J. agric. Sci., Camb. (1981), **96**, 167–186
With 11 *text-figures*
Printed in Great Britain

Growth of spring barley under drought: crop development, photosynthesis, dry-matter accumulation and nutrient content

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(*Received* 24 *July* 1980)

SUMMARY

The effects of water deficit on growth of spring barley were analysed under five irrigation treatments. One crop was irrigated at weekly intervals from emergence throughout the growing season, and one was not irrigated at all after emergence. Soil water deficits in the other treatments were allowed to develop early, intermediate or late in the crop's development.

Weekly irrigation produced a crop with a large leaf area index (maximum value 4) and maintained green leaf and awns throughout the grain-filling period. Early drought decreased leaf area index (maximum value 2) by slowing expansion of main-stem leaves and decreasing the number and growth of tiller leaves. Leaf senescence was also increased with drought. Drought late in the development of ears and leaves and during the grain-filling period caused leaves and awns to senesce so that the total photosynthetic areas decreased faster than with irrigation. Photosynthetic rate per unit leaf area was little affected by drought so total dry-matter production was most affected by differences in leaf area.

Early drought gave fewer tillers ($550/m^2$) and fewer grains per ear (18) than did irrigation (760 tillers/m^2 and 21 grains per ear). Late irrigation after drought increased the number of grains per ear slightly but not the number of ears/m^2. Thus at the start of the grain-filling period crops which had suffered drought early had fewer grains than irrigated ($9{\cdot}5$ and $18{\cdot}8 \times 10^3/m^2$ respectively) or crops which suffered drought later in development ($14 \times 10^3/m^2$).

During the first 2 weeks of filling, grains grew at almost the same rate in all treatments. Current assimilate supply was probably insufficient to provide this growth in crops which had suffered drought, and stem reserves were mobilized, as shown by the decrease in stem mass during the period. Grains filled for 8 days longer with irrigation and were heavier (36–38 mg) than without irrigation (29–30 mg). Drought throughout the grain-filling period after irrigation earlier in the season resulted in the smallest grains (29 mg).

Grain yield depended on the number of ears, the number of grains per ear and mass per grain. Early drought decreased tillering and tiller ear production and the number of grains that filled in each ear. Late drought affected grain size via the effects on photosynthetic surface area.

Drought decreased the concentrations of phosphorus, potassium and magnesium in the dry matter of crops, and irrigation after drought increased them. Concentration of nitrogen was little affected by treatment. Possible mechanisms by which water deficits and nutrient supply affect crop growth and yield are discussed.

INTRODUCTION

The maximum growth and grain yield a barley crop can achieve, its genetic potential, is possible only under optimum but unknown environmental conditions and may be assessed experimentally. In practical agriculture if one or more aspects of a crop's environment deviate from the optimum sufficiently to slow growth and decrease productivity then the crop will have been stressed. This paper concerns the response of barley to drought stress.

There is much information about the growth of spring barley in relation to its environment (Biscoe *et al.* 1975; Rackham, 1972), but analysis of the

0021-8596/81/2828-5060 $01.00

effects of drought is more difficult because in most studies there has been no, or only limited, control of rainfall. Distinguishing drought effects by comparison of growth and yield in different years (Gallagher, Biscoe & Hunter, 1976) is complicated by the differences in other environmental variables between seasons. Empirical relationships between yield and environmental conditions may be of practical importance for management and agronomic purposes (Dyson, 1977), but, as yet, the mechanisms through which environmental changes control crop productivity are little understood quantitatively. A knowledge of the underlying mechanisms involved in growth and production should provide better criteria for predicting yield, and in crop selection and breeding programmes.

In this paper we present results showing the effects of drought at different stages of growth on the development, dry-matter production, photosynthesis and nutrient uptake of spring barley under field conditions. The crop was protected from precipitation by mobile shelters which automatically covered the plots when rain fell (Legg *et al.* 1978). Drought treatments of different durations and at different stages of crop development were produced by withholding irrigation. There were 12 combinations of drought and irrigation: 11 of these had single drought periods, at different times and of different durations, while the 12th was irrigation throughout the season. Growth measurements presented here were made on the crops grown under five of these treatments.

METHODS

Experimental procedures

Use of the mobile rain shelters, the design of the experiment and the treatments applied have been described by Day *et al.* (1978). Each of the five treatments chosen for this study was applied to three plots (3·0 × 4·5 m). Each plot was halved, giving six half plots. Two half plots, in different plots, were sampled for growth analysis, two half plots, from different plots, were used for other measurements (e.g. photosynthesis) and two were used only for the final harvest. Soil water content was measured each week to 1·5 m depth by neutron moderation, on one half of two different plots. Spring barley (*Hordeum distichum* L. cv. Julia) seed was sown at 168 kg/ha in rows 15 cm apart on 31 March 1976 and received 376 kg/ha of fertilizer (20% N; 14% P_2O_5; 14% K_2O). The treatment designations are those used previously (Day *et al.* 1978; Legg *et al.* 1979). Drought was alleviated by applying water (amount determined from neutron moderation measurements) by trickle lines to return the soil to within 20 mm of field capacity at weekly intervals in the appropriate periods. These periods were chosen on the basis of the physiological development of the crop.

The treatments were: treatment 2, unirrigated after emergence until after anthesis; treatment 3, unirrigated (i.e. continuous drought); treatment 5, unirrigated from the middle of spikelet development on the ear, until anthesis; treatment 7, unirrigated from the middle of spikelet development until harvest; treatment 12, irrigated from emergence to final harvest.

The main periods of drought (Day *et al.* 1978) were: period 1 from 28 April to 1 June (approximately the time from differentiation of the first spikelet on the ear to the maximum number of spikelets); period 2, from 2 to 22 June when anthesis occurred, and period 3, 23 June to 21 July, when the crop was almost ripe. Thus the main drought was experienced by treatment 2 during periods 1 and 2, by treatment 3, during periods 1, 2 and 3; by treatment 5, during period 2 and by treatment 7, during periods 2 and 3.

Weather conditions

Temperatures in June and July 1976 were higher than the long-term averages (Table 1): there was more irradiance and a drier atmosphere than usual.

Crop sampling

Sampling design and procedure. After plant emergence, 25 cm lengths of row were marked for

Table 1. *Mean monthly maximum and minimum temperatures and departures from their long-term averages, mean daily radiation and open water evaporation for the period of spring barley growth in* 1976

Month	Temperature (°C) Mean max.*	Mean min.*	Radiation (mWh/cm² day)	Evaporation† (mm/month)
April	12·1 (0·0)	3·1 (−0·1)	369	64
May	17·3 (+1·4)	6·8 (+0·6)	479	90
June	23·7 (+4·8)	10·7 (+1·5)	586	140
July	25·1 (+4·5)	12·0 (+0·9)	533	152

* In brackets: departures from 1878–1975 averages.
† Symons evaporation tank.

sampling, on a pattern designed to minimize the effect of sample removal on the growth of the remaining crop. Emergence was measured for all marked row lengths. Samples of above-ground crop were removed for growth analysis at intervals of 2 weeks giving six harvests (H_1, H_2...H_6) from 10 May until 19 July. Each harvest consisted of the crop from two marked lengths of row per half plot giving 1 m of row from each treatment for analysis. Plants were severed from the roots at the base of the stem. Fresh mass and the number of main stems and tillers were recorded for each sample. The samples for each treatment were then combined and a subsample of one quarter to one half of the total was taken for detailed analysis; a second subsample was used to assess apical development.

Growth analysis. Plants were divided into main stems and those tillers visible outside the leaf bases. Tillers were considered dead if the youngest leaf was visibly yellowed. Main stem and tiller length were measured separately from base to ligule of the youngest leaf or the point of emergence from the leaf sheath. Leaf laminae were removed in order of insertion on the stem, and area measured with an electronic planimeter (Platon Industries, Australia). Ears were separated into awns, grain and rachis plus glumes. Awn area was measured on an image analysing computer (Quantimet, Metals Research, U.K.). Stem length and diameter at half height were measured to calculate stem surface area. All material was dried at 80 °C, and the total dry mass of each component was calculated.

Nutrient analysis. N, P, K and Mg content in the dry matter was measured for all plant parts at each harvest. Total free amino acids in ethanol/water (80% v/v) extracts of ground grain were measured spectrophotometrically. Total amino acids in grain were measured by automatic analyser (Technicon Ltd) after hydrolysis of ground grain in 1·0 N-HCl at 105 °C for 24 h.

Apical development. Apices were removed from 12 main stems in each treatment at each harvest and stored in formalin-acetic-alcohol prior to measurement of length, breadth and number of spikelet initials. Number of grains and distribution of the dried grain mass within the ear were measured from anthesis to ripening on main stems and first tiller ears from each treatment.

Root sampling

At final harvest, three soil cores 3·5 cm diameter and 1·0 m long were taken from the rows in treatments 2, 3, 7 and 12. Cores were divided into 15 cm lengths from the surface to 75 cm depth and then a 25 cm length to 1·0 m, and stored at 4 °C. The roots were washed out (Welbank & Williams, 1968) and their length estimated, using the image analysing computer, from photographs of the fresh roots. Root dry mass was also determined.

Stem and leaf extension

Leaf plus stem or ear plus stem length was measured by graduated rule several times a day, from reference markers in the soil, in the periods 20–29 May and 15–24 June, when the crops were growing rapidly.

Photosynthesis

Gross photosynthesis was measured on eight leaves (leaf 8) in each treatment on 6 days in June and July. Air containing $^{14}CO_2$ (300 μl CO_2/l; specific activity 0·84 μCi/mole) was supplied for 15 or 30 sec using a modified Shimshi (1969) apparatus. Discs were punched from the area of leaf. exposed to $^{14}CO_2$, dried, and radioactivity in them measured by planchette counting, with correction for self-absorption. In addition the photosynthesis of four main stem ears per treatment was measured on six occasions. Ears were exposed to $^{14}CO_2$ (specific activity as above) in a tubular 'perspex' chamber for 30 sec or 3 min. The ears were rapidly frozen, dried and combusted (Packard sample oxidizer); CO_2 produced was absorbed and the ^{14}C determined by scintillation counting. The temperature at which leaves and ears were fed was not controlled but was measured, as was irradiance (with a Kipp solarimeter), at the experimental site.

Soil water deficit and irrigation

Evaporation from the soil surface and from the emerged crops gave a soil water deficit of some 25 mm before the first irrigation. The deficit increased with time (Fig. 1) in treatments 2 and 3 (identical until anthesis, the end of period 2). The deficit for treatments 5, 7 and 12 (identical for the first 3 weeks) was decreased by irrigating each week. Figure 1 also shows that during June and July, even in the irrigated treatments, the hot dry conditions caused large increases in deficit within a week, up to 60 mm for treatment 12. However, with irrigation in this period (treatment 2, 5 and 12) some roots were in well watered soil, of high water potential, for much of the week. Soil water was depleted faster and the final deficit was greater for treatment 7 than for treatment 3, despite the latter being subject to drought for longer. Data for plant and soil water potential are given by Day, Lawlor & Legg (1981).

RESULTS

Plant emergence and tillering

Before 28 April all plots received the same treatment and emergence was uniform with 297 ± 17 plants/m^2 on 3 May. Late emergence increased the

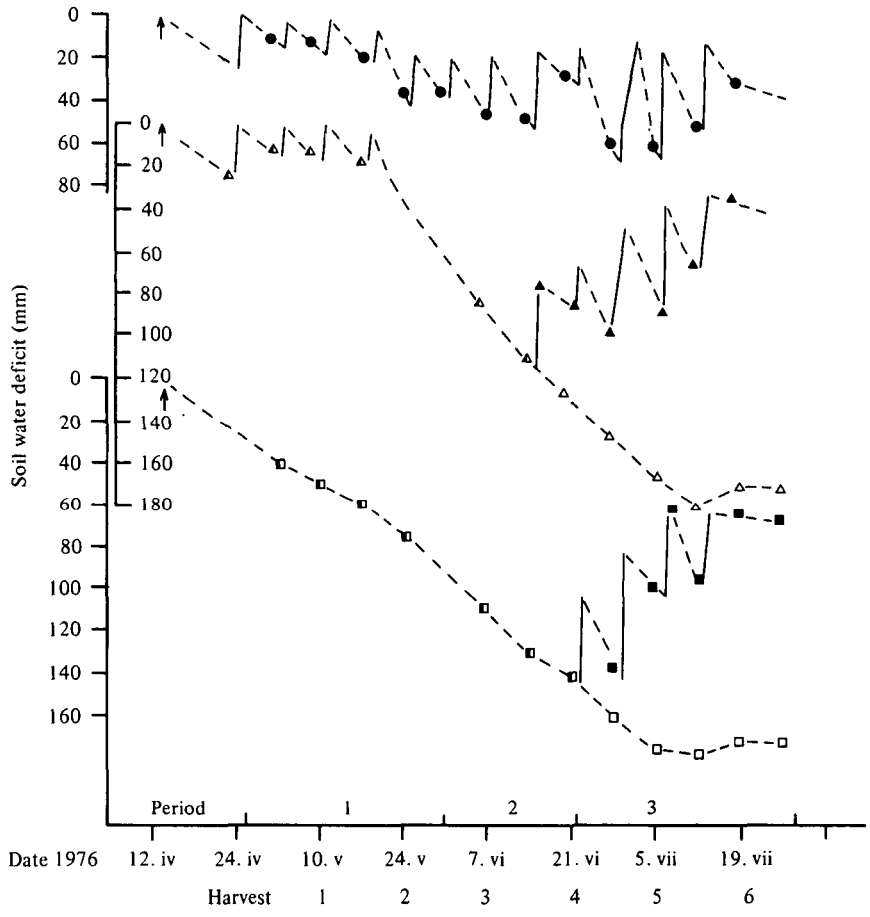

Fig. 1. Times of irrigation and development of soil water deficits under spring barley, using mobile rain shelters, 1976. The dates of growth analysis harvests (H_1–H_6) are given and the main periods (D_1, D_2 and D_3) over which growth and water deficits are compared. For clarity the deficit axes are displaced for different treatments. ●, Treatment 12; ▲, treatment 5; △, treatment 7; ◭, 5 and 7 combined: ■, treatment 2; □, treatment 3; ◧, treatment 2 and 3 combined. —, Irrigation; ---, drying. Arrows denote crop emergence.

number by 5% to 310 ± 21 plants/m², averaged over all treatments and harvests. There was no systematic relationship between emergence and subsequent treatment.

Irrigation produced more tillers; 4·0 per plant in treatments 5, 7 and 12 compared with 2·3 in treatments 2 and 3 (Fig. 2*a*). As the number of plants was constant, there were more stems/m² with irrigation than without. The number of tillers reached a maximum in late May with irrigation and about 2 weeks later without; it then decreased to a minimum at H_4 for both treatments. Many tillers died in all treatments; drought after irrigation (treatment 7) gave the same number of tillers as treatment 3 by H_4. A relatively brief drought (treatment 5) did not have this effect and almost as many tillers survived as in treatment 12. Some late tillering occurred in all treatments: these tillers only grew to any size with late irrigation (treatments 2, 5 and 12) and contributed to total dry matter but not grain yield.

Stem and leaf extension

Stems grew longer (Fig. 2*b*) and had a greater surface area (Fig. 2*c*) with irrigation than with drought. As drought developed in treatments 5 and 7, stem length and area were decreased; rewatering stimulated growth of plants only slightly (treatments 2 and 5).

The increase of stem and leaf length in May, and of stem and ear length in June (Fig. 3) was greater with irrigation than without. In late May there was

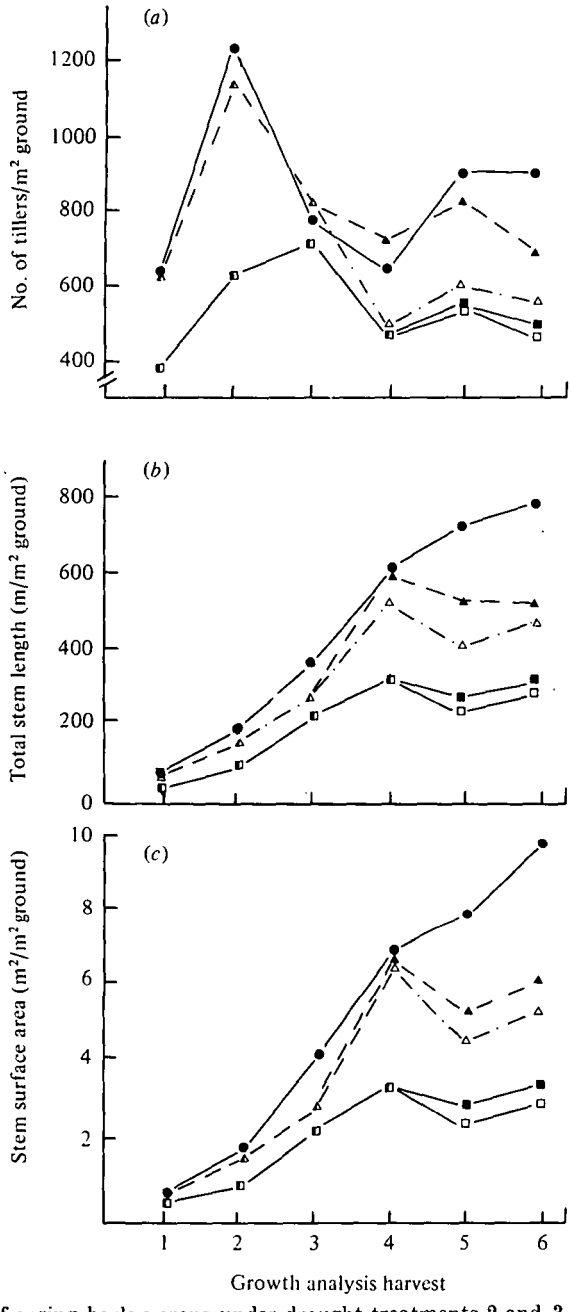

Fig. 2. Growth of spring barley crops under drought treatments 2 and 3 combined (◧), 2 (■), 3 (□), 5 and 7 combined (◭), 5 (▲), 7 (△), and 12 (●). (*a*) Number of tillers/m² ground; (*b*) total length of stem/m² ground: (*c*) total area of exposed stem and leaf sheaths/m² ground.

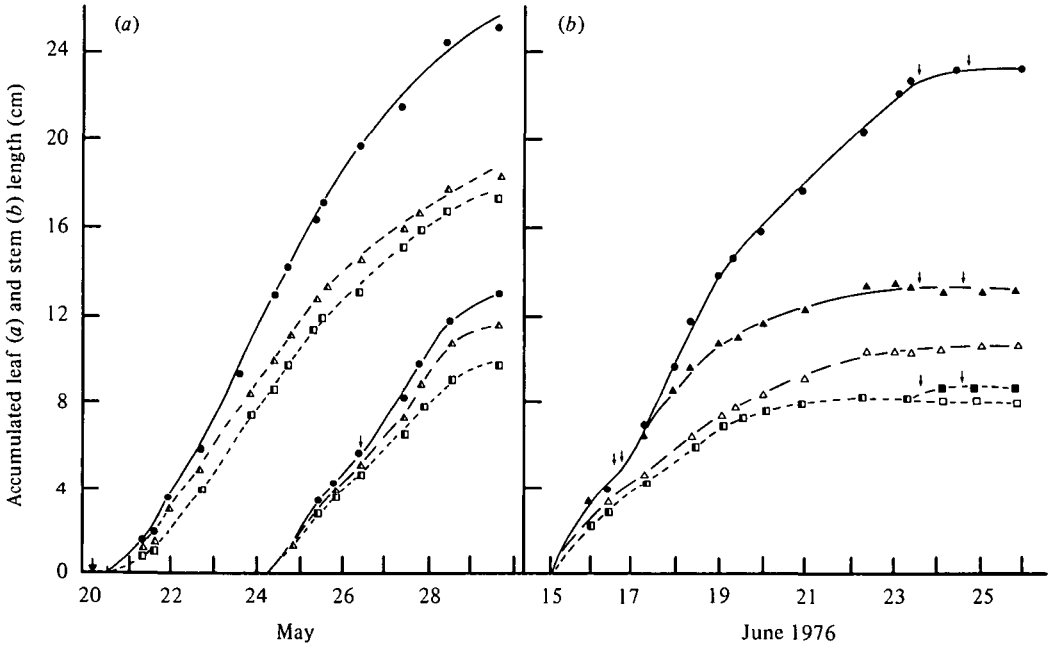

Fig. 3. Accumulated length of spring barley leaves (*a*) and total plant height (*b*) in treatments 12 (●); 5 (▲), 7 (△); 5 and 7 combined (◭); 2 (■); 3 (□) and 2 and 3 combined (◧). In (*a*) upper three curves the fifth oldest leaf, the lower three curves the sixth leaf. Arrows denote irrigation for the treatment.

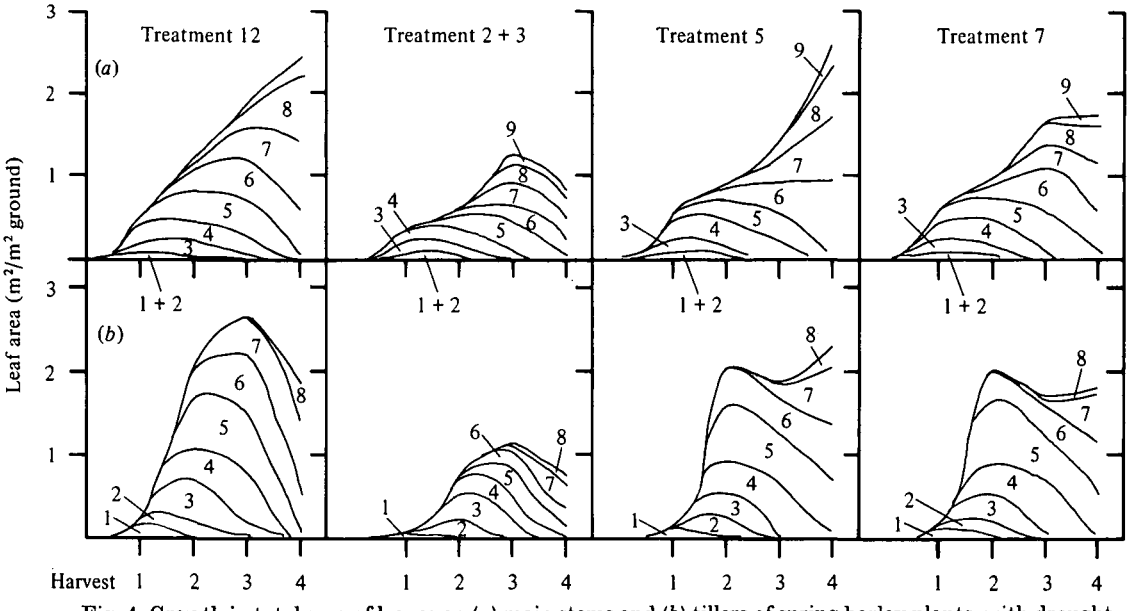

Fig. 4. Growth in total area of leaves on (*a*) main stems and (*b*) tillers of spring barley plants, with drought treatments and harvest. Leaf insertion 1, the oldest leaf: 9 the youngest.

little difference between treatment 7 and treatment 3, even though treatment 7 had received 3 weeks' irrigation in early May. In late June stems and ears of plants in treatment 12 grew faster and for some 3 days longer than did those of plants in other treatments. Re-watering after 5 weeks' drought stimulated extension growth (compare treatments 5 and 7), but did not stimulate them to grow as fast as the fully irrigated plants (treatment 12). Extension growth ceased earlier for plants without water since emergence (treatments 2 and 3) than for those which were watered in the early part of the growing season (treatment 7). Late irrigation in treatment 2 did not stimulate growth, as the crop was starting to mature.

Leaf area

Total leaf area is a function of number of stems, number of leaves per stem, and area per leaf. Figure 4 shows that for main stems drought decreased individual leaf size, and hastened senescence, as it did for tillers, where the number of surviving stems was also affected by drought (see above).

Number of leaves and area per leaf. Drought did not influence the time at which main-stem leaves appeared nor their number per live stem. However, there were fewer tiller leaves produced by crops which suffered drought and their rate of appearance was slowed.

Areas of all individual leaves present at H_4 were much smaller after prolonged drought than with full irrigation (Table 2). A short period of drought (treatments 5 and 7) decreased growth of all leaves except main-stem leaf 5. Re-watering plants after drought (treatment 5), during final expansion of the flag leaf, did permit some further growth but not to the same size as the flag leaf in treatment 12.

Leaf senescence. The oldest leaves, 1–3, died by H_3 in all treatments. The remaining older leaves survived longer in irrigated crops than in unirrigated (Fig. 4). The leaf area lost by H_3 was estimated for each treatment from the mass of dead leaf and the ratio of leaf area to dry mass. As a proportion of the total leaf area produced, losses were: treatment 12, 14%, treatments 5 and 7, 28%, treatments 2 and 3, 40%.

Total leaf area. Even slight drought greatly decreased leaf area by slowing early growth and causing earlier senescence. By H_1 unirrigated crops had 40% less leaf than irrigated, and by H_2 54% less (Fig. 5*a*). Maximum leaf area for treatments 12, 2 and 3 was reached at H_3 and for the others at H_4. All crops which were unirrigated at H_4 had little leaf then. Irrigation after drought (treatments 2 and 5) and weekly irrigation (treatment 12) kept the leaves green longer but by H_6 even irrigated treatments had only a few green leaves. Thus drought caused large differences in leaf area during grain growth.

The relative contribution of main-stem and tiller leaves to the total leaf area depended on the treatment (Fig. 4). Tiller leaf area was 24% of the total area for irrigated but 13% for the unirrigated crops respectively at H_1; at H_3, the proportion was similar in both.

Relative growth rate of leaf area. Errors in determining leaf area precluded accurate estimations of relative growth rates. Differences between treatments were small (Fig. 5*b*); drought slowed the rate initially and caused the fastest loss of leaf area (most negative relative growth rates) later in the season in treatments 3 and 7.

Awn area

Total projected area of awns was largest with weekly irrigation (treatment 12) and smallest with prolonged drought (treatments 2 and 3), particularly at H_6 when awns were dying (Fig. 5*c*). Awns contributed a large part of the photosynthetic

Table 2. *Area of laminae (cm²/leaf) of leaves of different insertion from main stems (MS) and tillers (T) at H_4* (21 June)

Leaf insertion		Treatment number 2+3	5	7	12
5	MS	4·4	7·8	7·8	8·1
	T	—	6·5	6·5	8·9
6	MS	7·5	15·8	15·5	16·8
	T	6·2	12·8	12·1	13·9
7	MS	9·9	16·5	16·5	21·5
	T	8·4	15·0	13·1	16·2
8	MS	8·2	13·6	13·0	18·1
	T	6·9	11·6	10·9	13·8
9 (flag leaf)	MS	2·5	4·5	3·7	6·4
	T	2·2	3·9	3·3	4·4

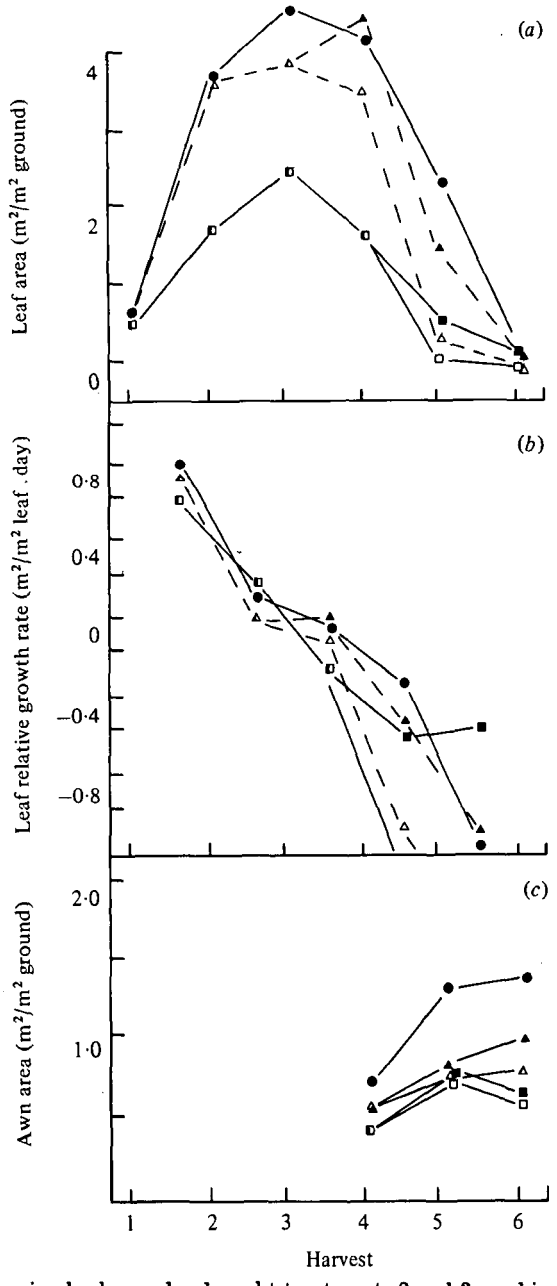

Fig. 5. Growth of spring barley under drought treatments 2 and 3 combined (◧), 2 (■), 3 (□), 5 and 7 combined (◭), 5 (■), 7 (△), and 12 (●). (*a*) Total leaf area of the crop (m^2/m^2 ground); (*b*) relative growth rate of leaf area calculated for the periods between growth analysis harvests (per day); (*c*) total projected area of awns (m^2/m^2 ground).

Table 3. *Length of main-stem apices (L, mm) (± S.E.) and number of floral initials (I) or grains (G) at each growth analysis harvest*

		Treatment number				
		2	3	5	7	12
Harvest						
1	L	0·7 ± 0·1		0·8 ± 0·1		
	I	12 ± 1		14 ± 2		
2	L	2·8 ± 0·2		3·2 ± 0·2		3·4 ± 0·2
	I	32 ± 3		33 ± 2		33 ± 1
3	L	26·6 ± 0·5		25·9 ± 3·4		22·6 ± 2·3
	I	27 ± 1		28 ± 1		29 ± 1
4	L	77 ± 10		83 ± 8	79 ± 11	76 ± 7
	I	—		—	—	—
5	L	64 ± 1	66 ± 8	72 ± 9	70 ± 6	74 ± 8
	G	19 ± 1	21 ± 1	21 ± 2	23 ± 1	24 ± 1
6	L	58 ± 2	60 ± 5	70 ± 4	71 ± 8	71 ± 5
	G	18 ± 1	17 ± 1	21 ± 1	20 ± 1	22 ± 1
Final harvest (main stem + tillers)	G	15	16	17	17	21

Table 4. *Green leaf dry matter as a percentage of total above-ground dry matter*

	Treatment number				
	2	3	5	7	12
Harvest					
1	57		72		
2	59		59		55
3	30		39		39
4	14		18	16	19
5	5	1	7	3	8

Table 5. *Dry matter per unit leaf area (mg/cm²) for main stem leaves from 4 (oldest) to 9 (youngest)*

		Treatment number		
Harvest	Leaf	2 and 3	5 and 7	12
1	4	4·1	4·0	
	5	4·1	3·7	
2	5	4·5	4·3	4·0
	6	4·3	4·1	3·8
3	6	4·7	4·2	3·6
	7	5·0	3·8	3·3
	8	5·2	3·8	3·8
4	7	4·4	3·6	3·3
	8	4·6	3·9	3·6
	9 (flag)	5·4	4·5	3·9

surface in all crops during the grain-filling period (compare Figs 5*a* and 5*c*) particularly for the unirrigated crops. At H_5 the proportion of the total photosynthetic surface area provided by the awns in crops receiving irrigation was: treatment 12, 36%; treatment 5, 33%; treatment 2, 62%. For unirrigated treatments the proportion was: treatment 3, 88%; treatment 7, 63%. Awns remained green for longer with irrigation than without, although irrigation after prolonged drought (treatment 2) did not significantly increase awn life.

Apical development and number of grains

Main-stem apices were differentiating at H_1, with well developed double ridges in all treatments. Early drought gave shorter apices, with fewer initials or spikelets (Table 3) than for irrigated plants, but in all treatments more initials were formed than survived to produce grain.

The numbers of grains per ear at final harvest (Table 3) were 10% less than at H_6, probably because the tiller ears, which were included at final harvest, contained fewer grains per ear. Treatments 2 and 3 produced fewer grains per ear than treatments 5 and 7, and treatment 12 had most. In treatments 3 and 7, fewer grains set at the base and considerably fewer at the tip of the ear, but all central grains developed.

Photosynthesis

Gross photosynthetic rate of leaves increased with irradiance, and the light compensation point was close to zero. On one occasion only was the photosynthesis rate, at equivalent irradiance, much smaller with drought than with full irrigation. This was for treatment 7 on June 24, after anthesis, when the leaves were senescing rapidly. Smaller differences between treatments were correlated with increased stomatal resistance on unirrigated crops (Day *et al.* 1981) but there was little correlation with soil water deficit or plant water potential. Photosynthesis by ears was little affected by light intensity, but measurements were only made at high light intensity. Differences in photosynthesis correlated with the stomatal resistance measured for the awns (Day *et al.* 1981).

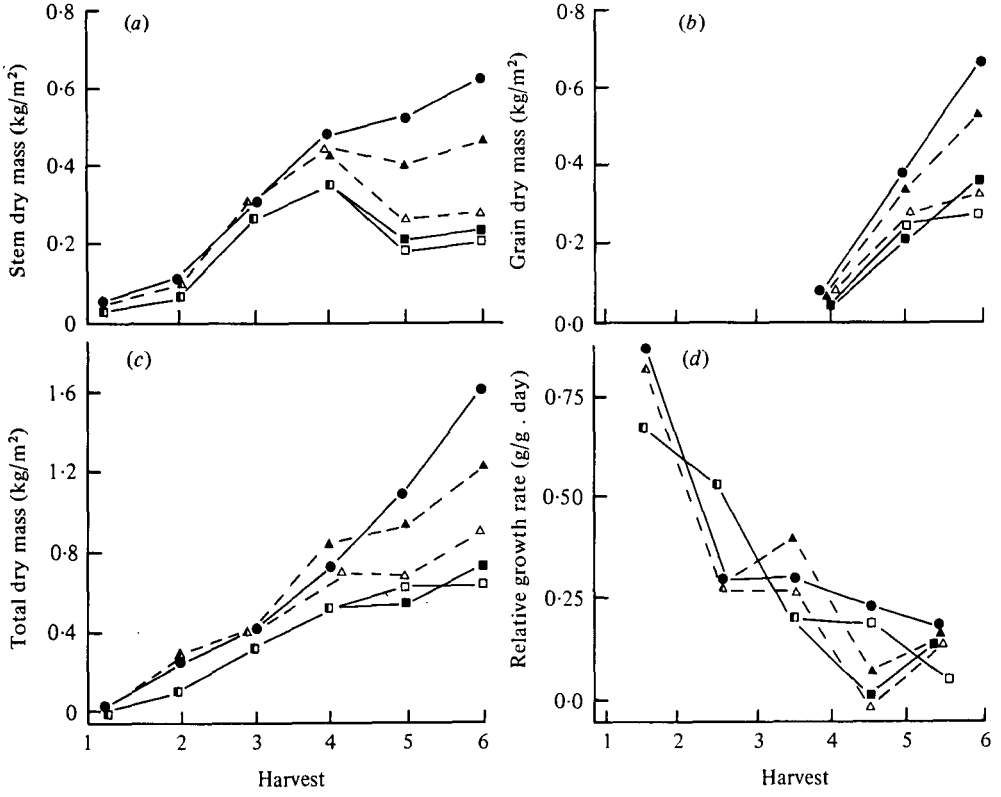

Fig. 6. Dry-matter accumulation of spring barley under drought treatments 2 and 3 combined (◧), 2 (■), 3 (□), 5 and 7 combined (◭), 5 (▲), 7 (△) and 12 (●). (*a*) Total stem dry mass (kg/m²); (*b*) grain dry matter (kg/m²) from H_4 to H_6; (*c*) total dry matter of aerial part of the crop (kg/m²), (*d*) relative growth rate of dry matter in crops for the 2 weekly periods between growth analysis harvests.

Leaf and stem dry matter

Total green leaf dry matter increased to a maximum at H_3 and decreased thereafter, as did leaf area. The proportion of the total dry matter in leaves (Table 4) decreased with age and with drought. Irrigated crops had appreciably less dry matter per unit leaf area than unirrigated (Table 5), whilst younger leaves tended to have more dry matter per unit area than did older leaves.

For irrigated plants (treatment 12) total stem dry matter increased between each harvest from H_1 to H_6 (Fig. 6*a*). Prolonged drought (treatments 2 and 3) slowed accumulation of dry matter in the stems, which grew until H_4 and then lost mass. This loss was little affected by late irrigation (treatment 2). Stems in treatment 7 also lost mass between H_4 and H_5.

The proportion of total dry matter in tillers increased from about 25% at H_1 to 56% at H_2 in treatment 12, and from 15% at H_1 to 48% at H_3 in treatments 2 and 3 (Table 6). The results suggest that tillers are more sensitive to late drought than are main stems (compare the contribution of tiller dry matter to total dry matter at H_3 and H_4 for treatments 5 and 7).

Root dry matter

At final harvest the amounts of root extracted to 1·0 m depth were 67, 81, 62 and 68 g/m² ground surface in treatments 12, 7, 3, and 2 respectively. Deeper roots, which crop water extraction measurements suggest extended to 1·5 m (Day *et al.* 1978), were not measured. The proportion of root to above-ground dry matter at final harvest was 5%, 10%, 11% and 10% in treatments 12, 7, 3 and 2 respectively. Other estimates of this ratio are about 10% (Welbank & Williams, 1968); the small value for treatment 12 was because of greater shoot production. Root distribution and soil water potential are discussed by Day *et al.* (1981).

Grain dry matter

Dry mass of grain per unit ground area increased almost linearly between H_4 and H_6 where irrigation was given, but did not increase after H_5 where water was not applied (Fig. 6*b*). Within each treatment, the number of grains per unit area was almost constant during the grain-filling period. The rate of dry-matter accumulation per grain (Table 7) was similar between H_4 and H_5 for all treatments. At H_5 treatment 3 had the heaviest grains and treatment 7 the lightest. Between H_5 and H_6 there was little grain growth with treatment 3 and the rate with treatment 7 was only half that with the irrigated treatments 2, 5 and 12 which had similar rates of filling. Irrigated crops filled grains for longer than did unirrigated. The mean grain mass on all treatments at H_6 was similar to that at final harvest, and was larger for irrigated than for un-

Table 6. *Dry matter in tillers as a percentage of the total dry matter (g/g) from plants grown under different drought treatments*

	Treatment			
Harvest	2+3	5	7	12
1	15	25		
2	42	52		56
3	48	53		48
4	47	52	48	56

Table 7. *Grain size of spring barley, from different drought treatments, measured on three occasions during grain growth, and the rates of grain dry-matter accumulation for* 14 *days* (H_4–H_5) *and* 14 *to* 28 *days* (H_5–H_6) *after the start of filling*

		Treatment				
	Harvest	2	3	5	7	12
Number of grains (1000/m²)	5	9·5	9·5	14·6	13·3	18·8
Grain mass (mg)	5	18·3	22·3	19·9	15·8	18·3
	6	37·0	29·6	37·9	27·5	36·8
	Final harvest	37·2	30·2	37·8	29·1	35·5
Rate of grain filling (mg/grain day)	4–5	1·31	1·50	1·41	1·10	1·30
	5–6	0·97	0·15	0·97	0·51	

irrigated treatments. Detailed analysis of grains from main-stem ears (Fig. 7) showed that grain filling lasted 7 to 9 days longer with irrigation (treatments 2, 5 and 12) than with drought (treatments 3 and 7): grain mass may have decreased in treatment 12 after reaching its maximum.

The distribution of grain mass within main-stem ears was measured just before H_6. The mass of individual grains was smaller with drought (treatment 3) particularly at the base and tip of the ear (Fig. 8). There were more large and small grains at final harvest for crops irrigated during the grain-filling period than for those unirrigated; 16% of grain in treatment 12 was heavier than 45 mg and 9% lighter than 15 mg, whilst in treatment 3 only 2% of the grains were heavier than 45 mg or

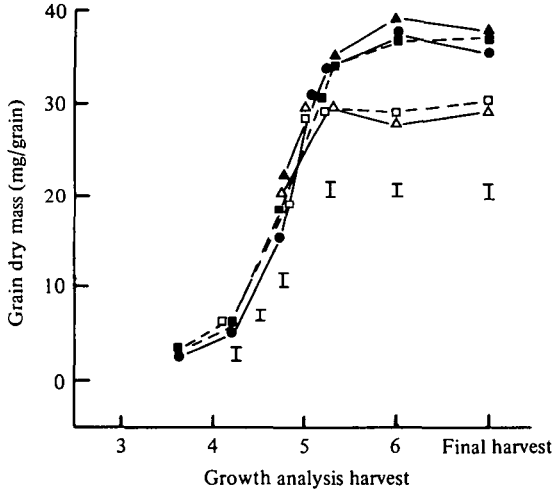

Fig. 7. Growth of grain dry mass, averaged over all grains in main-stem ears, for spring barley crops subjected to drought treatments 2 (■), 3 (□), 5 (▲), 7 (△), 12 (●). I represents the least significant difference (P = 0·05) between means.

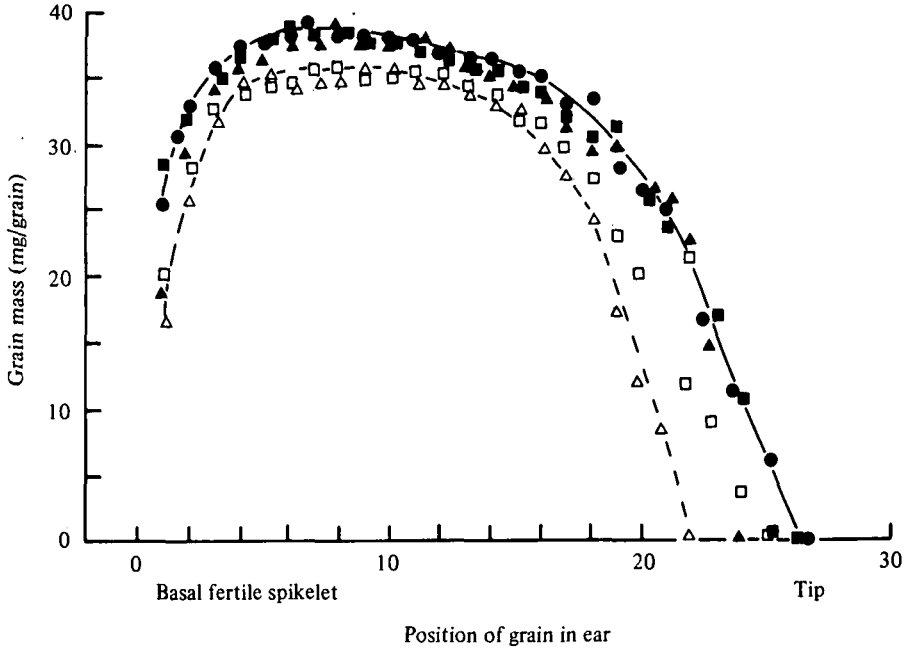

Fig. 8. Mass of individual grains, with position in the ear, for spring barley grown under drought treatments 2 (■), 3 (□), 5 (▲), 7 (△), 12 (●).

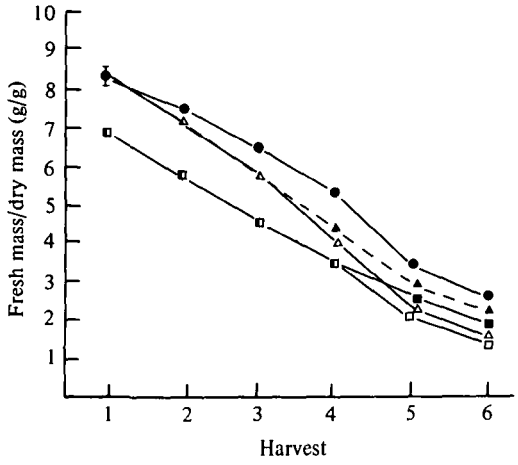

Fig. 9. Ratio of fresh mass to dry mass of the above-ground parts of crops of spring barley grown under drought treatments 2 and 3 combined (◧), 2 (■), 3 (□), 5 and 7 combined (◭), 5 (▲), 7 (△), 12 (●).

lighter than 15 mg. A somewhat greater proportion of grain was in the 25–35 mg/grain range in treatments 3 and 7 than in 2, 5 or 12. The proportion of light grains at final harvest may be underestimated as some light grain is carried over with straw during threshing.

Total dry matter and relative growth rate

Dry matter accumulated faster with irrigation than without, so there was more dry matter at all harvests with full irrigation. Differences in dry matter were small until H_3 but were considerable by the end of the season (Fig. 6*c*).

Root mass is not included in the total dry matter nor in calculating relative growth rates because of difficulties in extracting the roots, poor replication and their small contribution to crop dry matter.

The relative growth rate of dry matter (RGR = $(1/m)\ \Delta m/\Delta t$, where m is the above-ground crop dry mass, and Δt is the time interval for the change in mass Δm) decreased with time in all treatments (Fig. 6*d*), but did not differ between treatments.

Water content

Drought decreased not only the fresh mass of crops but also their percentage water content (Fig. 9). The water content of the above-ground crop declined with time, but the rate of decline was slower with irrigation after drought. The larger water content in irrigated crops was caused, in part, by more leaves relative to stems and more young tillers relative to old and dead tillers. Short-term (diurnal) fluctuations in water content were unimportant, for leaf relative water content was as large in unirrigated as in irrigated crops (Day *et al.* 1981).

Nutrient content

For each harvest, the percentage N, P, K and Mg in total dry matter, averaged for all above-ground parts of the crops, is shown for each treatment in Fig. 10. The nutrient concentration and amount per grain for final harvest grain samples is given in Table 8.

Nitrogen. Nitrogen concentration decreased from H_1 to H_4 and was constant thereafter (Fig. 10*a*). Leaves had a larger N concentration than stems, and tiller stems a larger concentration than main stems, probably as a result of a larger proportion of structural material in stems and older tissues. There were no significant differences ($P > 0{\cdot}05$) between treatments for any organ or harvest. Final harvest grain contained a mean of 2·3% N, with treatment 12 having the smallest and treatment 7 the largest concentration (Table 8) (for further data on nutrient content of the crop at final harvest, see Day *et al.* 1978). Hence the amount of N per grain was greatest in the biggest grain (0·91 mg N/35·5 mg grain) and least in the smallest grain (0·73 mg/29 mg grain).

The proportion, by mass, of amino acids in hydrolysed grain samples was not modified by drought treatment, and only average values of all treatments are given (Table 9). Free amino nitrogen in the grain was only 2% of the total hydrolysate amino N and was also unaffected by drought.

Phosphorus. Concentration of phosphorus decreased as the crops aged, reached a minimum at H_4 and increased towards final harvest in irrigated treatments (Fig. 10*b*). At H_1 unirrigated crops (treatments 2 and 3) contained almost 20% less P than irrigated (treatments 5, 7 and 12) and the

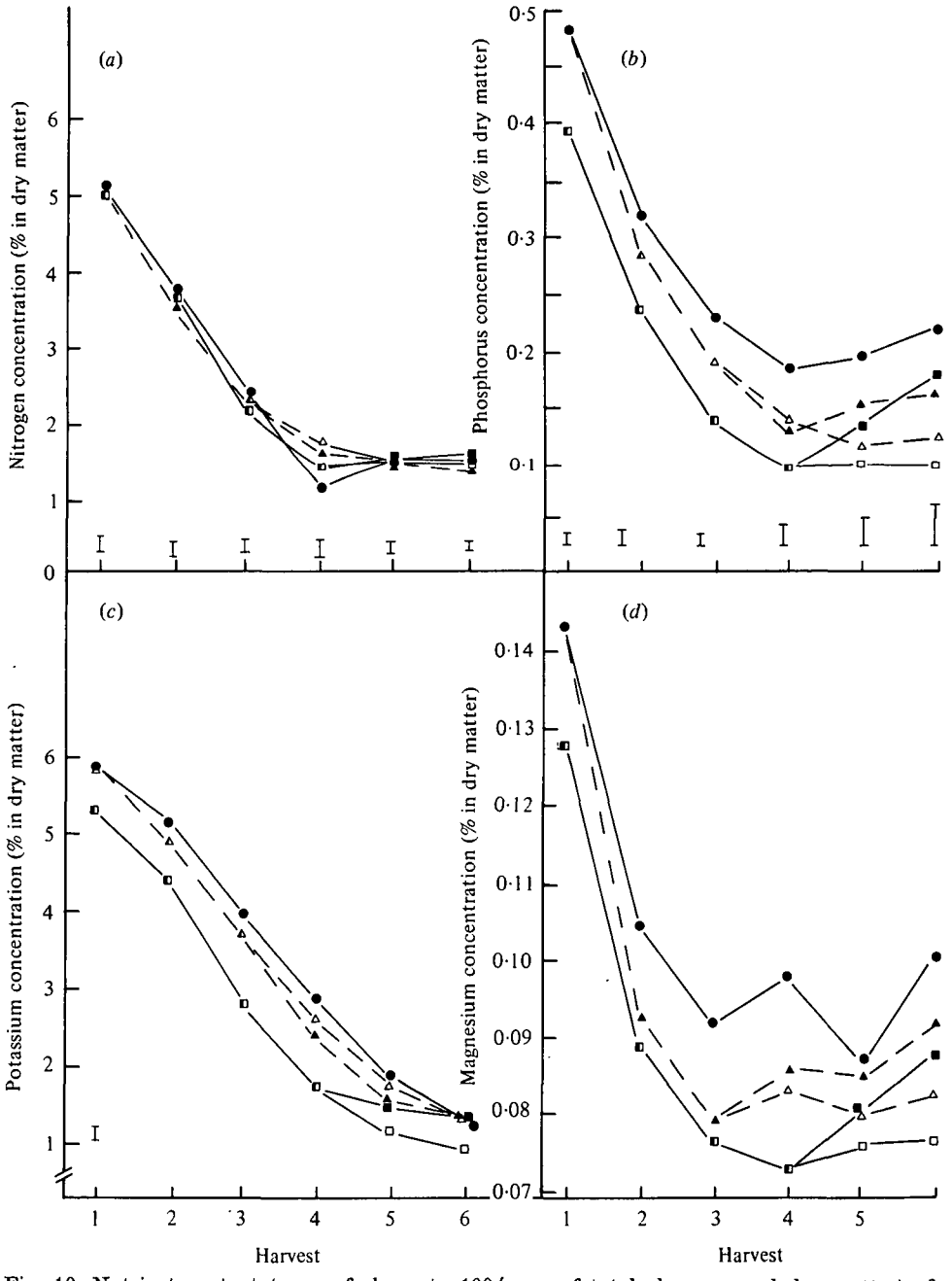

Fig. 10. Nutrient content (mass of element × 100/mass of total above-ground dry matter) of spring barley crops grown under drought treatments 2 and 3 combined (◧), 2 (■), 3 (□), 5 and 7 combined (◭), 5 (▲), 7 (△), 12 (●). I represents least significant difference ($P = 0{\cdot}05$). (*a*) Nitrogen, (*b*) phosphorus, (*c*) potassium, and (*d*) magnesium.

Table 8. *Nutrient content (% of dry matter) of final harvest grain samples and amount of nutrient per grain (mg/grain)*

	Treatment number					L.S.D.
	2	3	5	7	12	($P = 0.05$)
Nitrogen %	2·43	2·41	2·35	2·46	2·26	0·10
mg/grain	0·89	0·73	0·91	0·76	0·80	
Phosphorus %	0·38	0·23	0·38	0·24	0·41	0·04
mg/grain	0·14	0·07	0·15	0·07	0·14	
Potassium %	0·63	0·54	0·58	0·52	0·62	0·08
mg/grain	0·23	0·17	0·23	0·16	0·22	
Magnesium %	0·12	0·10	0·12	0·10	0·12	0·01
mg/grain	0·04	0·03	0·05	0·03	0·04	

Table 9. *Percentage distribution by mass, of amino acids in grain from spring barley averaged over drought treatments (± pooled standard deviations)*

Aspartic acid	5·0 ± 0·3
Threonine	3·4 ± 0·6
Serine	3·4 ± 0·3
Glutamate	27·2 ± 2·4
Proline	12·7 ± 1·1
Glycine	3·4 ± 0·5
Alanine	4·5 ± 0·6
Cystine	0·8 ± 0·7
Valine	5·9 ± 0·3
Methionine	1·3 ± 0·6
Isoleucine	4·4 ± 0·3
Leucine	7·3 ± 0·6
Tyrosine	3·0 ± 0·2
Phenylalanine	5·3 ± 0·8
Histamine	2·5 ± 0·5
Lysine	3·4 ± 0·5
Ammonia	1·3 ± 0·3
Arginine	5·2 ± 6·7

differences persisted. Drought after irrigation (treatments 5 and 7) decreased the P concentration, but not to so small a value as for prolonged drought. Irrigation after drought (treatments 2 and 5) greatly increased the P concentration. Leaves contained a greater proportion of P than stems, and tiller stems slightly more than main stems. At H_6 and final harvest (Table 8) there was little more than half the concentration and amount of P in grain from treatments 3 and 7 than treatment 12: straw also contained less P.

Potassium. Concentration of K decreased with time in all treatments and was lowest for the prolonged-drought treatment. Late drought (treatment 7) did not decrease the concentration as much as continuous drought. Irrigation after prolonged drought (treatment 2) checked the fall in K concentration, and, at H_6 only treatment 3 had a lower K concentration than the fully irrigated treatment. Grain from irrigated crops had a larger K concentration and amount per grain at H_6 and final harvest than did grain from unirrigated crops (Table 8); straw also had a larger K concentration with irrigation.

Magnesium. With all treatments the concentration of Mg decreased with time up to H_3 and there was less Mg where water was not applied (Fig. 10*d*). Leaves and ears had a larger concentration than stems. Grains from treatments 3 and 7, unirrigated during grain filling, had a smaller concentration of Mg and amount per grain than with irrigation (Table 8), but Mg concentration in straw was less affected by drought than was that of grain.

DISCUSSION

Quantifying drought

Soil water deficit and potential. There is no completely satisfactory method of quantifying drought. Water deficit, given here, shows the amount of water removed to a depth of 1·5 m, i.e. from most of the rooting zone. However, there is no unique correlation between water deficit and plant growth (Gardner, 1965) because the relationship between growth and water deficit will depend on the depth and density of the root system and soil type. Soils differ in water-holding capacity, and in the relationships between water potential, hydraulic conductivity and water content. Also both potential and conductivity decrease greatly as the soil dries (Gardner, 1965). In addition, the water balance of crops depends on the rate of transpiration. Thus a small water deficit may have a large effect on plants with poorly developed root systems, particularly if water loss is rapid and the soil shallow. Conversely a large deficit may have little effect on crop growth if water at high potential is available to some roots.

Soil water potentials at the sites of water ex-

traction may more accurately relate to the stress experienced by the plant, but they are difficult to measure and to integrate over the root system.

In this experiment, deficits were allowed to develop in three periods, corresponding to (1) growth of main-stem tillers and leaf area, (2) ear growth to anthesis, and (3) grain filling and early ripening. The deficits were greater the later and longer they were allowed to develop, and comparison of drought effects in different periods cannot be made at a given soil water deficit.

Plant water content and potential. Plant water potential often correlates closely with plant growth in short-term stress experiments under controlled conditions (Lawlor, 1972). In the field, changes in plant water potential are due to the diurnal variation of evaporation rate, as well as to changes in soil water potential. For example, in late May the leaf water potential of irrigated crops in this experiment decreased rapidly from close to zero at dawn to about -12 bar for much of the day, and increased again during the night. In crops suffering drought leaf water potential changed similarly but was generally 2–4 bar lower. The problems of how, where and when to measure water potential in the plant and of integrating it throughout growth have yet to be solved.

The relative water content of leaves in this experiment was close to 100%, even in unirrigated crops, so that leaf cells were not suffering obvious water deficiency (Day *et al.* 1981). The smaller water content and larger dry matter per unit area of leaf (specific leaf mass) observed in the unirrigated crops were probably due to smaller cells with relatively thicker walls and smaller vacuoles (Hsiao, 1973). Drought treatments in our experiments had little effect on the osmotic potential of the cell sap but turgor was smaller (Day *et al.* 1981).

Here we relate growth to soil water deficit and give typical plant and soil water potentials to illustrate the effects of stress treatments, though aware of the limitations discussed above.

Drought and nutrient concentration of crops

The effect of the drought treatments on nutrient concentration at final harvest have been discussed by Day *et al.* (1978). Here the trends with time and the effects of treatment are considered.

The concentration of N, P, K and Mg in the irrigated crop (treatment 12) decreased as the plants grew and accumulated more structural and storage material of low nutrient concentration. Nitrogen concentration remained almost constant after H_4 whereas potassium decreased and phosphorus and magnesium increased. Dry matter increased throughout growth and nitrogen was accumulated in proportion, whereas potassium was accumulated at a slower rate and phosphorus and magnesium at a higher rate after H_4. Changes in concentration are complex as the proportion of leaf, stem and grain alters with age, and nutrients are remobilized and translocated.

Drought had little effect on nitrogen concentration of the crop throughout the season, or on the concentration in grain or straw at final harvest (Day *et al.* 1978). The soil was well supplied with nitrogen and as the nitrogen concentration in the dry matter was not affected by drought, it would appear that N was not limiting (Day *et al.* 1978).

Phosphorus, potassium and magnesium concentrations decreased with drought, as absorption lagged behind dry-matter accumulation. Early drought decreased phosphorus concentrations by 20% at H_1 and the effect persisted; smaller effects were observed on potassium and magnesium concentrations. Phosphorus in the soil was probably sufficient for growth of the irrigated crop, as similar crops did not respond to added P fertilizers. However, in dry soil, particularly the top 30 cm where fertilizer was applied, the combined effects of decreased fertilizer solubility, reduced mass flow of water, less root production and poorer contact between soil and root, restricted P supply (Day *et al.* 1978). Irrigation after drought only partially offset the drought effects.

The low concentrations of phosphorus in the unirrigated crops were probably limiting growth, but this would not be distinguishable from the direct effects of water deficit. Indirect evidence suggests (Day *et al.* 1978) that potassium and magnesium were probably not the primary limitations to growth.

Early drought: effects of tiller growth and grain development

Roots of spring-sown cereals are produced mostly during period 1. They proliferate mainly in the top 20 cm of soil, with less than 1% reaching 1·5 m depth at maturity (Welbank, 1974). In our experiment where no drought treatments were applied until after emergence, roots of the unirrigated crops were growing in soils rapidly drying by evaporation from the soil surface and from the plants. Thus the early check to growth was probably because the deeper roots did not proliferate fast enough to obtain sufficient water to compensate for the diminishing supply from the top soil. At H_1 there was a 50 mm deficit in the unirrigated plots while those which were watered had a maximum deficit of 30 mm just prior to irrigation; minimum soil water potentials at 15 cm depth were about $-1·0$ bar and $-0·5$ bar respectively. By H_2 near the end of period 1, soil water potential had decreased with continuous drought to $-2·0$ bar at 15 cm, whereas in irrigated soil the minimum potential was $-0·5$ bar at that depth.

Drought in period 1 was important for tillering; by H_2 when the soil water deficit under treatment 3 was 60 mm, there were only half the number of tillers, and they were smaller than those on irrigated plots. During period 2 the deficit increased to 140 mm, and the soil water potential at 20 cm fell to −12 bar in the unirrigated treatment. Tillers died in this period on all treatments. By final harvest there were only 0·7 ears per plant after continuous drought (treatment 3) whereas full irrigation gave 1·6 ears per plant.

Regression of number of ears per unit ground area on mean deficit in period 1 (Day *et al.* 1978) accounted for 25% of the variance in number of ears whereas the deficit in period 2, i.e. during the phase of tiller death, accounted for 62% of the variance. Regression analysis also showed that the final number of grains per ear was most dependent on mean soil water deficit in the period of flower spike and grain primordia development, i.e. period 1. Most of the grain primordia which contributed to crop yield were formed by the end of period 1, although more primordia were formed than eventually filled (Gallagher, Biscoe & Scott, 1976). Death of primordia during period 2 was little affected by soil water deficit at that time. Conditions during period 1 may have determined the ability of primordia to develop and survive drought in period 2. The effect of drought on grain that did develop was not uniform throughout the ear. Grains at the tip and the base of the ear died or grew less, whilst the central grains were little affected, suggesting a complex response of grain development and assimilate distribution to grains. The combined effect of drought in periods 1 and 2 was to give crops with fewer ears and fewer grains per ear than with irrigation. The effects of drought on barley have often been studied (Husain & Aspinall, 1970) but the mechanisms by which water deficits modify the production, growth and death of tillers and grain primordia are not understood. Competition for assimilates and nutrients between main stems, tillers and roots or between developing grains in the ear, is important (Spiertz 1978); in this experiment, phosphorus was at a low concentration in unirrigated crops (Day *et al.* 1978) and this may have contributed to decreased growth. The observed variation in number of tillers shows that the biomass distribution in the crop alters when under stress. The ability of barley to produce many tillers, and their sensitivity to stress, enables this crop to adapt to a wide range of climatic conditions.

Straw yield depends on tillering and the growth of the stems, so it was most affected by drought during periods 1 and 2 (Day *et al.* 1978). Some of the straw in the irrigated crops was accumulated in period 3; it derived from late tillering and contributed nothing to grain yield and delayed harvest. The tendency for excessive vegetative growth is often observed with irrigation (Salter & Goode, 1967) and/or abundant nitrogen (Thorne, 1974).

Effect of drought on the photosynthetic surface

Growth of leaves and stems was greatly decreased by drought at any time; for example, by H_1 there was 40% less leaf area and 20% fewer tillers on unirrigated plots than those on irrigated. The time of main-stem leaf emergence was not affected by stress, suggesting that in this experiment leaf primordium initiation and development was insensitive to drought. This was not so for tillers. Their rate of emergence was slowed by stress, resulting in fewer tiller leaves, which, together with decreased leaf size, reduced their contribution to the total leaf area. The rate of leaf expansion in unwatered crops was always less than that in the watered, and as width as well as length was affected, the total leaf area was very sensitive to water deficit.

As leaf growth had almost stopped by anthesis, relieving drought then had little effect on total leaf area. Leaf senescence began earlier on unirrigated crops, and this greatly affected green leaf area in the grain-filling period.

Awn area was smallest in crops unirrigated from emergence to anthesis as they had fewer ears with smaller awns. Drought during grain filling, in period 3, caused water potential of ears to drop from −25 to −35 bar, and awns died faster, at a time when leaves, stems and leaf sheaths were also senescing. Thus, the total assimilatory surface of crops suffering drought was smaller and shorter-lived than in irrigated crops.

Photosynthesis and dry-matter yield

There was little direct effect of soil or plant water potential on photosynthesis per unit leaf area. A possible exception was the crop severely stressed after early irrigation (treatment 7). Stomatal resistance increased with drought (Day *et al.* 1981), and this partial stomatal closure would have decreased total daily photosynthesis by at most 11% in the unirrigated crops, compared with the irrigated (Legg *et al.* 1979).

Published evidence showing that decreasing water potential inhibits photosynthesis by closing stomata, and affecting metabolism (Hsiao, 1973; Lawlor, 1979) is mainly from laboratory experiments in which plants were rapidly stressed. In our experiments, the late stressed crop (treatment 7) may have approached this condition. With early and prolonged drought, plants adjusted to stress by having smaller leaves and fewer tillers, not by major readjustment of metabolism or decrease in photosynthetic rate.

Leaf area duration was of much greater import-

ance to total assimilate production than was the rate of photosynthesis per unit leaf area. Between 21 June and 5 July, the period of grain filling and of greatest irradiance, crops in treatments 2, 3, 5 and 7 intercepted 76, 64, 97 and 80% respectively of the radiation 1400 MJ/m^2) intercepted by crops in treatment 12 (Legg *et al.* 1979). Allowing for lower photosynthetic efficiency and stomatal closure, assimilation by crops given treatments 3 and 7 may have been some 50–60%, and in treatments 2 and 5, 70–90% of that of the continuously irrigated crop. Differences in radiation interception were even greater after 5 July as the unirrigated crops were nearly ripe then, some 2 weeks before the irrigated.

Harvest index, the ratio of grain to grain plus straw dry matter, shows how dry matter was distributed at final harvest. Final yields of grain ranged from 2·8 to 5·6 t/ha and of straw from 3·1 to 7·6 t/ha. The harvest index ranged from 0·42 to 0·48 and was largest for crops stressed early. Weekly irrigation gave the smallest value, but this was associated with high yield. The values obtained were similar to those quoted by Gallagher & Biscoe (1978) for other crops of spring barley.

Grain growth in relation to drought, assimilatory surface and straw mass

In considering grain growth, particularly its early phase between H_4 and H_5, three points are important: (1) Number of grains per unit ground area differed by a factor of 2 between treatments; the numbers on treatments 2, 3, 5 and 7 were 50, 50, 78 and 72% respectively of the number on treatment 12. (2) The total green surface area of unirrigated crops (treatments 3 and 7) was very small, less than 20% of the surface of the weekly irrigated crop (treatment 12). (3) Despite these differences in the ratio of numbers of grains to assimilatory surface area, the rate of dry matter accumulation per grain for the 14-day period from H_4 to H_5 was similar for all treatments (Table 7).

Current assimilation was probably insufficient to supply all the material required to fill grain in unirrigated crops because they had little photosynthetic area. Following Gallagher, Biscoe & Scott (1975) and plotting the grain and straw mass changes in the 2 weeks from H_4 to H_5, normalized for number of grains, against the change in total crop dry mass in this period (Fig. 11) shows that

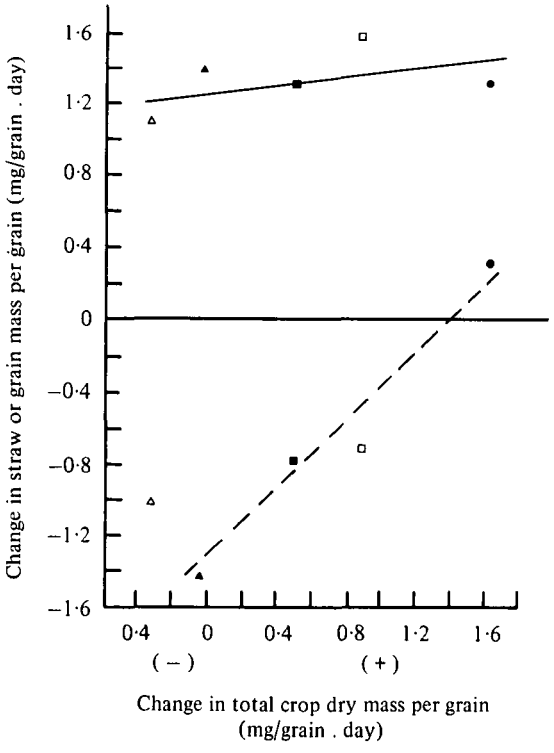

Fig. 11. Change in grain mass and straw mass, normalized for number of grains, in relation to the change in total above-ground mass/grain during early grain filling between H_4 and H_5 for spring barley crops grown with drought treatments 2 (■), 3 (□), 5 (▲), 7 (△) and 12 (●). Grains mass shown by —, and straw mass by — — —.

grain growth was almost constant, over a wide range of changes in crop dry mass. With weekly irrigation (treatment 12) there was a net gain in straw mass suggesting that assimilate supply was adequate to fill grain and that excess material was used for vegetative growth. In all other treatments straw dry matter decreased in this period, presumably as stem reserves were mobilized to provide material for grain filling. The crop under treatment 7 had probably the smallest assimilate production per grain and so was most dependent on stored material, more so than the long-term stressed crop (treatment 3) in which straw mass per grain changed less. Thus the grains' capacity to store assimilate would appear to have been saturated (i.e. sink capacity limited; Spiertz, 1978) as all treatments filled grain at the same rate, independent of assimilate production in the period.

Between H_5 and H_6 grain almost stopped filling on unirrigated treatments and straw mass changed little; little light was intercepted and the crop ripened. Lack of assimilate and reserve material may have stopped grain filling (i.e. source capacity limited, Spiertz, 1978). With irrigation, grain mass increased, though by less than in the previous 2 weeks.

The almost constant rate of early grain filling in 1976, over a wide range of crop production, and the compensation provided by reserves in drought-stressed plants, agrees with the concept (Gallagher *et al.* 1975) that reserves contribute significantly to grain filling in adverse conditions. Bidinger, Musgrave & Fischer (1977) concluded from a drought experiment that there was little contribution of stored assimilate to grain growth in their unirrigated crop. However, total crop dry-matter increase per grain was very large in their study, even in the unirrigated crop, indicating that assimilate supply per grain was large and therefore demand for stored assimilate may have been limited. This may have been because drought was not particularly severe in their experiments.

There is little doubt that reserves can contribute to grain growth in cereals when current assimilate is limiting. The amount of reserves used, rate of mobilization and importance to the crop will depend on 'sink demand', supply of assimilate from the leaves, i.e. the 'source', and reserves (Spiertz, 1978) which, as we have shown, are affected by drought.

Our measurements of grain growth on main stems indicate that it was the duration of grain filling rather than its rate that was primarily affected by the drought treatments. This contrasts with the work of Brocklehurst, Moss & Williams (1978) showing that grain of unirrigated wheat filled at a slower rate than that of irrigated, and that the duration of filling was unaffected. Gallagher, Biscoe & Hunter (1976) concluded that temperature alone controlled the duration of grain filling, but, in our experiment, irrigation extended the filling period despite high temperatures.

The range of grain mass we obtained was similar to that for 'Julia' in other years (Gallagher *et al.* 1975). The physiological factors which control potential grain size and the rate and duration of filling are unknown. Potential grain size depends, in part, on the number of endosperm cells per grain. Cool, moist conditions during development slow cell division but increase its duration, giving more potential storage sites (Brocklehurst, 1977) and hence potentially larger grains (Brocklehurst *et al.* 1978). However, in our experiments, although early drought affected growth and the concentrations of P, K and Mg in the plants, these early stressed plants produced large grain when irrigated after anthesis, suggesting that nutrient or assimilate supply during early grain development had not affected potential grain size. The similar amount of nitrogen per grain and the constant amino acid composition suggest that the ability to accumulate N and synthesize proteins was little changed by drought conditions. However, the effects of nutrient deficiency during late grain filling may be important. Phosphorus deficiency, particularly, may decrease the efficiency of starch synthesis by ADP glucosepyrophosphorylase (Preiss, 1978) as the enzyme is dependent upon P concentration and is therefore a potential control stage.

The authors wish to thank A. T. Day for organizing the irrigation; B. K. French and J. Croft for measurement of soil water content by neutron probe, Sheila Davis for ^{14}C analyses, J. Hill for the amino acid determination, and J. G. Pearlman for the statistical analyses; many others helped in nutrient analyses and ear measurements.

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