The ability of wheat cultivars to withstand drought in UK conditions: formation of grain yield

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SUMMARY

Experiments in three dry years, 1993/94, 1994/95 and 1995/96, on a medium sand at ADAS Gleadthorpe, England, tested responses of six winter wheat cultivars to irrigation of dry-matter growth, partitioning of dry matter to leaf, stem and ear throughout the season, and to grain at final harvest. Cultivars (Haven, Maris Huntsman, Mercia, Rialto, Riband and Soissons) were selected for contrasts in flowering date and stem soluble carbohydrate. Maximum soil moisture deficit (SMD) exceeded 140 mm in all years, with large deficits (> 75 mm) from early June in 1994 and from May in 1995 and 1996. The main effects of drought on partitioning of biomass were for a decrease in the proportion of the crop as lamina in the pre-flowering period, and then earlier retranslocation of stem reserves to grains during the first half of grain filling. Restricted water availability decreased grain yield by 1·83 t/ha in 1994 ($P < 0·05$), and with more prolonged droughts, by 3·06 t/ha in 1995 ($P < 0·001$) and by 4·55 t/ha in 1996 ($P < 0·001$). Averaged over the three years, grain yield responses of the six cultivars differed significantly ($P < 0·05$). Rialto and Mercia lost only 2·8 t/ha compared with Riband and Haven which lost 3·5 t/ha. Losses for Soissons and Maris Huntsman were intermediate. In the two years with prolonged drought, the biomass depression was on average greater for Haven (6·0 t/ha) than for Maris Huntsman (4·2 t/ha) ($P < 0·05$). Thus, the grain yield sensitivity of Haven to drought derived, in part, from a sensitivity of biomass growth to drought. Harvest index (HI; ratio of grain to above-ground dry matter at harvest) responses of the six cultivars to irrigation also differed ($P < 0·05$) and contributed to the yield responses. The smallest decrease in HI of the six cultivars with restricted water availability was shown by Rialto ($-0·033$); this partially explained the drought resistance for this cultivar. The largest decrease was for Maris Huntsman ($-0·072$). The cultivars differed in flowering dates by up to 9 days but these were poorly correlated with grain yield responses to irrigation. Stem soluble carbohydrate at flowering varied amongst cultivars from 220 to 300 g/m² in the unirrigated crop; greater accumulation appeared to be associated with better maintenance of HI under drought. It is concluded that high stem-soluble carbohydrate reserves could be used to improve drought resistance in the UK's temperate climate, but that early flowering seems less likely to be useful.

INTRODUCTION

Under drought, grain yield is determined by the amount of water the crop extracts from the soil, the efficiency with which this water is converted into above-ground biomass and the fraction of this which is partitioned to grains. All of these processes must have some genetic control. The effects of cultivar traits of winter wheat (*Triticum aestivum* L.) on the responses of resource capture and biomass production

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to UK drought were previously reported by Foulkes *et al.* (2001). We now report, for the same set of field experiments, the effects of cultivar traits on responses of partitioning to grain and hence yield formation to drought.

In dry regions with predictable early-season rainfall, early flowering has been shown to confer drought resistance in wheat through escape effects. For example, Fischer & Maurer (1978) working with 34 cultivars of spring wheat when drought was created by withholding irrigation in northern Mexico showed that each day of earliness conferred a yield advantage of 30 kg/ha. The degree of earliness required for

drought escape in such environments is generally considered a compromise, permitting the development of sufficient dry matter without reducing soil water to a level that will limit reproductive growth after flowering. Recent studies on the pleiotropic effects of photoperiod-insensitive genes in wheat suggest that summer stress avoidance associated with early flowering promotes a yield advantage of about 30% in southern Europe and 15% in central Europe (Borner et al. 1993; Law et al. 1994). In north-western Europe, there are relatively few reports as to whether early flowering is associated with drought escape in winter wheat. Innes et al. (1985), examining F_5 selections from a Norman × Talent cross differing in ear emergence by 7 days, observed earliness to increase yield under late-season drought but found no effect of earliness under early-season drought. Effects of photoperiod-insensitive genes in winter wheat in England have generally been reported to be neutral averaged over a run of years (Law et al. 1994; Worland 1996), although in dry years increases in the region of 5% have been observed (Worland 1996), possibly suggesting earliness to confer summer drought avoidance. In the work reported here, we examine whether cultivars differing in flowering date differ in their ability to maintain harvest index and hence grain yield in response to UK drought.

By flowering, reserves of water soluble carbohydrate (WSC), mostly as fructans, have accumulated in the stems and leaf sheaths of the crop. Maximal amounts are reached shortly after flowering (Austin et al. 1977; Foulkes et al. 1998a). A significant proportion of these reserves can be subsequently retranslocated to grains under drought (Bidinger et al. 1977; Schnyder 1993). At flowering, the proportion of stem dry matter as WSC has been shown to vary in UK cultivars from 0·20–0·30 (Austin et al. 1977; Makunga et al. 1978) and more recently from 0·29–0·36 by Muchingami (1994). Similarly for a set of 17 UK genotypes, Foulkes et al. (1998b) reported values in the range 0·29–0·39, equivalent to 250–400 g/m² dry matter of stem WSC. Cultivars allocating more dry matter to stem reserves should be better positioned to buffer grain yield formation, and hence maintain harvest index with drought. In the work reported in this paper, we examine whether cultivars differing in stem WSC accumulation differ in their ability to maintain harvest index and hence grain yield in response to UK drought.

In the present study, responses of six winter wheat cultivars to irrigation of partitioning of biomass to leaf, stem and ear throughout the season, and to grain at final harvest were tested in experiments in three dry years, 1993/94, 1994/95 and 1995/96, on a medium sand at ADAS Gleadthorpe, England. The biomass responses of the six cultivars to irrigation were previously reported by Foulkes et al. (2001). The six cultivars were chosen to examine contrasts in flower-

ing date and stem soluble carbohydrate reserves, to examine whether these traits have any effect on grain partitioning and hence yield formation under drought. The flowering date was widened by including the French-bred photoperiod insensitive cultivar, Soissons (Worland et al. 1994) and a late developing, photoperiod sensitive, UK-bred cultivar, Haven. A wide range in the amount of stem-soluble carbohydrate was intended by including contrasting genotypes from preliminary field screening for this trait (Muchingami 1994).

The objectives were to test whether cultivars differ in responses of partitioning to grains and hence grain yield formation to restricted water availability and whether associations can be detected between responses and two specific target traits: flowering date and stem-soluble carbohydrate. It was hoped that information gained on drought-resistant traits would be of value to growers when choosing cultivars, to testers when assessing cultivars and to breeders when developing new cultivars for drought-prone environments.

MATERIALS AND METHODS

Experimental design and treatments

One experiment of standard design was undertaken in each of three seasons, 1993/94, 1994/95 and 1995/96. All experiments were located at ADAS Gleadthorpe, Nottinghamshire (55°13′ N, 1°6′ W). The wheat was grown following maincrop potatoes in each year.

A randomized block, split-plot design was used. There were three replicate blocks within which two irrigation treatments, unirrigated (I_0) and fully irrigated (I_1), were randomized on main plots, and six cultivars (Haven, Maris Huntsman, Mercia, Rialto, Riband and Soissons) randomized on subplots (4 × 18 m with 12 cm between rows). The irrigation treatments were:

I_0: *Unirrigated*

I_1: Water applied using a linear overhead irrigator to maintain soil moisture deficit < 60 mm up to GS61 + 4 weeks and < 75 mm thereafter. SMD was calculated using the ADAS Irriguide model (Bailey & Spackman 1996), assuming 1·2 m maximum rooting depth.

The six cultivars were selected mainly from current commercial cultivars so as to provide a range for flowering date and stem-soluble carbohydrate. Four of the six cultivars (Haven, Riband, Rialto and Soissons) were semi-dwarfs containing either the *Rht2* or *Rht1* gene; and two (Haven and Rialto) contained the 1BL/1RS wheat–rye chromosome translocation (Zeller & Hsam 1983). Maris Huntsman was first introduced in the UK in 1969; dates of introduction for the remaining cultivars ranged from 1983 for Mercia to 1991 for Rialto.

Plot management

Full details of plot management and husbandry inputs in the three years were described by Foulkes *et al.* (2001). All experiments were autumn-sown first wheats. Plots were treated prophylactically with fungicides at GS 31, GS 39 and GS 59 to keep diseases to very low levels and with pesticides and herbicides as necessary to minimize the effects of pests and weeds. Seed rate was adjusted to achieve a target seed number of 325 per m².

Crop measurements

In 1994 and 1995, growth analysis was performed in all subplots. All above-ground plant material was harvested in one $1·2 \times 0·6$ m quadrat per subplot at seven sample times according to growth stage (Tottman 1987): (i) onset of stem extension (GS 31), (ii) flag leaf emergence (GS 39), (iii) onset of flowering (GS 61), (iv) early grain fill (taken as GS 39 + 550 °Cd, base temperature 0 °C), (v) late grain fill (taken as GS 39 + 750 °Cd, base temperature 0 °C) (vi) complete canopy senescence (green area index = 0) and (vii) harvest. Cultivars were sampled on the particular calendar dates when they reached the specific stage. In 1996, all cultivars were sampled on 15 June (two replicates) and harvest (three replicates) only. Two cultivars, Haven and Soissons, were assessed at the seven developmental stages as in 1994 and 1995.

At sample times (i)–(vi) above-ground crop dry weight was assessed from a 30 % sub sample (by fresh weight) from all above-ground material sampled within a $1·2 \times 0·6$ m quadrat area dried to constant weight at 80 °C (Gay *et al.* 1998). To estimate the proportion of the crop as different components, material in a 10 % subsample by fresh weight was separated into: (i) leaf lamina, (ii) stem plus attached leaf sheath, and (iii) ear (after GS 39). Each component was dried to constant weight at 80 °C. For brevity, the 'stem and leaf sheath' fraction of biomass is referred to as 'stem' in the following text.

In each year, percentage water-soluble carbohydrate of stems and attached leaf sheaths was assessed in six randomly selected fertile shoots (those with an ear) per subplot at GS 61 + 75 °Cd (base temperature 0 °C). The six shoots were dried at 102 °C for 2 h and analysed for %WSC as described by Gay *et al.* (1998). In 1994 and 1995, stem dry weight at GS 61 + 75 °Cd was calculated from linear interpolation of estimates at GS 61 and early grain fill. In 1996, it was calculated from the product of: (i) stem dry weight per shoot (from the six fertile shoots sampled for WSC analysis) and (ii) the number of fertile shoots per m² (obtained from growth analysis samples at harvest).

At final harvest, all above-ground material in the $1·2 \times 0·6$ m quadrat per subplot was separated into straw and ears. Straw dry weight was assessed from a 30 % subsample (by fresh weight) from all straw material sampled with the $1·2 \times 0·6$ m quadrat dried to constant weight at 80 °C. All ears within the $1·2 \times 0·6$ m quadrat were counted and immediately threshed using a laboratory thresher, and the grain and chaff collected separately. The weight of each was measured after drying to constant weight at 80 °C. Harvest index was calculated as the ratio of the grain to above-ground dry matter.

Combine grain yield and yield components

In each experiment for all subplots, combine grain yield was assessed in a 5×3 m area, and values adjusted to 15 % moisture. Harvest dates were judged according to grain moisture content, for irrigated and unirrigated treatments separately. Thousand grain weight was estimated by counting all grains in a 250 g sample from the combine and then drying to constant weight at 80 °C. Grains per ear was calculated as:

$$\frac{hand\text{-}harvested\ grain\ yield\ (g/m²@100\%\ DM)}{ears/m² \times grain\ weight\ (g@100\%\ DM)}$$

Soil moisture deficit

In each year, volumetric soil water content to 1·65 m soil depth was measured at 3–4 day intervals from mid-April to harvest in all subplots of two replicates using a Wallingford neutron probe inserted in one aluminium access tube per subplot.

RESULTS

Weather patterns and soil moisture deficits

The seasonal rainfall and soil moisture deficits in the three experiments were described previously by Foulkes *et al.* (2001). In summary, in 1994 large soil moisture deficits (> 75 mm) did not occur until early June about 10 days before flowering (Table 1) thereafter progressively increasing to 175 mm by late July. In 1995 and 1996, the onset of large deficits was earlier, in May, and thereafter increased to 145 mm by late July. Drought was more prolonged in these seasons. In the irrigated treatment, deficits were restricted to less than 80 mm prior to mid-June and to less than 100 mm prior to mid-July in all years.

Crop development

The behaviour of the cultivars was consistent in the individual seasons (Table 2). In all years, Soissons and Rialto were earliest to GS 31, and Haven latest. At GS 39 and GS 61, the rank order was broadly maintained from GS 31, with the exception of Rialto, which, as a result of an extended stem-extension

Table 1. *Soil moisture deficits (mm) in irrigated (Irr) and unirrigated (Unirr) treatments in 1994, 1995 and 1996*

	1994		1995		1996	
	Irr	Unirr	Irr	Unirr	Irr	Unirr
SMD 1 June	47	59	50	84	72	103
SMD 15 July	111	167	90	148	79	139
Days SMD > 75 mm 1 Apr–31 May	0	0	0	23	2	19
Days SMD > 100 mm 1 June–15 July	7	32	3	36	0	46

Table 2. *Dates of developmental stages and harvest in 1994 and 1995 in unirrigated treatment for six cultivars*; and in 1996 for Haven and Soissons (most rapid and slow developing cultivars) (values in parentheses are number of days delay in irrigated treatment)*

	GS 31	GS 39	GS 61	Harvest
Haven				
1994	30 Apr	5 Jun	24 Jun	9 Aug (3)
1995	17 Apr	23 May (−1)	16 Jun (4)	3 Aug (5)
1996	30 Apr	29 May	15 Jun (2)	14 Aug (5)
Maris Huntsman				
1994	30 Apr	27 May	21 Jun	9 Aug (3)
1995	16 Apr	18 May (−1)	10 Jun (5)	3 Aug (5)
1996	–	–	–	–
Mercia				
1994	19 Apr	24 May	19 Jun	9 Aug (3)
1995	10 Apr	13 May (−1)	8 Jun (5)	3 Aug (5)
Rialto				
1994	16 Apr	3 Jun	24 Jun	9 Aug (3)
1995	6 Apr	19 May	13 Jun (4)	3 Aug (5)
1996	–	–	–	–
Riband				
1994	26 Apr	29 May	21 Jun	9 Aug (3)
1995	13 Apr	21 May	10 Jun (5)	3 Aug (5)
1996	–	–	–	–
Soissons				
1994	16 Apr	17 May	17 Jun	9 Aug (3)
1995	6 Apr	7 May	3 Jun (2)	3 Aug (5)
1996	19 Apr	22 May	8 Jun (2)	14 Aug (5)
Mean				
1994	23 Apr	27 May	21 Jun	9 Aug (3)
1995	11 Apr	17 May (−1)	10 Jun (4)	3 Aug (5)
1996	25 Apr	26 May	12 Jun (2)	14 Aug (5)

* Year of first harvest in NIAB National List trials: Maris Huntsman (1969), Mercia (1983), Riband (1985), Haven (1987), Soissons (1989) and Rialto (1991).

phase, was relatively later at these stages (Table 2). The effects of water availability were up to 5 days. They mainly occurred after flowering in 1994 and, except for Soissons, before flowering in 1995. At harvest, all cultivars were affected similarly.

Grain yield

Irrigation increased combine grain yield significantly in all years, by 1·8 t/ha in 1994 ($P < 0.05$) and, with more prolonged deficits, by 3·1 t/ha in 1995 ($P < 0.001$) and by 4·6 t/ha in 1996 ($P < 0.001$; Table 3). In each season, cultivars in irrigated conditions reflected their performance on the UK Recommended List (NIAB, 1996 and preceding publications) (Table 3). Thus, averaged over the 3 years, the modern wheats of high yield potential, Haven, Riband and Rialto, yielded more than the modern wheats of low yield potential, Mercia and Soissons, or the older, feed wheat, Maris Huntsman ($P < 0.01$).

Averaged across the 3 years, the cultivars responded differently to restricted water availability ($P < 0.05$)

Table 3. *Combine grain yield (t/ha 85% DM), harvest index, ears/m², grains/ear and individual grain weight (mg 100% DM) for six cultivars in irrigated and unirrigated treatments in 1994, 1995 and 1996*

	1994					1995					1996					Mean 1994–1996				
	Yield (t/ha)	HI	Ears /m²	Grains /ear	G. wt mg	Yield t/ha	HI	Ears /m²	Grains /ear	G. wt mg	Yield t/ha	HI	Ears /m²	Grains /ear	G. wt mg	Yield t/ha	HI	Ears /m²	Grains /ear	G. wt mg
Irrigated																				
Haven	11·59	0·55	478	40·4	46·8	9·77	0·51	435	45·2	44·4	11·21	0·54	462	46·5	43·2	10·86	0·53	458	44·0	44·8
M. Huntsman	9·89	0·51	450	36·9	48·4	8·08	0·48	417	36·9	49·5	9·71	0·52	475	39·9	48·1	9·23	0·50	448	37·9	48·6
Mercia	10·11	0·53	621	34·6	39·6	8·22	0·48	503	40·4	39·2	9·67	0·52	576	37·4	38·6	9·34	0·51	567	37·5	39·1
Rialto	10·81	0·52	472	44·0	41·9	9·12	0·49	445	47·1	41·5	10·81	0·54	421	52·2	42·4	10·25	0·52	446	47·8	41·9
Riband	11·28	0·56	451	47·5	45·5	9·81	0·52	419	45·8	43·6	10·19	0·54	482	45·9	42·3	10·43	0·54	450	46·4	43·8
Soissons	9·41	0·51	600	29·9	42·5	9·34	0·51	638	33·4	39·6	10·01	0·52	668	36·9	38·4	9·59	0·51	635	33·4	40·1
Mean	10·52	0·53	512	38·9	44·1	9·06	0·50	476	41·5	43·0	10·27	0·53	514	43·1	42·2	9·95	0·52	501	41·2	43·1
Unirrigated																				
Haven	9·82	0·51	488	39·4	41·0	6·01	0·46	385	40·5	33·4	5·87	0·46	399	32·9	39·9	7·23	0·48	424	37·6	38·1
M. Huntsman	7·55	0·48	455	33·5	43·3	5·52	0·42	386	33·4	42·4	5·31	0·42	393	28·9	44·1	6·13	0·44	411	31·9	43·3
Mercia	8·40	0·49	628	30·9	36·0	6·05	0·45	462	34·4	34·1	5·24	0·42	451	32·3	32·4	6·56	0·46	513	32·5	34·2
Rialto	9·54	0·51	428	41·9	40·7	6·34	0·48	377	48·1	35·2	6·21	0·47	395	41·8	38·3	7·37	0·48	400	43·9	38·1
Riband	8·71	0·52	407	42·6	40·8	6·13	0·46	359	44·8	35·1	5·87	0·48	388	37·6	40·9	6·90	0·49	384	41·6	39·0
Soissons	8·13	0·50	607	27·8	39·2	5·93	0·46	684	23·5	34·4	5·83	0·44	597	27·7	31·9	6·63	0·47	629	26·3	35·2
Mean	8·69	0·50	502	36·0	40·2	6·00	0·46	442	37·5	35·8	5·72	0·45	437	33·5	37·9	6·80	0·47	460	35·7	38·0
S.E. irrigation (D.F. = 2)*	0·164	0·006	7·1	0·47	0·36	0·163	0·003	5·9	0·49	0·30	0·056	0·001	10·5	0·35	0·40	0·079	0·002	4·7	0·26	0·21
S.E. cultivar (D.F. = 20)	0·204	0·005	14·0	0·69	0·47	0·177	0·006	11·2	0·99	0·31	0·162	0·004	15·8	1·26	0·47	0·105	0·003	8·0	0·58	0·24
S.E. int'n (D.F. = 20)	0·310	0·009	19·4	1·01	0·70	0·281	0·008	15·6	1·37	0·50	0·216	0·006	23·0	1·66	0·72	0·138	0·004	11·3	0·79	0·38

* D.F. for individual seasons given in table. D.F. for cross-year mean (1994–1996): irrigation effect = 6, cultivar effect = 60, interaction = 60.
HI, harvest index.

Table 4. *Grains/m² measured at harvest for six cultivars in irrigated and unirrigated treatments in 1994, 1995 and 1996*

	1994	1995	1996	Mean
Irrigated				
Haven	19256	19693	21444	20131
Maris Huntsman	16628	15394	18964	16995
Mercia	21483	20370	21543	21132
Rialto	20712	20935	21946	21198
Riband	21367	19201	22096	20888
Soissons	17887	21291	24580	21253
Mean	19556	19480	21762	20266
Unirrigated				
Haven	19196	15551	13046	15931
Maris Huntsman	15227	12893	11368	13162
Mercia	19357	15865	14125	16449
Rialto	17932	18078	16485	17498
Riband	17286	16043	14557	15962
Soissons	16850	16055	16518	16474
Mean	17641	15747	14350	15913
S.E. of mean, irrigation (D.F. = 2)	53·7	387·9	402·4	165·1
S.E. of mean, cultivar (D.F. = 20)	400·4	531·0	451·6	239·4
S.E. of mean, interaction (D.F. = 20)	519·7	787·7	708·3	350·4

(Table 3). Rialto and Mercia lost only 2·8 t/ha without irrigation whereas Riband and Haven lost 3·5 t/ha. Losses for Soissons and Maris Huntsman were intermediate. Rialto maintained yield better than the average, Riband was more affected by drought than the average and Maris Huntsman showed intermediate responses consistently in all years. However, for other cultivars, the pattern of response differed in the 3 years. Haven showed an intermediate response in 1994 but evidence for marked drought susceptibility in the 2 drier years ($P = 0.06$). Although the mean response of Mercia indicated that it was drought resistant this was heavily influenced by its performance in 1995; in the other years the effect was marginal. Soissons showed a smaller depression than average in 1994, although its response in other years was intermediate.

Components of yield

Irrigation treatment effects

Effects on components of yield depended on the timing of drought. With drought mainly after flowering in 1994 ears/m² was not affected (Table 3), but grains/ear and individual grain weight were decreased by 2·9 ($P < 0.05$) and 3·9 mg ($P < 0.05$), respectively. With the more prolonged droughts in 1995 and 1996, all yield components were affected. In 1995, there were 34 fewer ears/m² ($P = 0.06$), 4·0 fewer grains/ear ($P < 0.05$) and 7·3 mg lighter grains ($P < 0.05$) with restricted water availability. In 1996, there were 77 fewer ears/m² ($P < 0.01$), 9·6 fewer grains/ear ($P < 0.01$) and 4·2 mg lighter grains ($P < 0.05$), respectively.

Cultivar effects in irrigated conditions

Cultivar differences were expressed consistently in the 3 years (Table 3). Cultivars could be classed broadly into three groups according to yield components. Firstly, the modern, high-yield-potential genotypes, comprising Haven, Riband and Rialto, which had comparatively few ears/m² (446–458), more grains/ear (44–48) and heavier grains (42–45 mg). Secondly, the modern, low-yield-potential genotypes, Mercia and Soissons, which had more ears/m² (567–635), fewer grains/ear (33–38) and lighter grains (39–40 mg). Finally, the older, feed genotype, Maris Huntsman, which had few ears/m² (448), few grains/ear (38), but heavy grains (49 mg).

Cultivar responses to restricted water availability

Differences in yield components of themselves seemed to have little bearing on the ability to maintain yield under drought. Drought-resistant (Rialto) and drought-susceptible (Haven, Riband) genotypes had similar yield structures. Conversely, cultivars with different yield structures, e.g. Soissons and Maris Huntsman, showed broadly similar responses to drought. The drought susceptibility of Haven in 1995 and 1996 related to larger losses in grains/ear and individual grain weight. The drought resistance of Rialto was similarly linked with smaller losses for these two yield components.

In the individual years, the irrigation/cultivar interaction for ears/m² and grains/ear was only statistically significant in 1995 ($P < 0.05$) (Table 3). Soissons lost fewer ears/m² compared to other

Table 5. *Stem-and-leaf-sheath dry matter and above-ground dry matter at GS 61 for six cultivars in irrigated and unirrigated treatments in 1994, 1995 and 1996*

	Stem and leaf sheath DM (g/m²)			Above-ground DM (g/m²)		
	1994	1995	1996	1994	1995	1996
Irrigated						
Haven	801	830	766	1186	1215	1121
Maris Huntsman	690	774	673	1039	1091	1046
Mercia	704	704	673	1070	1042	1064
Rialto	805	827	726	1244	1201	1120
Riband	669	725	628	1023	1054	1004
Soissons	702	737	765	1015	1059	1099
Mean	729	766	705	1096	1111	1076
Unirrigated						
Haven	758	649	579	1176	943	951
Maris Huntsman	690	664	621	1042	940	1032
Mercia	742	548	554	1129	793	912
Rialto	749	715	610	1149	1041	1028
Riband	706	610	575	1075	875	948
Soissons	710	552	612	1001	775	978
Mean	726	623	592	1095	895	975
S.E. of mean, irrigation (D.F.)	5·0 (2)	1·4 (2)	26·9 (1)	7·0 (2)	4·6 (2)	21·9 (1)
S.E. of mean, cultivar (D.F.)	13·3 (20)	21·1 (20)	19·3 (10)	23·3 (20)	28·8 (20)	24·0 (10)
S.E. of mean, interaction (D.F.)	17·9 (20)	20·2 (20)	41·8 (10)	30·8 (20)	37·5 (20)	37·9 (10)

Table 6. *Leaf lamina dry matter and stem-and-leaf-sheath dry matter at GS 39 for six cultivars in irrigated and unirrigated treatments in 1995*

	Leaf lamina DM (g/m²)	Stem-and-leaf-sheath DM (g/m²)
Irrigated		
Haven	179	456
Maris Huntsman	177	324
Mercia	152	245
Rialto	182	349
Riband	203	380
Soissons	150	293
Mean	174	341
Unirrigated		
Haven	144	385
Maris Huntsman	125	324
Mercia	123	303
Rialto	140	408
Riband	121	355
Soissons	114	321
Mean	128	349
S.E. of mean, irrigation (D.F. = 2)	6·5	6·7
S.E. of mean, cultivar (D.F. = 20)	5·8	10·9
S.E. of mean, interaction (D.F. = 20)	10·0	15·6

cultivars without irrigation, and Rialto lost fewer grains/ear than Riband and Haven. For individual grain weight, the interaction was significant in all years ($P < 0.05$), with Rialto generally maintaining grain weight better than Riband and Haven.

Grain number per m²

Grain number per m² was calculated as the product of ears/m² and grains/ear. Effects of irrigation related to the extent of the SMD in the unirrigated crop
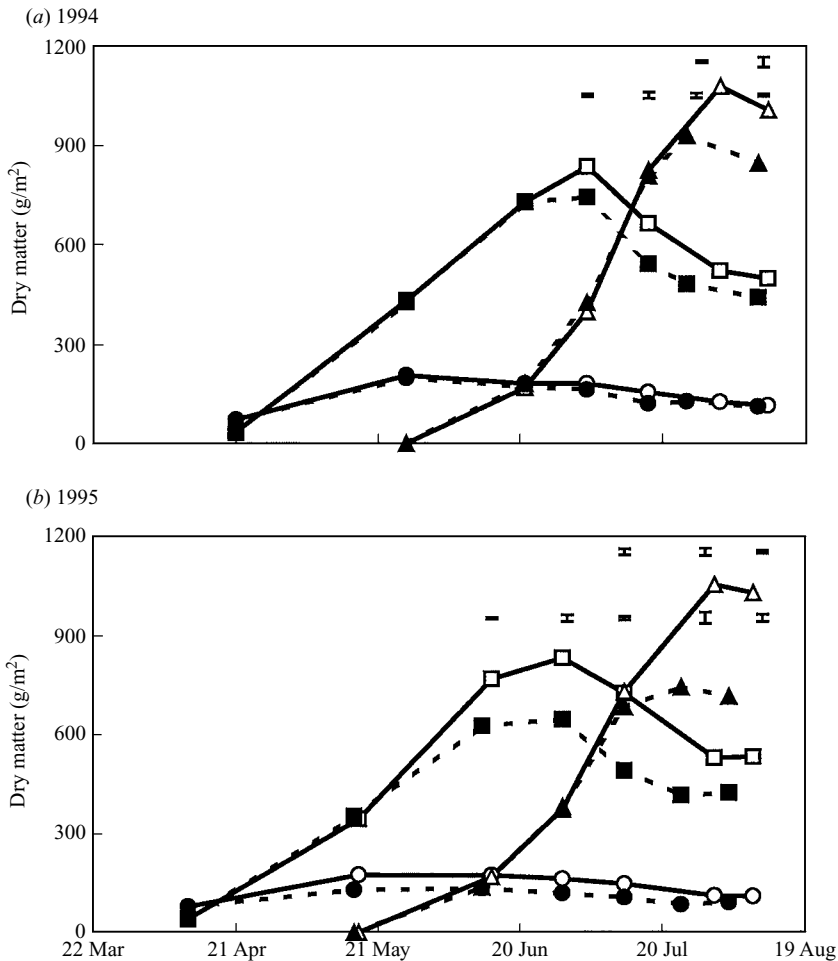
Fig. 1. (*a*) Dry matter (means of the six cultivars) of the leaf lamina in the irrigated crop ○; the leaf lamina in the unirrigated crop ●; the stem and leaf sheath in the irrigated crop □; the stem and leaf sheath in the unirrigated crop ■; the ear in the irrigated crop △, and the ear in the unirrigated crop ▲ in 1994. Upper series of error bars show the S.E. of mean for the irrigation/cultivar interaction for the ear dry matter (D.F. = 20); the lower series of error bars show the S.E. of mean for the irrigation/cultivar interaction for the stem-and-leaf-sheath dry matter (D.F. = 20). (*b*) Dry matter (means of the six cultivars) of the leaf lamina in the irrigated crop ○; the leaf lamina in the unirrigated crop ●; the stem and leaf sheath in the irrigated crop □; the stem and leaf sheath in the unirrigated crop ■; the ear in the irrigated crop △, and the ear in the unirrigated crop ▲ in 1995. Upper series of error bars show the S.E. of mean for the irrigation/cultivar interaction for the ear dry matter (D.F. = 20); the lower series of error bars show the S.E. of mean for the irrigation/cultivar interaction for the stem-and-leaf-sheath dry matter (D.F. = 20).

before flowering. Where deficits in the 20 day period prior to flowering were greater in 1995 and 1996, the loss in grains/m² under drought was larger. Thus, the decrease in 1994 (1915 per m²) was less than in 1995 (3733 per m²) and much less than in 1996 (7412 per m²) (Table 4).

Averaged over the three years, cultivars in irrigated conditions produced from 16995 to 21198 grains/m² ($P < 0.001$). Differences amongst five of the genotypes were small, from Rialto (21198 per m²) to Haven (20131 per m²), but Maris Huntsman had consider-

ably fewer grains (16995 per m²). Averaged over the 3 years, losses with restricted water availability varied from 3699 (Rialto) to 4926 per m² (Riband), but these responses were not statistically significant.

Crop biomass growth and partitioning

Effects in the pre-flowering phase

Cultivars differed in crop dry weight at flowering in irrigated conditions, with values varying from 1015

Table 7. *Proportion of above-ground dry matter as leaf lamina and as stem-and-leaf-sheath at GS 39, GS 61 and late grain fill for six cultivars in irrigated and unirrigated treatments in 1994 and 1995*

|	1994						1995					
	GS 39		GS 61		Late grain fill		GS 39		GS 61		Late grain fill	
	Lamina	Stem	Lamina	Stem	Lamina	Stem	Lamina	Stem	Lamina	Stem	Lamina	Stem
Irrigated												
Haven	0·30	0·70	0·16	0·69	0·10	0·36	0·28	0·72	0·15	0·69	0·09	0·40
Maris Huntsman	0·41	0·59	0·18	0·68	0·10	0·44	0·35	0·65	0·15	0·71	0·09	0·47
Mercia	0·36	0·64	0·17	0·68	0·11	0·43	0·38	0·62	0·18	0·68	0·10	0·48
Rialto	0·29	0·71	0·16	0·66	0·10	0·39	0·34	0·66	0·15	0·70	0·10	0·45
Riband	0·28	0·72	0·17	0·66	0·09	0·36	0·35	0·65	0·14	0·70	0·08	0·43
Soissons	0·35	0·65	0·16	0·69	0·09	0·44	0·34	0·66	0·17	0·70	0·09	0·50
Mean	0·33	0·67	0·17	0·68	0·10	0·40	0·34	0·66	0·16	0·70	0·09	0·45
Unirrigated												
Haven	0·28	0·72	0·17	0·66	0·08	0·31	0·27	0·73	0·14	0·69	0·08	0·33
Maris Huntsman	0·38	0·62	0·18	0·68	0·08	0·40	0·28	0·72	0·16	0·71	0·08	0·42
Mercia	0·39	0·61	0·17	0·67	0·09	0·38	0·29	0·71	0·15	0·69	0·09	0·40
Rialto	0·28	0·72	0·14	0·66	0·09	0·36	0·26	0·75	0·15	0·69	0·09	0·36
Riband	0·28	0·72	0·16	0·67	0·08	0·34	0·25	0·75	0·14	0·70	0·08	0·35
Soissons	0·34	0·66	0·14	0·72	0·09	0·43	0·26	0·74	0·15	0·72	0·09	0·44
Mean	0·33	0·67	0·16	0·68	0·09	0·38	0·27	0·73	0·15	0·70	0·09	0·39
S.E. of mean, irrigation (D.F. = 2)	0·006	0·006	0·006	0·003	0·005	0·007	0·004	0·004	0·002	0·003	0·001	0·001
S.E. of mean, cultivar (D.F. = 20)	0·010	0·010	0·011	0·005	0·009	0·012	0·008	0·008	0·004	0·004	0·004	0·001
S.E. of mean, interaction (D.F. = 20)	0·013	0·013	0·015	0·006	0·013	0·017	0·011	0·011	0·006	0·006	0·004	0·001
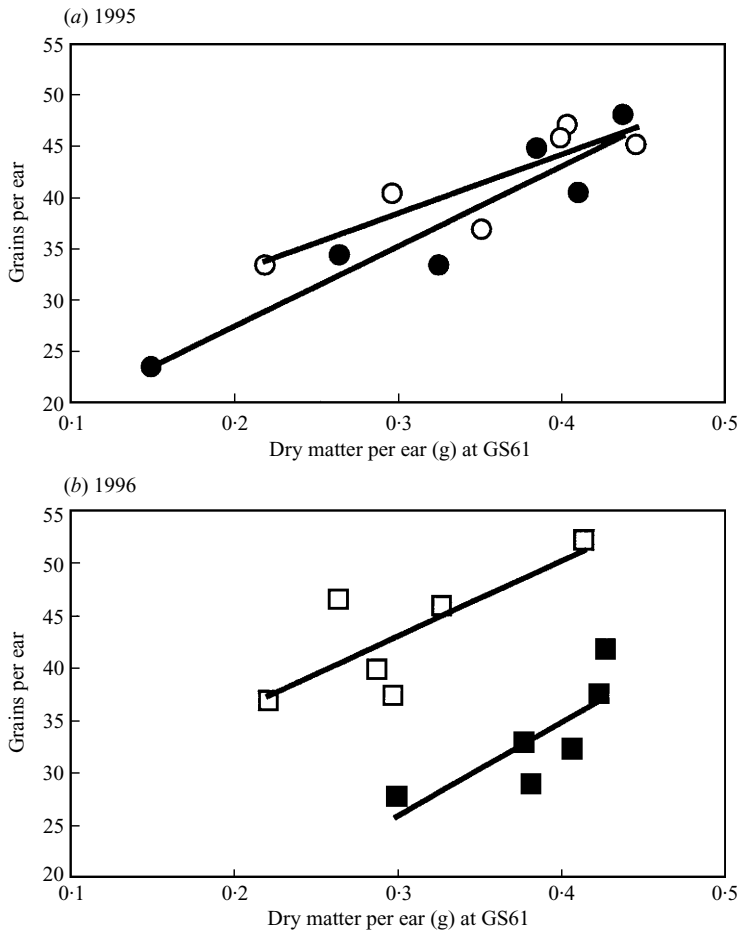
Fig. 2. Regression of grains per ear on dry matter per ear at GS 61 for six cultivars in irrigated and unirrigated treatments in (a) 1995 and (b) 1996: 1995 irrigated (○) $y = 21 \cdot 2$ (S.E. $\pm 5 \cdot 97) + 57 \cdot 5$ (S.E. $\pm 16 \cdot 6)x$ ($r^2 = 0 \cdot 75$, D.F. $= 4$); 1995 unirrigated (●) $y = 11 \cdot 8$ (S.E. $\pm 4 \cdot 65) + 78 \cdot 3$ (S.E. $\pm 13 \cdot 61)x$ ($r^2 = 0 \cdot 89$, D.F. $= 4$); 1996 irrigated (□) $y = 21 \cdot 5$ (S.E. $\pm 9 \cdot 02) + 71 \cdot 7$ (S.E. $\pm 29 \cdot 43)x$ ($r^2 = 0 \cdot 60$, D.F. $= 4$); and 1996 unirrigated (■) $y = -1 \cdot 1$ (S.E. $\pm 13 \cdot 53) + 89 \cdot 8$ (S.E. $\pm 34 \cdot 75)x$ ($r^2 = 0 \cdot 63$, D.F. $= 4$).

(Soissons) to 1244 (Rialto) g/m² in 1994 ($P < 0 \cdot 001$) and from 1042 (Mercia) to 1215 (Haven) g/m² in 1995 ($P < 0 \cdot 01$; Table 5). In both years, cultivars with later flowering dates tended to have larger crop dry weight at flowering. In 1994, biomass was not decreased by restricted water availability at this stage. In 1995, where biomass decreased on average under drought from 1111 to 895 g/m² ($P < 0 \cdot 001$), the irrigation/ cultivar interaction was not significant, and genotypes ranked similarly with and without irrigation.

In 1995, leaf lamina weight deceased from 174 to 128 g/m² without irrigation at GS 39 (Table 6 and Fig. 1b), but by flowering, although crop dry weight was reduced by 221 g/m², the proportion of the crop as leaf, stem and ear was not greatly affected. Growth of stem and ear was also checked by flowering, following the earlier check on leaf lamina, such that

there was a broadly proportionate decrease in the weight of all three plant components (Table 7). The decrease in the proportion of the crop as leaf lamina at GS 39 for five cultivars was similar at c. 0·09, but for Haven it was only 0·01. Haven exhibited a large decrease in stem weight of 71 g/m² in addition to a decrease in lamina of 35 g/m² at this stage, whereas other cultivars showed only small or negligible decreases in stem weight. The poor maintenance of stem growth under drought for Haven was again evident at GS 61 in both 1995 and 1996 (Table 5).

For the 2 years with prolonged drought, individual ear weight of the cultivars at flowering was linearly regressed on grains/ear, fitting separate regressions to the irrigated and unirrigated values in each year (Fig. 2). The fitted regressions were significant ($P < 0 \cdot 05$) for both the irrigated and unirrigated plots in each

Table 8. *Post-flowering growth, derived as increase in above-ground dry matter from GS 61 to complete canopy senescence (ΔWg), stem-and-leaf-sheath dry matter loss from GS 61 to harvest (ΔWs), grain growth, derived as increase in ear dry matter from GS 61 to harvest (ΔWe), proportion of above-ground dry matter at GS61 retranslocated to grains, derived as ΔWs divided by above-ground dry matter at GS61, and proportion of grain growth from stored carbohydrate, derived as $\Delta Ws/\Delta We$ for six cultivars in irrigated and unirrigated treatments in 1994 and 1995*

	Post-flowering growth (ΔWg g/m²)			Stem-and-leaf-sheath DM loss (ΔWs g/m²)			Grain growth (ΔWe g/m²)			Proportion of above-ground DM at GS61 retranslocated (ΔWs/DM at GS61)			Proportion grain growth from stored carbohydrate ($\Delta Ws/\Delta We$)		
	1994	1995	Mean	1994	1995	Mean	1994	1995	Mean	1994	1995	Mean	1994	1995	Mean
Irrigated															
Haven	571	492	531	347	324	336	880	890	885	0·29	0·26	0·28	0·40	0·37	0·39
Maris Hunstman	744	517	630	167	206	186	791	788	790	0·16	0·23	0·17	0·22	0·27	0·24
Mercia	638	590	614	214	170	192	834	859	847	0·20	0·25	0·18	0·26	0·20	0·23
Rialto	552	600	576	300	279	290	820	907	864	0·24	0·28	0·24	0·37	0·31	0·34
Riband	741	637	689	165	236	200	952	850	901	0·16	0·28	0·19	0·18	0·28	0·23
Soissons	572	651	611	211	208	209	742	893	818	0·21	0·27	0·20	0·29	0·23	0·26
Mean	636	581	609	234	237	236	836	864	850	0·21	0·26	0·24	0·29	0·28	0·28
Unirrigated															
Haven	422	320	371	305	276	290	737	514	626	0·27	0·29	0·27	0·42	0·53	0·48
Maris Hunstman	483	376	429	244	145	195	633	571	602	0·19	0·15	0·19	0·39	0·26	0·32
Mercia	368	453	410	281	155	218	662	567	615	0·17	0·19	0·22	0·42	0·28	0·35
Rialto	389	240	315	327	289	308	662	644	653	0·23	0·28	0·28	0·50	0·46	0·48
Riband	479	346	412	299	187	243	657	577	617	0·22	0·21	0·25	0·46	0·33	0·39
Soissons	478	378	428	273	162	218	641	598	620	0·19	0·20	0·23	0·44	0·28	0·36
Mean	436	352	394	288	202	245	666	579	623	0·21	0·22	0·21	0·44	0·36	0·40
S.E. mean, irrigation (D.F. = 2*, 4†)	45·5	28·2	26·8	8·9	11·2	7·1	2·7	18·9	9·5	0·008	0·010	0·007	0·007	0·022	0·012
S.E. mean, cultivar (D.F. = 20*, 40†)	37·8	48·6	30·8	17·4	25·4	15·4	20·2	27·6	17·1	0·014	0·023	0·013	0·030	0·044	0·027
S.E. mean interaction (D.F. = 20*, 40†)	66·8	68·8	47·9	24·3	34·7	21·2	26·2	40·3	24·1	0·020	0·032	0·019	0·040	0·061	0·036

* D.F. for individual years; † D.F. for cross-year comparison from cross-year split-plot ANOVA: Year 1, Reps (Year) 4, Irrigation 1, Year × Irrigation 1, Error A 4, Cultivar 5, Year × Cultivar 5, Irrigation × Cultivar 5, Year × Irrigation × Cultivar 5, Error B 40.

Table 9. *Amount of water-soluble carbohydrate in stems and leaf sheaths for six cultivars in irrigated and unirrigated treatments at GS 61+75 °Cd in 1994, 1995 and 1996*

	1994 (WSC g/m²)	1995 (WSC g/m²)	1996 (WSC g/m²)
Irrigated			
Haven	332	363	359
Maris Hunstman	191	298	249
Mercia	210	252	254
Rialto	314	329	278
Riband	233	278	280
Soissons	246	273	357
Mean	253	298	296
Unirrigated			
Haven	299	278	293
Maris Hunstman	205	251	281
Mercia	219	229	213
Rialto	294	272	333
Riband	256	235	252
Soissons	253	225	278
Mean	254	248	275
S.E. of mean, irrigation (D.F. = 2)	3·7	8·6	9·0
S.E. of mean, cultivar (D.F. = 20)	10·1	13·2	25·4
S.E. of mean, interaction (D.F. = 20)	13·6	19·1	34·0

year, with heavier ears at flowering having more grains/ear at harvest. The regression slopes were not affected by irrigation in either year, but in 1996 there was a displacement between the two linear regressions for the irrigated and unirrigated data ($P < 0.05$). In this year, individual ear weights were broadly similar in irrigated and unirrigated conditions, but there was an average decrease in grains/ear of 10 with restricted water availability. This displacement suggested that in this year grains/ear may have been diminished under drought by direct stress effects on pollination.

Effects in the post-flowering phase

For the two years with a full set of measurements on all cultivars, the amount of growth in the period from flowering to harvest (Δ Wg) was estimated from the difference between crop dry weight at GS 61 and that at the end of grain fill (taken as complete canopy senescence). Post-flowering growth decreased with restricted water availability by 190 g/m² in 1994 ($P = 0.09$) and 229 g/m² in 1995 ($P < 0.05$) (Table 8). In irrigated conditions, Δ Wg did not differ significantly amongst cultivars in either year, with values in the range 552 (Rialto) to 741 g/m² (Maris Hunstman) in 1994 ($P = 0.06$) and from 492 (Haven) to 651 g/m² (Soissons) in 1995 ($P = 0.43$). On average, though, there was a trend for less growth for Haven (531 g/m²) and more for Riband (689 g/m²) compared with other genotypes (cultivar mean 609 g/m²) during this period. The decrease in Δ Wg with restricted water availability varied amongst cultivars from 103 to

270 g/m² in 1994 and from 137 to 339 g/m² in 1995 but the irrigation/cultivar interaction was not significant in either year.

During the first half of grain filling, drought increased the proportion of crop DM in ears and decreased that in stems, suggesting earlier retranslocation of stored stem sugars to the ear in the unirrigated crop (Figs 1a and 1b). This was also suggested by the observation that ear weight was hardly depressed under drought in either year until late grain filling (although by the end of grain-fill ear weight was depressed by 149 g/m² in 1994 and 310 g/m² in 1995; Figs 1a and 1b). Estimates of the amount of assimilate available for redistribution from stems to grains were attained in two ways: firstly through direct measurement of water-soluble carbohydrate in the stems, shortly after flowering (Table 9), and secondly through the loss in stem weight from GS 61 to harvest (Δ Ws) (Table 8). In 1994 stem WSC at flowering was not affected by restricted water availability. In subsequent years with more prolonged drought, stem WSC was less where the crop was not irrigated by 50 g/m² in 1995 and 21 g/m² in 1996. A similar picture emerges for Δ Ws: in 1995, Δ Ws was on average 35 g/m² less without than with irrigation.

The proportion of pre-flowering growth redistributed to grain was calculated as the ratio of Δ Ws to crop dry weight at GS 61. This increased with drought from 0·21 to 0·26 in 1994 ($P < 0.01$), and from 0·21 to 0·22 in 1995 ($P < 0.05$). The proportion of grain yield derived from redistribution was calculated as Δ Ws/Δ

We, where Δ We is the grain yield, calculated as the ear biomass increment from GS 61 to harvest. This increased with drought from 0·29 to 0·44 in 1994 ($P < 0.05$) and from 0·28 to 0·36 in 1995 ($P < 0.05$). Previously the contribution of reserves to grain yield of barley has been reported to be in the order of 0·17 (Bidinger *et al.* 1977) and 0·44 (Austin *et al.* 1980*a*) under dry conditions, and 0·12 (Bidinger *et al.* 1977) and 0·11 (Austin *et al.* 1980*a*) in irrigation/normal conditions. Similar relationships have been observed in wheat crops (Bidinger *et al.* 1977). The proportional contribution of reserves in irrigated conditions in this study was therefore somewhat greater than in these previous studies.

Averaged across 1994 and 1995, the post-flowering stem weight loss in irrigated conditions was larger for Haven (336 g/m²) and Rialto (290 g/m²) than for other cultivars, with values in the range 186 to 209 g/m² ($P < 0.001$). This indicated that these two cultivars accumulated larger amounts of remobilizable stem reserves. Amounts were roughly similar from the direct measurements at flowering, with values in the range 239 to 351 g/m², and cultivars ranked similarly in both assessments (Table 8 and 9).

In the two seasons with prolonged drought, values for both direct measurements and Δ Ws indicated that the ability to amass reserves under early drought tended to be more affected for Haven. For example, in 1995 the reduction in Δ Ws for Haven was greatest at 48 g/m² whereas the value for Rialto was not diminished by drought.

Effects on growth and partitioning at final harvest

The accumulation of effects occurring in the pre- and post-flowering phases was ultimately expressed as the harvest biomass and the harvest index. The harvest biomass responses of the cultivars to restricted water availability were described by Foulkes *et al.* (2001). In summary, with later drought in 1994 restricted water availability decreased biomass by 220 g/m² ($P < 0.01$). In 1995 and 1996, with more prolonged drought, there was a reduction of 440 and 526 g/m², respectively. There were consistent differences amongst cultivars in crop dry weight in irrigated conditions ($P < 0.01$), with values, averaged over the three years, ranging from Rialto (1721 g/m²) to Mercia (1620 g/m²). In the two driest years, 1995 and 1996, the biomass depression was, on average, greater for Haven (599 g/m²) than for Maris Huntsman (420 g/m²) ($P < 0.05$). Thus, the grain yield sensitivity of Haven to drought derived, in part, from a sensitivity of total biomass growth to drought.

Averaged over the three years, HI was also diminished with restricted water availability from 0·52 to 0·47 ($P < 0.001$) (Table 3). The decrease was smaller in 1994 (0·03) than in 1995 (0·04) and 1996 (0·08). Averaged over the 3 years, in irrigated conditions HI differed amongst the cultivars from 0·50 (Maris Huntsman) to 0·54 (Riband) ($P < 0.001$). It was greater for the UK-bred semi-dwarfs Riband (0·54), Haven (0·53) and Rialto (0·52) than for the non semi-dwarfs Maris Huntsman (0·50) and Mercia (0·51), reflecting their greater yield potential. This is consistent with previous analyses on the effects of the *Rht2* semi-dwarf gene (e.g. Gale & Youseffian 1985).

Averaged over the 3 years, Rialto (0·033) showed a smaller decrease in HI without irrigation than Maris Huntsman (0·055) and Haven (0·056) ($P < 0.05$). The smaller decrease for Rialto was expressed consistently in each season and related to its smaller than average grain yield depression with restricted water availability. The larger decrease for Maris Huntsman did not lead to a larger than average grain yield depression because it was countered by a smaller than average decrease in harvest biomass. Averaging over the 2 years with prolonged deficits, Rialto (0·043) again maintained HI best and Maris Huntsman poorly (0·072), but Haven (0·066) was more similar to the other three cultivars, for which the decrease ranged from 0·061 to 0·064.

DISCUSSION

The results in the present study allow us to consider responses to restricted water availability in yield-forming processes beyond the responses in harvest biomass (Foulkes *et al.* 2001). We can then consider the traits which may offer the basis for genetic improvement of ability to maintain HI under drought.

Evidence for drought resistance

Yield responses to irrigation in 1995 and 1996 were larger than those reported previously for UK wheat of *c.* 2 t/ha (Innes *et al.* 1985; Bailey 1990). There were three principal reasons for this. Firstly, where rain shelters have been used in previous studies, sites were located on soils of greater AW, e.g. at PBI, Cambridge (Innes *et al.* 1985). Secondly, where irrigation has been applied at the same site (ADAS Gleadthorpe) in previous years, it has normally been applied only up to flowering and not, as in this study, up to harvest (Bailey 1990). Rainfall was also significantly less than previously reported.

Under irrigated conditions, the three UK-bred semi-dwarfs, Riband, Haven and Rialto, outyielded other cultivars, largely through producing more grains/ear, confirming previous reports of improved spikelet fertility conferred by the *Rht2* gene (Gale & Youseffian 1985). But, the cultivars differed in their grain yield responses to restricted water availability in this study. The drought resistance of Rialto and susceptibility of Riband were consistently expressed. Haven, though, only showed susceptibility in the 2

driest years. Similarly Mercia only showed resistance in these years, particularly 1995. Although drought is more commonly encountered later in the season in the UK after flowering (Foulkes *et al.* 1993), growers cannot predict with certainty whether drought will occur early or late in any season. Therefore, a drought-resistant cultivar must, in practice, be resistant to both early and late droughts. This seems to preclude Mercia from categorization as a drought-resistant cultivar. Rialto, in contrast, showed a pattern for resistance in all years.

We therefore conclude that differences in drought resistance were detected amongst cultivars and that such information, if routinely available at an early stage of the national usage of new cultivars in the UK, could offer growers the opportunity to increase yields on drought-prone soils through judicious choice of genotype.

Contribution of HI responses to drought resistance

The approach taken in this study is to analyse yield responses of the six cultivars to restricted water availability, firstly in terms of the ability to maintain harvest biomass under drought, and secondly in terms of the ability to maintain partitioning to grains. Different harvest biomass responses to drought were only found between two cultivars in the dry years of 1995 and 1996: Maris Huntsman (drought resistant) and Haven (drought susceptible) (Foulkes *et al.* 2001). The susceptibility of Haven was linked with restricted water uptake and the resistance of Maris Huntsman to high WUE. Rialto showed a trend for drought resistance across the 3 years at the harvest biomass level, but this did not reach statistical significance in any year.

Harvest index has been reported to be a relatively stable feature for a given cultivar in the absence of severe stress (Gallagher & Biscoe 1978), but effects are commonly reported with drought. For example, the decreases of 0·03, 0·02, 0·09 and 0·09 reported for wheat by Innes *et al.* (1981, 1984), Innes & Blackwell (1983) and Fischer & Wood (1979), respectively. In our experiments, the average decrease from 0·52 to 0·47 under drought was similar to these findings. Improved HI through UK breeding during the 1970s and 1980s has been well documented (Austin *et al.* 1980*b*, 1989; Hay 1995), one of the principal mechanisms being the introduction of the semi-dwarf *Rht2* gene in the mid 1970s (Gale & Youseffian 1985). In this study, this improvement was evident, the semi-dwarfs generally showing greater indices. However, averaged across the 3 years, HI responses of the cultivars to drought differed in these experiments ($P < 0.05$). For example, the decrease of 0·043 for Rialto compared with 0·072 for Maris Huntsman; and these differences contributed to the differences in yield responses to drought.

Traits for maintenance of partitioning to grains under drought

The traits targeted in this study were flowering date and stem-soluble carbohydrate. It was expected that early flowering and large amounts of stem-soluble carbohydrate would confer better maintenance of HI and hence grain yield under drought (Foulkes *et al.* 1993). The cultivars selected broadly represented the full range of genotypic variation available for these traits in UK wheat cultivars, as indicated by the findings of Foulkes *et al.* (1998*b*) for a wider set of 17 UK genotypes. There was evidence for an interdependence between the traits, in that earlier flowering tended to be associated with smaller amounts of stem-soluble carbohydrate. Thus the theoretically desirable combination for drought resistance of early flowering and large stem-soluble carbohydrate was not represented in the six genotypes tested.

Flowering date

Cultivars in this study expressed consistent differences in flowering date within a range of 9 days, but flowering date was found to be poorly correlated with HI responses to restricted water availability. In these experiments, it had been expected that early flowering would be linked with smaller biomass at flowering, and that this would favour post-flowering growth and hence maintenance of HI under drought. Early flowering did lead to smaller biomass at flowering. However, no association was found between the size of the crop at flowering without irrigation and the amount of subsequent post-flowering growth. This could be because, although pre-flowering water uptake was strongly correlated with flowering date in unirrigated conditions, the uptake of water post-flowering was not (Foulkes *et al.* 2001). Thus, the latest to flower (Haven) used *c.* 30 mm less water than Soissons and Mercia during the post-flowering period in 1995, but other later flowering types used only in the region of 5–10 mm less than these two early-flowering cultivars. This was a result of the later flowering types generally showing a larger season-long water uptake, presumably due to an extended period for root growth up to GS61.

In the 2 years with prolonged droughts, cultivar differences in flowering date could be examined in relation to their effects on maintenance of grains/ear. The pattern of depression in grains/ear in these 2 years reflected the extent of drought during the period from ear emergence to the end of flowering, with larger deficits and reductions observed in grains/ear in 1996. Grains/ear seemed, however, to be reduced by two different mechanisms in these years. In 1995, decreases in individual ear weight at flowering under drought were associated with fewer grains/ear, although the extent of the decrease in grains/ear was poorly correlated with flowering date amongst the six

cultivars. This overall effect indicated floret survival to be linked to assimilate supply to the ear, as suggested by Slafer (1996). In 1996, though, individual ear weight was not reduced at flowering, yet grains/ear was diminished most of any season. This implied that ear fertility was reduced due to direct-stress effects in this season, probably at around the time of pollination during flowering. The average maximum temperature during the flowering window was 15 °C in 1995, but 21 °C in 1996 and higher temperature could explain the catastrophic effect in 1996. Equally, corresponding SMDs of 87 and 118 mm – and a greater loss of evaporative cooling with increased water stress in 1996 – could explain the effects. The fact that SMD increased steadily through the flowering window in 1996 but temperature did not, coupled with the observation that the decreases in 1996 were larger for the later flowering cultivars, pointed to SMD as the more likely cause.

In summary, flowering date seemed to have a marginal effect on maintenance of partitioning to grains and grain yield performance in these experiments. The main reason for this appeared to be that under drought the earlier flowering cultivars showed evidence of smaller seasonal water uptake and this countered the advantage of their more favourable distribution of water uptake with respect to the grain-filling period. This result is different from that reported by Innes *et al.* (1985), who found no differences in season-long water uptake between F_5 selections from a Norman × Talent cross differing in ear emergence by 7 days under late drought. The greater grain yield with earliness those authors reported under late drought presumably resulted from more favourable distribution of water uptake with respect to grain filling, although they did not report the proportion of water uptake occurring before and after flowering. In the present study, although a trend for improved maintenance of grains/ear with early flowering was detected in 1996, perhaps associated with avoidance of direct-stress at flowering, this did not lead to improved maintenance of grain yield under drought stress. This suggested that maintenance of assimilate supply (source) rather than grain number (sink) was the more important determinant of the grain yield responses of the cultivars to drought in these experiments. The ability to maintain 'source' was also highlighted as determining cultivar drought resistances by Richards (1983) and Turner (1986).

Stem-soluble carbohydrate reserves

In the experiments described in this paper, cultivars differed in the amount of stem-soluble carbohydrate accumulated shortly after flowering ($P < 0.05$). There was an apparent trend in relation to date of introduction (Table 2) with the more recently introduced cultivars (e.g. Rialto and Haven) tending to accumulate greater amounts of reserves. This trend

with date of introduction has also been observed in experiments testing a wider set of 17 UK genotypes by Foulkes *et al.* (1998*b*). It seems that UK breeders may have inadvertently selected for lines with greater stem-soluble carbohydrate in recent decades when increasing yield potential. It was expected that those cultivars accumulating larger amounts of stem-soluble carbohydrate at flowering would maintain partitioning to grains better under drought. In irrigated conditions, in 2 out of the 3 years, there was a trend for a positive linear regression between the absolute amount of stem WSC dry weight accumulated shortly after flowering and grain yield amongst the six cultivars: 1994 ($R^2 = 0.40$) and 1996 ($R^2 = 0.32$). A similar relationship was found by Foulkes *et al.* (1998*b*) for a wider set of 17 UK genotypes. It seems therefore that stem sugars contributed to grain yield in irrigated conditions in these experiments. In unirrigated conditions, however, the amount of stem WSC proved to be an even more reliable indicator of grain yield in this study. Without irrigation, there was an improvement in the fit of the linear regression of stem WSC on yield, the respective R^2 increasing from 0.40 to 0.84 in 1994 and from 0.32 to 0.54 in 1996. In the other year of 1995, the respective regressions had an R^2 of 0.17 (irrigated) and 0.04 (unirrigated). In this year, crop growth at GS 61 was decreased more without irrigation than in any other season (2·2 t/ha cf. 0·0 t/ha in 1994 and 1·1 t/ha in 1996); this may have prevented the potential differences amongst the six cultivars in stem-soluble carbohydrate being fully expressed. As a result of this work, the UK variety evaluation system has recently added stem WSC to the list of traits of agronomic importance routinely recorded in their Recommended List trials (NIAB, 1997), with the intention of providing early indications of potential drought resistance of cultivars to growers.

Exploitation of traits for drought resistance

Present findings would indicate that the increase in post-flowering water uptake under drought with early compared with late flowering dates reported previously for these cultivars of *c*. 5–10 mm (Foulkes *et al.* 2001) did not lead to improved maintenance of HI under drought, and that flowering date was generally neutral in its effect on HI responses of cultivars to drought. The effect of the small increase in water uptake which was apparent in these experiments may have been countered by a tendency for the early flowering genotypes to amass a smaller amount of stem-soluble carbohydrate. The susceptibility of Haven, the latest flowering genotype examined, in seasons with prolonged drought, seemed to relate to greater sensitivity of stem growth to drought rather than to an effect directly associated with late flowering. The ability to amass greater amounts of stem-soluble carbohydrate shortly after flowering seemed to be

associated with better maintenance of grain yield under drought in this study. Rialto particularly showed a capacity to accumulate large reserves and an enhanced ability to maintain this production in conditions of early-season drought compared to other genotypes. The ability of Rialto to maintain stem growth under drought may have derived, in part, from its longer stem-extension phase, this period coinciding with the period of maximum crown root growth and proliferation (Gregory *et al*. 1978). Future work seems justified to test this and also whether there is a link between the duration of this period and the development of a more extensive root system. Of traits not originally targeted in this study, the duration of this period would seem to offer scope for improving drought resistance. In addition, as previously reported by Foulkes *et al*. (2001), high water use efficiency may have contributed to the better maintenance of biomass for Maris Huntsman. It was suggested that breeders might screen candidate lines for this character using the $^{13/12}$C technique to improve drought resistance.

There were too few varieties in the present work to conclude with certainty about desirable combinations of traits for drought resistance. Nevertheless it can be tentatively suggested that a combination of: (i) an extended phase for stem extension, (ii) the ability to allocate large amounts of biomass to stem carbohydrate reserves and (iii) high water use efficiency might provide a feasible ideotype for drought resistance in the UK's temperate climate. All these traits are known to be heritable and all can be monitored and favoured in breeding programmes with relative ease. With predicted climate change and more frequent summer droughts (Marsh 1996), we conclude that such an approach should be valuable for breeding programmes in future years.

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