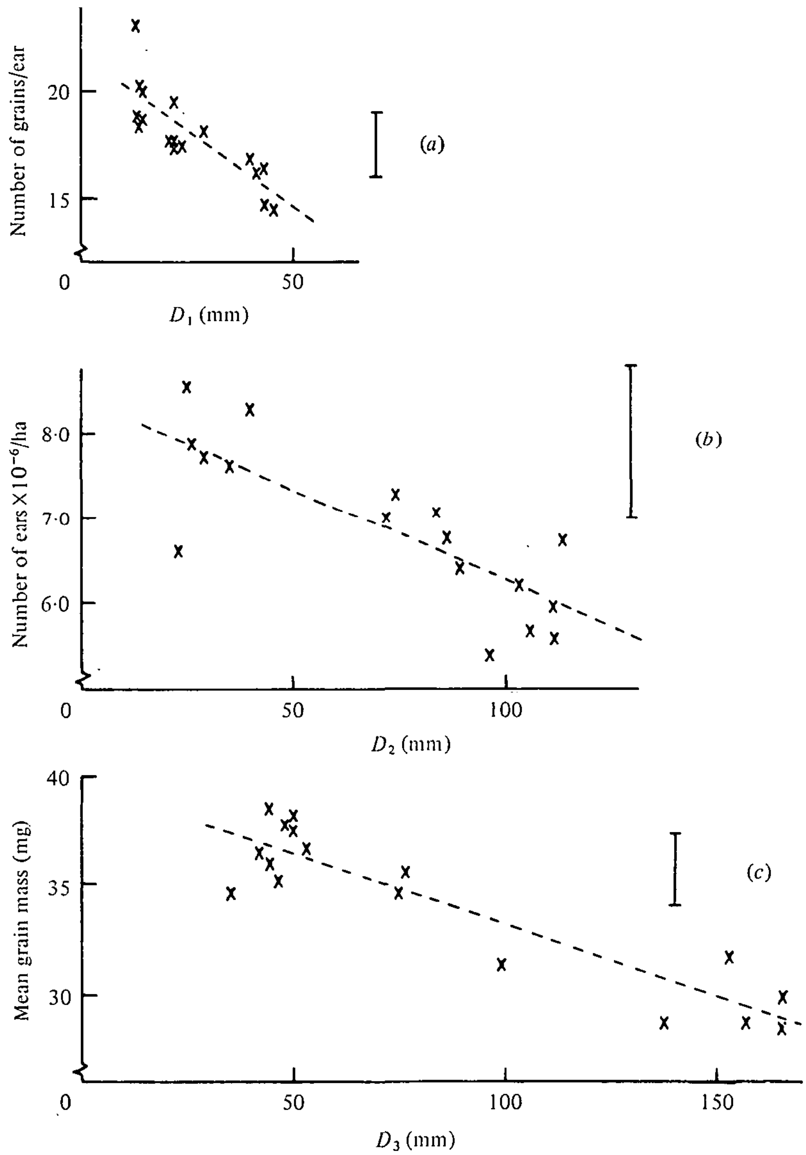

Fig. 7. The components of grain yield, each against the deficit in one period. The periods used are those which accounted for most of the variance. There is one point for each plot on which soil water content was measured. The regression lines and error bars indicating L.S.D. ($P = 0·05$) are also shown.

with a large number of grains (i.e. those that include little or no stress in periods 1 and 2) drought in period 3 decreased not only mean grain mass, but also the number of grains. For example, treatment 9 had 12% less grains than treatment 8, and treatment 10 had 7% less grains than treatment 12. Thus the number of grains was largely determined before anthesis, in agreement with the results of Gallagher *et al.* (1975), but some loss of grain did occur in severe late drought.

Grain yield. There were significant correlations of grain yield with mean deficit in each of the three periods. In the first order regressions (Table 6) most variation was accounted for by the regression against D_2, but this was due, in part, to the correlation between D_2 and D_1 ($r = 0·57$) and between D_2 and D_3 ($r = 0·59$). The deficits in the three periods were not independent because a large deficit can only be produced by a long drought, extending into more than one period. Though regression against D_1 or D_3 after D_2 was not significant, there was a 12% increase in the variance accounted for when the regression included D_1 and D_3 after D_2 ($P < 0{\cdot}01$). The second order partial correlation coefficients (Table 6) show that the deficit in each of the three periods had an independent effect on the grain yield. The regression equation giving the best fit was

$$\text{grain yield} = 6{\cdot}74 - 0{\cdot}033\,D_1 - 0{\cdot}013\,D_2 - 0{\cdot}0083\,D_3 \text{ t/ha}$$

with deficits in mm. It is clear from this equation and Fig. 7 that yield was affected by smaller deficits in the early periods than in the later. This is largely because the depth of soil exploited by the roots increased through the season. The mobile shelter experiment included treatments with extremes of water availability in each period of growth after emergence, i.e. regular irrigation at one extreme and no irrigation or rainfall at the other. Therefore the percentage decrease in each component of the grain yield over the measured range of deficits is a good indication of the sensitivity to drought for that component. The decrease, calculated from the fitted regressions, was 28% for the number of ears per unit ground area and 24% for the number of grains per ear, indicating a similar sensitivity to drought. Mean grain mass also decreased by 24% over the range of deficits in period 3, but the secondary correlation with D_2 was positive, and indicated a 5% increase in mean grain mass for the range of deficits in period 2.

Table 7. *Partial correlation coefficients for grain yield and straw yield with mean deficits*

	$r_{1x.23}$	$r_{2x.13}$	$r_{3x.12}$
x = grain yield	−0·68**	−0·52*	−0·64*
x = straw yield	−0·81**	−0·49 NS	−0·42 NS

$r_{1x.23}$ = correlation between the deficit in period 1 and x after allowing for the correlation of x with the deficits in periods 2 and 3. NS, $P > 0{\cdot}05$; *, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$.

Straw yield. The straw yield was most closely correlated with the deficit in period 1, linear regression accounting for 67% of the variation (Table 6). Multiple regression against the deficits in periods 1 and 2, and 1 and 3 significantly increased the amount of variance accounted for ($P < 0{\cdot}01$), but the second order partial correlation coefficients do not indicate whether one period was more important than the other (Table 7).

After anthesis there is little accumulation of dry matter in the straw, and Gallagher *et al.* (1975) interpreted decreases in the dry weight of stems and leaves between anthesis and harvest in terms of translocation to the grain. In the mobile shelter experiment there was a marked difference in straw yield between treatments that differed only after anthesis and for which the number of grains per unit ground area was large (treatments 8 and 9, 12 and 10; Fig. 8). This difference may have been due to translocation of dry matter from the stems to the grain when demand for assimilate was large but supply restricted.

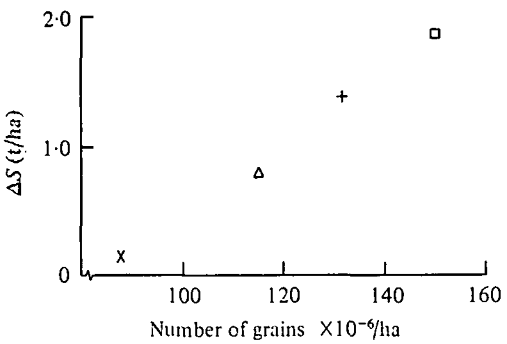

Fig. 8. The decrease in straw yield, ΔS, due to a drought in period 3, against the number of grains per unit ground area at harvest. The straw yield differences are between treatments 2 and 3 (×, D_3 = 140 mm for treatment not irrigated in period 3), the mean of 5 and 6, and 7 (Δ, D_3 = 160 mm), 8 and 9 (+, D_3 = 160 mm), and 12 and 10 (□, D_3 = 100 mm).

Yield and potential deficit

In order to relate the results from the present experiment to those from other field irrigation experiments, it is useful to consider the response of yield to some measure representing the degree of drought over the whole season. Penman (1971) related loss of yield to the maximum potential deficit, finding a linear relationship when deficit exceeded some limiting value.

In this experiment each treatment included only one drought period, so yield can be directly related to the potential soil water deficit at the end of the drought period for each treatment. This deficit is the maximum potential soil water deficit, D_M,

$$D_M = \int_{\text{drought}} E_{12}\, dt,$$

where E_{12} is the measured evaporation rate from the fully irrigated treatment. This evaporation rate is used in preference to a meteorological estimate because, although it is based on a limited number of observations, it is a direct measurement on site. The values of D_M are, however, exaggerated because advection between small plots increases evaporative demand from rapidly transpiring plants and decreases that from stressed plants (Legg *et al.* 1978). The value of D_M for treatment 12 has been taken as the maximum deficit at the end of a single week.

Total dry-matter yield generally decreased with increasing maximum potential deficit (Fig. 9*a*) though early drought caused a greater decrease than drought late in the season.

Grain yield decreased linearly with D_M for all treatments except treatment 2 (Fig. 9*b*). There is little evidence of a limiting deficit below which yield is constant, but this is principally because the hot weather gave high weekly evaporation totals, and few treatments had a very small maximum potential deficit. Treatment 4 indicates that the limiting deficit is between 80 and 100 mm for barley on this soil, and the gradient, excluding treatment 2, is $-0{\cdot}008$ t/ha/mm.

Treatment 2 shows a greater response to drought than the other treatments, and indicates a 'critical stage' in the crop's drought response. The crop had so few grains per unit ground area by anthesis when the drought ended that although all grains filled (mean mass 37·2 mg) the yield was still exceptionally low. The number of grains per ear, and the number of ears per unit ground area were not measured accurately enough to determine which component suffered most.

The relationship between straw yield and potential deficit shows much more scatter (Fig. 9*c*). Early drought (treatments 1 and 4) decreased straw yield more than did the same deficit in any other period. Drought in period 2 also decreased straw yield (compare treatment 2 with 1, and 8 with 12). But the effect of drought in period 3 depended on whether there had been an earlier drought. After an earlier drought there was little further depression of straw yield (compare treatment 3 with 2, and 7 with 6); with no earlier drought, a drought in period 3 caused a large decrease in straw yield (compare treatment 10 with 12).

The differing response of straw and grain yield

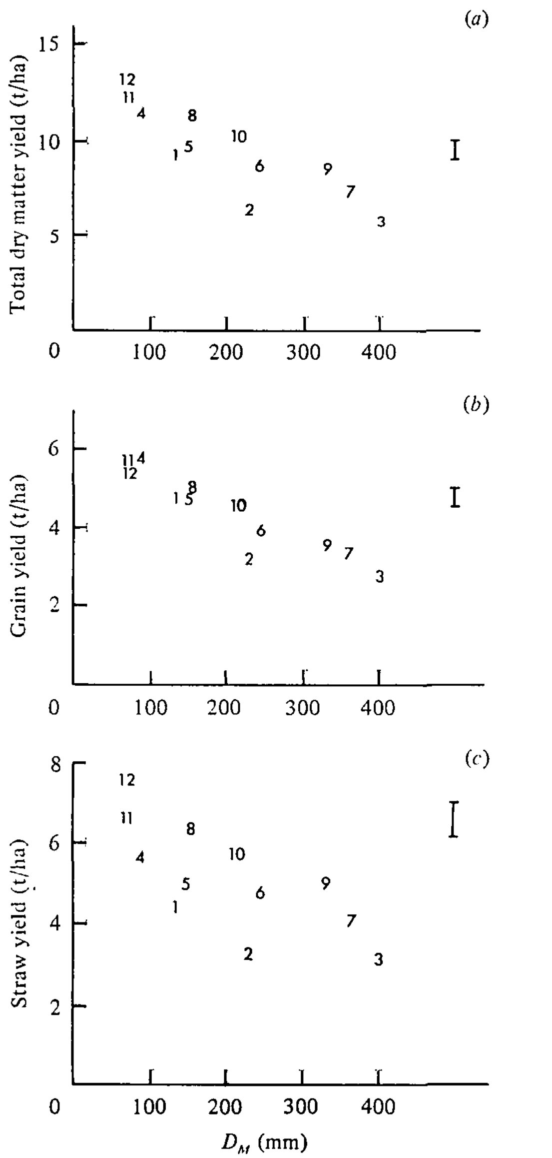

Fig. 9. (*a*) The total dry-matter yield, (*b*) grain yield and (*c*) straw yield against the maximum potential soil water deficit, D_M. Each treatment is represented by its treatment number. The error bars indicate L.S.D. (P = 0·05).

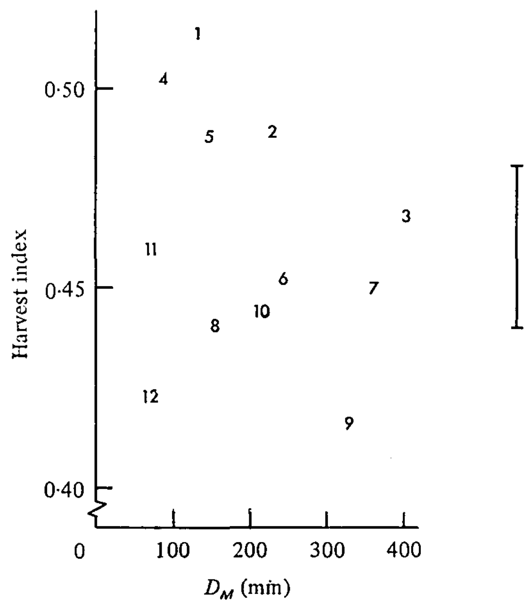

Fig. 10. The harvest index (grain yield/total dry-matter yield) against maximum potential soil water deficit, D_M. The error bars indicate L.S.D. (P = 0·05).

to drought is also shown by the harvest index, the ratio of grain to total dry-matter yield (Fig. 10). Early drought depressed straw yield and gave an increased harvest index (e.g. treatments 1 and 4); as the drought extended later into the season, the index progressively declined (treatments 1 → 2 → 3; treatments 4 → 5 → 6 → 7).

Yield and water use

Drought has been shown to affect both yield and water use, and the effect on each is remarkably similar, total dry-matter, grain and straw yields being nearly linearly related to water use (Fig. 11*a–c*).

The grain yield from treatment 2 was an exception from the relation of yield to potential deficit (Fig. 9*b*) but not from the relation to water use. Any exceptional effect of the drought modified both the yield and water use, possibly via decreased leaf area and stomatal conductance. Interference with pollination (Skazkin, 1961) is not likely to have mediated the drought effect, because such interference is unlikely to have caused equal decreases in both water use and grain yield.

The scatter in the relationship between straw yield and water use (Fig. 11*c*) is largely explained by the within-treatment variance, but there is an indication that severe early stress decreases straw yield more than water use (treatments 1 and 2).

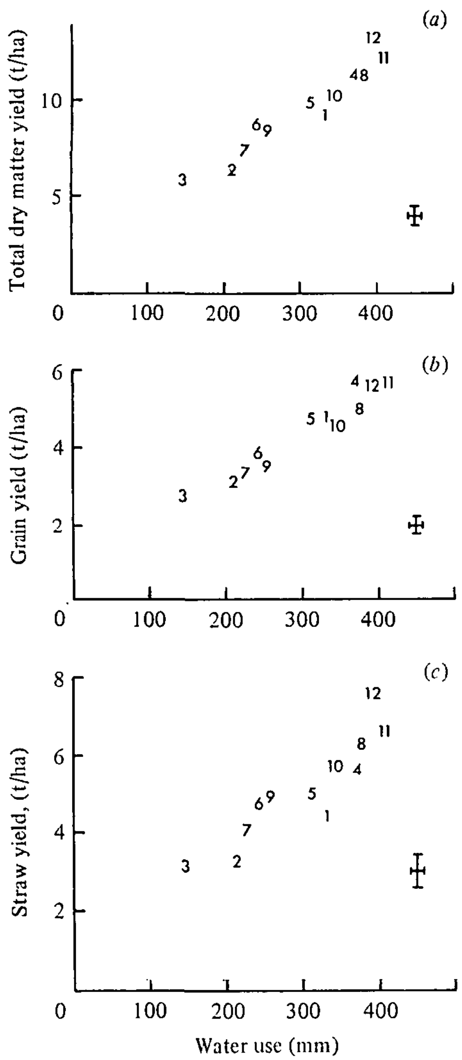

Fig. 11. (*a*) Total dry-matter yield, (*b*) grain yield and (*c*) straw yield, against water use. The error bars indicate L.S.D. ($P = 0{\cdot}05$).

Yield comparison with the Great Field experiments

From the response to drought in the mobile shelter experiment, the effect on yield in the Great Field experiment can be predicted, and compared with the measured effect. Differences between the experimental sites, for example the residual effects of previous cropping, can be expected to cause differences in the absolute yields. However, the effect of drought within an experiment should be comparable between experiments. For this reason, comparisons will be made in terms only of the decrease in yield from that of the fully irrigated treatment in each experiment.

The grain yield and mean grain mass were measured on both experiments in Great Field, and they can be compared in three ways with the results from the mobile shelter. First, the effect of mean measured deficit on the components of yield can be tested. Secondly, the yield decreases due to drought can be compared on the basis of the measured water use. These two comparisons are only possible for the plots in which soil water content was measured (M_0, M_I, X_0, X_F), though a good estimate can be made of the mean deficit for treatments X_E and X_L. Thirdly, yields can be related to the maximum potential deficit, which can be calculated, for all treatments, from treatment irrigation amounts and water use on the fully irrigated treatments.

To apply to the Great Field yields the results of the regression analysis of components of yield for the small plots, periods equivalent to periods to 1, 2 and 3 must be defined. The crop in Great Field emerged 2 weeks before that under the shelters, but by late June the crops were at nearly the same stage of development. The equivalent periods chosen for the Great Field crops were then 21 April to 28 May, 29 May to 21 June, 22 June to 10 July.

Table 8 compares the measured effect of drought on mean grain mass and the number of grains per unit ground area with that predicted from the results of the mobile shelter experiment. The predicted values are based on the deficits in the two

Table 8. *Grain yield and its components on Great Field*

		M_0	M_I	X_0	X_E	X_L	X_F
Mean grain mass (mg)		31·9	30·9	33·0	34·5	36·8	36·8
Decrease from fully irrigated treatment	Measured	−1·0	—	3·8	2·3	0·0	—
	Predicted from actual deficits	+2·2	—	4·2	2·4	0·8	—
Comparison of measured and predicted decreases		**	—	NS	NS	NS	—
Number of grains $\times 10^6$/ha		110	139	125	138	118	137
Decrease from fully irrigated treatment	Measured	30	—	12	−1	19	6
	Predicted from actual deficits	34	—	29	−9	29	—
Comparison of measured and predicted decreases		NS	—	**	NS	*	—
Grain yield t/ha		3·51	4·29	4·14	4·77	4·33	5·06
Decrease from fully irrigated treatment	Measured	0·78	—	0·92	0·29	0·73	—
	Predicted from water use	0·8	—	0·8	—	—	—
	Predicted from potential deficit	1·0	—	1·0	0·3	0·6	—
Comparison of measured and predicted increases		NS	—	NS	NS	NS	—

M_0 and X_0 were non-irrigated plots, X_E was irrigated until 12 June, X_L was irrigated between 21 June and 9 July, and M_I and X_I were fully irrigated plots. The decreases from the value for the fully irrigated treatment in each experiment are shown, together with the predicted decreases, based on comparisons of mean actual deficits, water use and maximum potential deficit with those in the mobile shelter experiment. NS, $P > 0{\cdot}05$; *, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$.

Table 9. *The straw yield on Great Field*

	M_0	M_I	X_0	X_E	X_L	X_F	S.E.
Straw yield (S), t/ha	2·16	2·95	2·92	3·90	2·83	3·83	0·2
S/S_W	0·57	0·59	0·75	—	—	0·78	0·05
S/S_{PD}	0·48	0·45	0·60	0·60	0·54	0·54	0·05

S_W is the straw yield predicted from measured water use, and S_{PD} is the straw yield predicted from the maximum potential deficit.

important periods, 2 and 3 for grain mass, and 1 and 2 for the number of grains. The decreases in mean grain mass for treatments X_0, X_E and X_L are in good agreement with prediction. However M_0 has a greater mean grain mass than does M_I. M_I was last irrigated on June 24, so though it was a 'fully irrigated' treatment, there was a major late drought. This would seem to have had a greater effect than predicted by the linear regression. The agreement between measured and predicted decreases in number of grains per unit ground area is good for the M plots, though only fair for the X plots. Table 8 also compares the measured decreases in final grain yield with the predictions on the basis of the water use and the maximum potential soil water deficit. There is good agreement, showing that the effect of drought was comparable at the two sites.

Comparison of straw yields is more difficult, as the crop in Great Field was combine harvested, whilst that on the mobile shelter site was hand harvested. The proportion of straw harvested by the two methods will differ markedly. Table 9 gives the ratio of the measured straw yield to that predicted from water use and potential deficit. Although the ratio is different for X and M plots and for the two methods of prediction, it varies little between treatments, indicating good prediction.

Nutrient uptake

The relationship between nutrient uptake and drought is complex. The rate of supply of nutrients is decreased in a dry soil (Russell, 1973, pp. 545–7) because the mobility of ions, and water uptake, and hence mass flow of nutrients, is less in dry soil than in wet soil. The rate of production of new

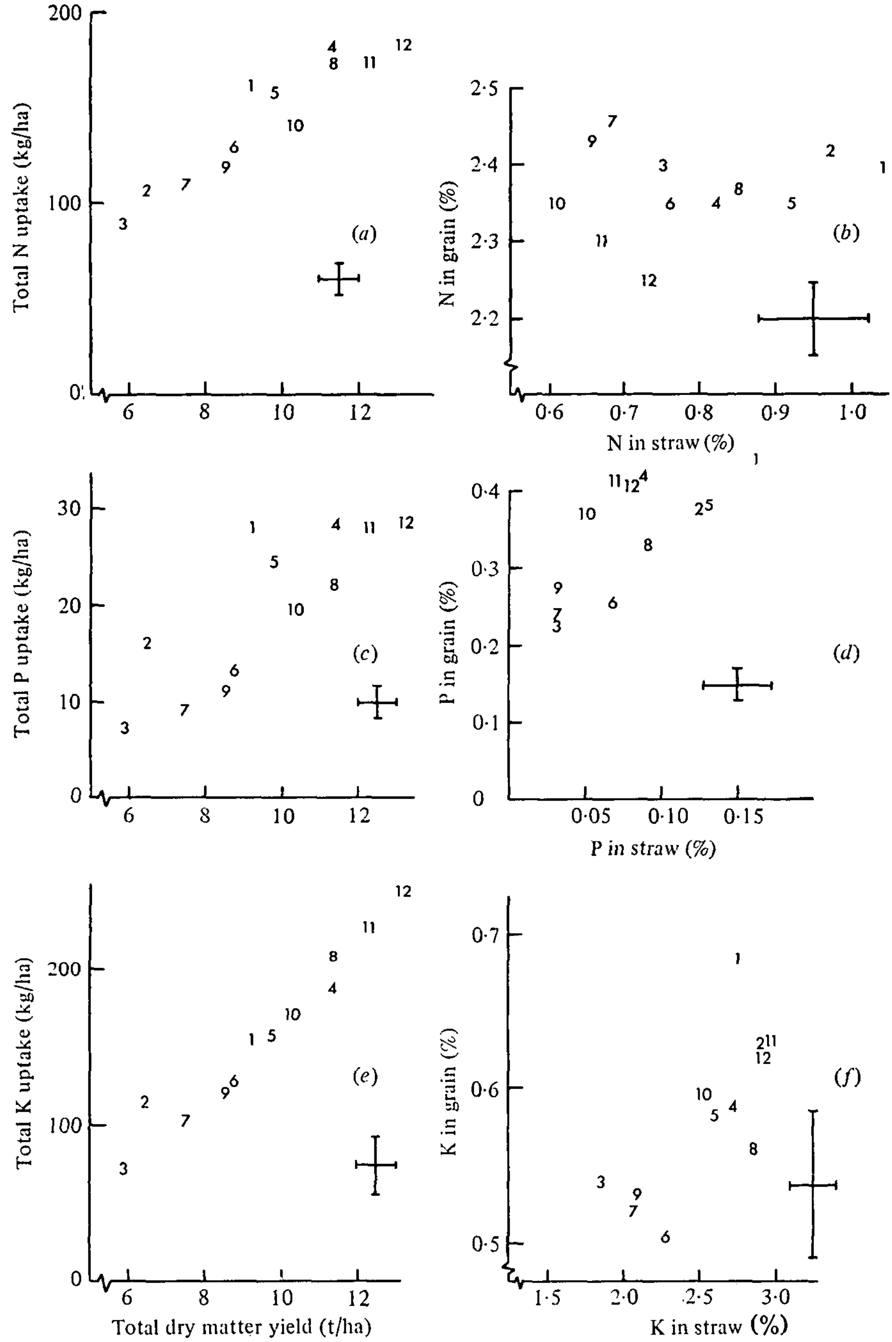

Fig. 12. Total uptakes of N, P and K against total dry-matter yield, and concentration of each nutrient in the grain dry matter against concentration in the straw dry matter. The error bars indicate L.S.D. ($P = 0{\cdot}05$), (*a*) and (*b*) nitrogen; (*c*) and (*d*) phosphorus; (*e*) and (*f*) potassium.

roots and extension of existing roots is decreased, as is the root absorbing power for some nutrients (e.g. phosphate; Dunham & Nye, 1976). Finally the heterogeneity of nutrient availability through the soil profile is important. For example, most available phosphate is in the top soil, and thus, in any prolonged drought period, when the surface soil is dry and root activity transferred to depth, phosphate uptake will be decreased. Nutrient uptake is not related simply to water use because diffusion either towards or away from the root surface is important for many nutrients (Nye & Tinker, 1977). Hence, rigorous interpretation of the measured uptake of N, P, K, Mg, Na and Ca (Figs 12 and 14) in terms of the effect of drought on uptake processes is not possible, but some conclusions may be drawn.

The total uptake of each nutrient generally increased with increasing dry-matter yield, and for N, K, Mg and Ca the relationship was nearly linear. Thus the effect of drought on the uptake of these nutrients paralleled the effect on yield. The effect on P uptake is considered below.

Nitrogen

Nitrogen uptake ranged from 90 to 180 kg N/ha, and the largest amounts were from the most irrigated treatments 4 and 12 (Fig. 12*a*). These large uptakes resulted from both large yield and high N concentration in the dry matter, though neither was abnormal. Fertilizer supplied 75 kg N/ha and a further 21 kg N/ha were supplied in the irrigation water to the fully irrigated plots (Legg *et al.* 1978). Therefore at least 84 kg N/ha was obtained from the soil by the irrigated crop. This amount can be compared with the results of other experiments on similar soil.

Winter wheat given no N and growing on soil without N fertilizer for many years recovered 26 kg N/ha on a soil cropped in the previous year and 56 kg N/ha after a fallow year (Johnston, 1969). Spratt & Gasser (1970) reported that spring wheat recovered 90 kg N/ha from the soil when given full irrigation but no N fertilizer. In both these experiments, less than 60% of applied nitrogen fertilizer was recovered from accompanying fertilized treatments.

The uptake in the present experiment was large because the site was fallowed in 1975, and winter rainfall was small (277 mm, November 1975–March 1976). Thus mineralization of organic nitrogen in the fallow year, and restricted leaching during the winter (drainage from a 1·5 m deep gauge at Rothamsted was 125 mm, compared with the 1960–9 average of 292 mm) caused much nitrogen to be available, and irrigation increased nitrogen uptake. Because large amounts of nitrogen were available in the soil, the nitrogen added in irrigation water (maximum 21 kg N/ha) should not be a significant complication in any watering treatment.

All plots received the same amount of nitrogen fertilizer, and any interaction between N and irrigation was therefore not measured. However, it is unlikely that nitrogen supply limited yield in this experiment, because total N uptake was so large and there was little variation with treatment in the nitrogen concentration in the grain (Fig. 12*b*). The concentration was large, even for the largest yields, also indicating adequate N supply. Nitrogen concentration was largest in the most stressed treatments and smallest in the fully irrigated, in general agreement with previous work (reviewed by Richards & Wadleigh (1952) and Viets (1972)). The N concentration in the straw varied more, and was smallest for the late stressed and largest for the early stressed treatments.

Phosphorus

Phosphate uptake is not closely correlated with dry-matter yield (Fig. 12*b*), and is not therefore closely correlated with water use (see relation between dry-matter yield and water use, Fig. 11). A better relationship can be expected between phosphate uptake and the soil water content in the topsoil, as most available phosphate is in this zone, and its availability diminishes rapidly with decreasing soil water content (Dunham & Nye, 1976). A simple empirical relationship between phosphate uptake and the measured water content in the topsoil was tested. It was assumed that phosphate uptake rate was constant until the soil water content fell below a fixed value, when uptake ceased abruptly. This is an oversimplification, as the effects of root density and crop development are neglected, but should allow comparison between treatments.

A deficit of 45 mm in the top 30 cm of the soil profile (cf. total available water in this zone of 64 mm) was selected, by inspection of the results, as being a suitable criterion for the cut-off point for phosphate uptake. Psychrometer measurements of soil water potential indicate that, for this soil, this deficit corresponded to a water potential of about −2 bars at 30 cm depth, with soil above this depth considerably drier. Figure 13 shows that phosphate uptake decreased linearly with the number of days that the topsoil was 'dry' during the drought period.

There was no direct measure of the effect of phosphate fertilizer in this experiment. Johnston, Warren & Penny (1970*a*) showed that spring barley (cv. Plumage Archer) grown on a similar soil, with 15 mg/kg of bicarbonate-soluble P, gave only a small response to added phosphate. The soil

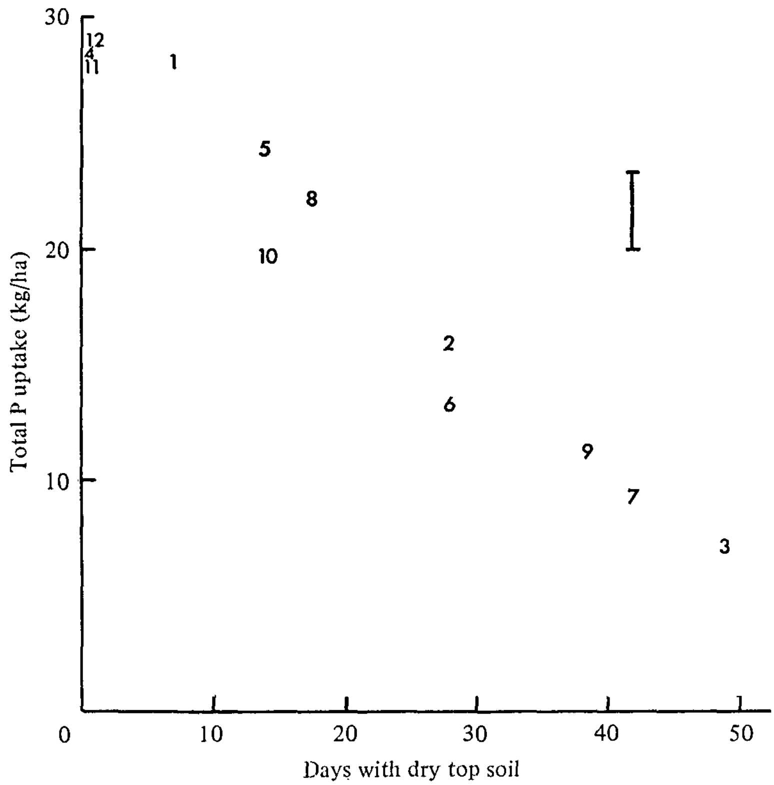

Fig. 13. Total phosphorus uptake against the number of days that the soil was dry during each drought. The soil was considered to be dry when the deficit in the top 30 cm was greater than 45 mm. The error bar indicates L.S.D. ($P = 0.05$).

on the mobile shelter site contained about 25 mg/kg of bicarbonate-soluble P, and a response to additional P would not be expected. However, drought does decrease the uptake of P markedly (Fig. 13) and applied phosphate may then affect yield (Ivanova, Spiridovskaya & Mosma, 1972).

The total phosphate uptake in the non-irrigated treatment 3 was similar to that for a barley crop grown on phosphate deficient soil and with no applied phosphate (Johnston *et al.* 1970*a*). The P concentration in the grain from the unirrigated treatment 3 was also as low as that for a phosphate deficient crop. Thus it is possible that the effect of drought on crop growth and yield was in part due to inadequate phosphate uptake.

The relationship between P content of grain and straw (Fig. 12*d*) shows that though late irrigation increased P uptake, the extra P raised the concentration in grain and straw almost equally (compare treatment 2 with 3, and 5 with 7). The extra P was not as successfully translocated to the grain as was P taken up earlier (comparing treatments 9, 7 and 3).

Potassium

Under all treatments, much more potassium was taken up than the 42 kg K/ha applied as fertilizer (Fig. 12*e*). The percentage K in the grain, 0·5% and more (Fig. 12*f*), suggests that K was not limiting yield, whilst that in the straw was much larger than usual (see, for example, Johnston, Warren & Penny, 1970*b*). The large K concentration in the straw probably arose because the straw was not washed by rain.

The K concentration in grain and straw increased with irrigation (Fig. 12*f*). This means that potassium uptake was more sensitive to drought than was dry-matter production. The increase in the K concentration in the crop with irrigation agrees with the results of most previous experiments (Richards & Wadleigh, 1952) but contrasts with those of Jenne *et al.* (1957) for maize.

Calcium, magnesium and sodium

The Ca concentration in the grain and straw increased with irrigation (Fig. 14*b*). This increase

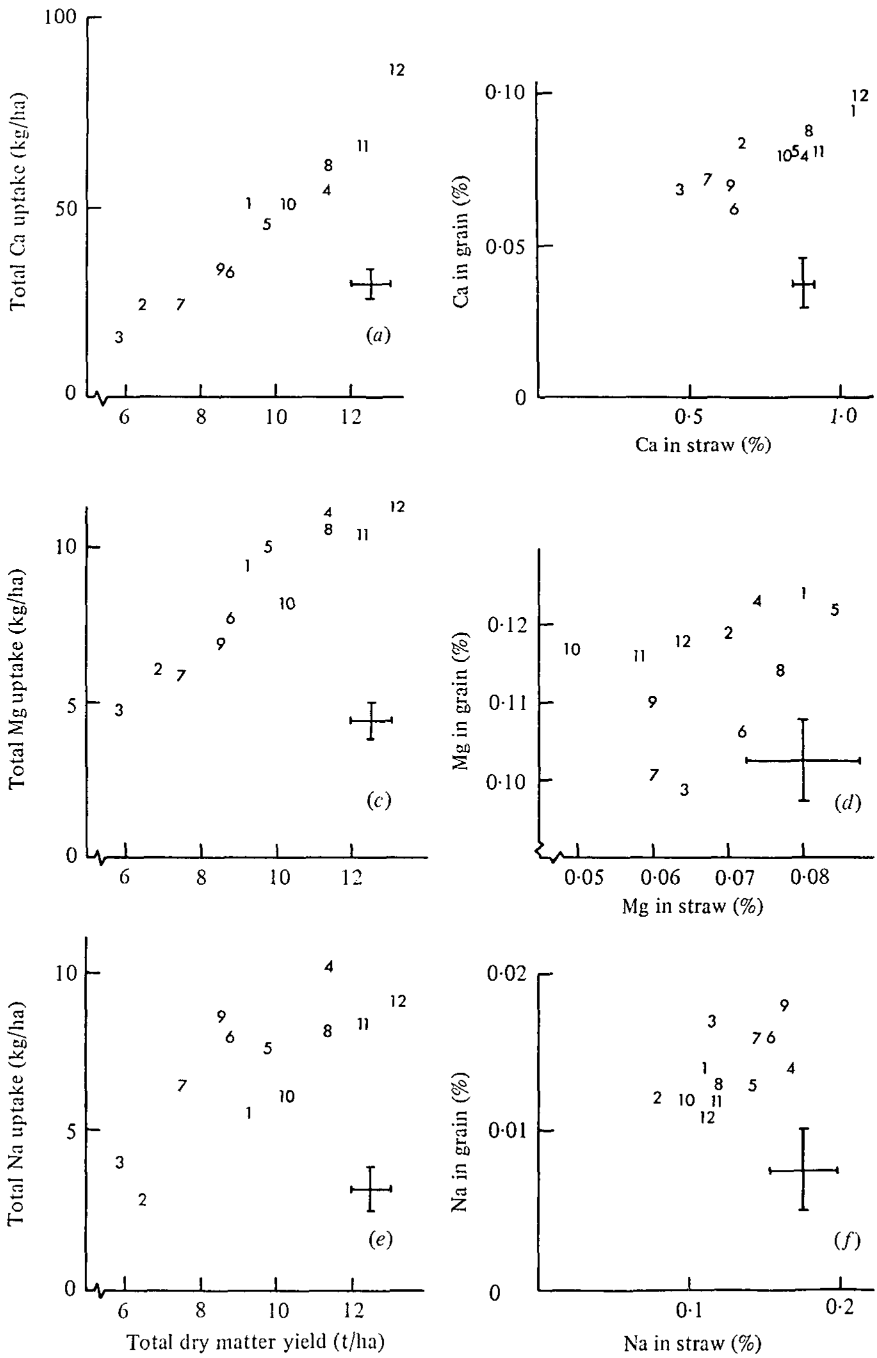

Fig. 14. Total uptakes of Ca, Mg and Na against total dry matter yield, and concentration of each nutrient in the grain dry matter against concentration in the straw dry matter. The error bars indicates L.S.D. ($P = 0.05$). (*a*) and (*b*) calcium; (*c*) and (*d*) magnesium; (*e*) and (*f*) sodium.

may be due to the large amounts of calcium applied in the irrigation water. The fully irrigated treatment 12 received about 400 kg Ca/ha because the irrigation water contained 113 mg Ca/kg. However, concentration in the soil water was probably greater than 113 mg/kg as the soil had a pH in water of 7·2.

There is no evidence that magnesium concentration was affected by drought (Fig. 14*d*). Our results therefore do not support Richards & Wadleigh's (1952) conclusion that irrigation decreases the concentration in the dry matter.

The total sodium uptake (Fig. 14*e*) was approximately proportional to dry-matter yield. As with calcium, much sodium was applied in the irrigation water: for treatment 12 about 24 kg Na/ha was applied through irrigation, and this was more than twice the total uptake.

CONCLUSIONS

Drought caused large decreases in yield, but there was little evidence that any development stage was particularly sensitive. The values for each component of grain yield had a range of about 25%, and the variation between treatments was largely accounted for by the soil water deficit in one of three periods. The number of grains per ear was closely related to the deficit early in the season, the final number of ears per unit ground area was related to the mid-season deficit, and grain mass was related to the deficit in the grain filling period.

First order linear regressions against soil water deficit accounted for much of the variation in yield and its components, though there were more complicated effects. The final number of grains was affected by water stress in the grain filling period for some treatments. A decrease in straw yield due to stress during the grain-filling period was observed for treatments with a large number of grains per unit ground area: this may be indicative of translocation from the stems to the grain when there was competition for restricted assimilate, as suggested by Gallagher *et al.* (1975).

The relationship between grain yield and maximum potential deficit showed that, for 11 of the 12 treatments, the same grain yield decrease resulted from a particular maximum potential deficit independent of timing. For the other treatment, where drought extended from emergence to anthesis, the decrease was greater. By anthesis, the potential for yield, i.e. the number of ears and viable grains per ear, was so low for this treatment that rewatering after anthesis did not have a large effect.

The relationship between grain yield and water use was nearly linear. No treatments deviated markedly from the line, indicating that the effect of drought on grain yield had a parallel effect on water use. An important consequence of this is that potential yield can be defined, based on the total stored soil water plus irrigation and rainfall. Further, the response of yield to maximum potential deficit shows that, for our soil, if the deficit exceeds 100 mm then the maximum yield will not be achieved. Late irrigation gave an increase in yield contrary to Penman's (1971) results.

The maximum depth of root activity at any time, as indicated by water uptake, was not significantly affected by treatment. However, the amount of water extracted from different depths was greatly affected by the soil water content. The rate of water uptake by the crop in a drought period followed atmospheric demand until about 50% of the available water in the rooting zone had been used. The uptake rate then decreased rapidly.

The results for nutrient uptake suggest that the effect of drought was in part via phosphate shortage. The lack of phosphate in the deeper soil layers, and the rapid decrease in root uptake of phosphate as the soil dries, both contribute to the sensitivity of total phosphate uptake to drought. The total uptake in the most stressed treatments was very small, and concentration in the plants was as low as in crops grown in phosphate deficient soils.

The results from the mobile shelter experiment compared quite well with those from the Great Field experiments. Water use on both sites was comparable, and any differences were explained by advection between the small plots on the mobile shelter site, and by the absence of early and late irrigation on the Great Field experiments. The effects of drought on yield on the two sites were similar and, in particular, the decreases in yield due to increasing maximum potential deficit were in good agreement.

When considering the results of the mobile shelter experiment in a wider context, it must be remembered that the effects of drought will not only depend on the irrigation regime, but also on soil fertility, water holding capacity and depth of soil. The soils on the mobile shelter site and on Great Field have a large water holding capacity throughout the rooting depth, and they contain about 3% organic matter and not less than 25 mg/kg bicarbonate-soluble phosphorus. In a shallower, lighter or less fertile soil, drought may have more sudden or severe effects, as may drought during the germination of the crop, a treatment specifically excluded from the present experiment.

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