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Predictability of wheat growth and yield in light-limited conditions

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SUMMARY

In seeking better predictions of grain yield under light-limited conditions, shading was applied to field-grown winter wheat cv. Slejpner during each of five consecutive phases (canopy expansion, ear expansion, pre-flowering, grain expansion and grain filling). Absolute measures were taken of solar radiation and its effects on growth in three seasons, at a site where water and nutrient supplies were not limiting. Replicate mobile shades automatically occluded 0·80 of incident light when mean total solar radiation exceeded 250 J/m^2 per s. Mean effects over seasons of shading on incident total solar radiation were −296, −139, −78, −157 and −357 MJ/m^2 for the five phases respectively, and corresponding effects on shoot dry weight were −236, −184, −58, −122 and −105 g/m^2. Estimated efficiency of radiation use after flowering was 1·2 g/MJ unshaded, tending to increase with shading. Shading in all phases reduced grain dry matter yield: mean effects over seasons were −106, −64, −61, −93 and −281 g/m^2 for the five consecutive shading periods. Shading from GS31–39 increased mean maximum area of the two top leaves from 2700 to 3100 mm^2 per leaf but, with fewer stems, canopy size remained unaffected. This and the next shading, from GS39–55, reduced specific leaf weight from 42 g/m^2 by 4 and 3 g/m^2 respectively, but effects on shoot dry weight were largely due to stem and ear. By flowering, stem weights, and especially their reserves of water-soluble carbohydrates, had partially recovered. Effects on yield of shading from GS31–39 were explained by a reduction in grains/m^2 of 3070 from 26 109. Shading from GS39–55 reduced grains/m^2 by 4211 due to fewer grains per ear, whilst mean weight per grain increased in compensation. Shading from GS55–61 decreased grains/ear by 2·5. Shading from GS61–71 decreased ear growth and reduced stem weight, and at harvest resulted in 4·3 less grains/ear. Effects of the final shading from GS71–87 were fully explained by a reduction in mean dry weight/grain of 10·3 mg. Except for shading from GS71–87, source- and sink-based explanations of grain yield both proved feasible, within the precision of the measurements. Constraints to accurate comparison of source- and sink-based approaches are identified, and the implications for yield forecasting are discussed.

INTRODUCTION

Given the importance of wheat as a global food and energy source, and as a subject of scientific research, it is unsatisfactory that the predictability of wheat yields remains poor (e.g. Porter *et al.* 1993; Landau *et al.* 1998) and that physiological models are rarely used to support commercial production, either at farm, regional or national scales (Stone & Hochman 2004).

Irresolution between sink- and source-determination of grain yield (Sinclair & Jamieson 2006) is one obstacle to its predictability. Current simulation models of wheat take the principal determinant of yield to be radiation intercepted during the grain-filling period, with some contribution from pre-anthesis assimilate, i.e. they are primarily source-driven (Ritchie & Otter 1985; van Laar *et al.* 1992; Jamieson *et al.* 1998; Keating *et al.* 2001), although sink constraints have sometimes been added

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(Moreno-Sotomayor & Weiss 2004). Also, insofar as they are rationalized physiologically, crop management decisions on protection and nutrition tend to target leaf area and longevity, hence use a source-driven analysis (e.g. Waggoner & Berger 1987; Bryson *et al.* 1997; Sylvester-Bradley *et al.* 1997; Milne *et al.* 2003; Audsley *et al.* 2005). This is despite many findings that yields are sensitive to light-limitation in the pre-anthesis period when grain numbers are determined (Fischer & Stockman 1980; Fischer 1985; Calderini *et al.* 2001), and that responses to nutrition relate well to grain number (Demotes-Mainard *et al.* 1999), suggesting that they are sink-driven. The majority view on sink versus source limitation (e.g. Thorne 1974; Evans & Wardlaw 1996) now appears to be that unstressed (i.e. light-limited) yields are generally determined by sink size (e.g. Evans 1978; Woodruff & Mawhood 1978; Fischer & Stockman 1980; Fischer 1985; Savin & Slafer 1991; Slafer & Savin 1994; Richards 1996; Borras *et al.* 2004; Shearman *et al.* 2005). However, most of the evidence has come from lower yielding environments than the dull, moist regions of north-west Europe.

Two difficulties arise in trying to develop a predictive approach from sink-based analyses of wheat yields. Firstly, the sink has not been convincingly defined in absolute terms; no observable determinant of potential weight/grain has emerged. Secondly, effects of shading on yield, used to conclude that wheat is sink-limited, have generally been expressed in relative terms (e.g. Slafer & Savin 1994). Few shading experiments have provided the absolute measures of both incident radiation and crop structure necessary to develop a predictive approach. For instance, shading has often been defined by a relative reduction of incident radiation, without presenting associated measures of ambient conditions (e.g. Willey & Holliday 1971; Kemp & Whingwiri 1980; Grabau *et al.* 1990). Also, some of the other experimental methods used to test the balance between source and sink limitation may have exaggerated source size (for instance through use of de-tillered plants; Slafer & Savin 1994), or tested unrealistically large variation in source (the review of Borras *et al.* (2004) includes two- to five-fold increases in assimilate availability/seed).

Most above-ground wheat dry matter (DM) in north-western Europe is formed from May to July. Mean daily solar radiation in May, June and July is similar at ~18 MJ/m^2, but weather is often cloudy (sun hours in eastern UK are about one third of daylight hours) and variation in radiation is large (being distributed rectangularly, with a negative skew; Thomas & Norris 1982). The cyclonic climate frequently imposes periods of cloud or sun which can last several days or weeks. Thus, important components of grain yield are often determined under contrasting light conditions, and this may have significant implications for yield predictions, and consequently for crop management.

Table 1. *Dates of the start of stem extension and subsequent durations of phases used to define the shading treatments in three seasons at ADAS Terrington*

Season	1993/94	1994/95	1995/96
Development stage		*Date of stage*	
First node detectable (GS31)	2 May	12 Apr	30 Apr
Development phase		*duration of phase (days)*	
Canopy expansion (GS31–39)	27	42	35
Ear emergence (GS39–55)	17	14	7
Pre-flowering (GS55–61)	8	14	6
Grain expansion (GS61–71)	14	14	14
Grain filling (GS71–87)	26	26	28

The work described in the present paper quantified, in absolute terms, the influences on wheat crops of variations in sunlight during successive development phases from stem extension to grain filling, at a site representative of high-yielding conditions in north-west Europe. An analysis is presented of how yield formation might be best explained in terms of energy receipts. Shading periods were defined to affect particular yield-forming processes as distinctly as possible (accepting that some processes overlap, or are concurrent), although this resulted in shading periods of unequal length. Periods were defined by growth stage (Tottman 1987), with the predominant processes being canopy expansion, stem extension and shoot survival (from GS31–39), ear expansion and floret formation ('booting'; GS39–55), stem reserve deposition pre-flowering (GS55–61), grain expansion (GS61–71) and grain filling (GS71–87). A shading technique was developed for field plots, to mimic the effect of cloudy periods, and to have minimal effects when ambient conditions were dull, dark or raining. Absolute measurements were made of meteorological conditions, growth and partitioning after each phase of crop development, and grain yield.

MATERIALS AND METHODS

Experimental design, treatments and husbandry

One experiment in each of harvest years 1994, 1995 and 1996 tested five shading treatments and an unshaded control (Table 1) applied to winter wheat (cv. Slejpner) on a deep, stoneless silty clay loam over silty clay at ADAS Terrington, Norfolk, UK, (0°17′E, 52°44′N). Previous crops were peas, linseed and linseed in 1994, 1995 and 1996, respectively. In 1994 there were two blocks, each with six main-plots receiving

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randomly allocated shading treatments; data were collected from all plots on all dates. In 1995 and 1996 the shading treatments were arranged in a Latin square of six rows and six columns. In addition to the fungicide-treated subplots described in the present paper, three further subplots, untreated or partially treated with fungicide, were included within each main-plot (18 × 8 m); results from these are to be reported elsewhere. Thus in each year six shading treatments are considered, applied to fungicide-treated plots measuring 8 × 5 m; these were replicated twice in randomized blocks in 1994, and six times in a Latin square in 1995 and 1996. Experiments were sown on 5 November 1993, 24 September 1994 and 30 September 1995 with 350–380 seeds/m². Applications of fertilizers and agrochemicals were made to avoid effects of nutrient deficiency, weeds, pests or diseases on crop growth or grain yield. All subplots were assessed weekly for foliar diseases, pests, lodging and other problems. No adverse effects were noted other than those described in the results.

Shading technique

Mobile shades were constructed of a similar design to the automatic rain shelters described by Weir & Edwards (1985), such that (except on the few days when there was a malfunction) direct light was occluded only during periods when ambient solar radiation exceeded a pre-set threshold (daily data are shown in Fig. 1; shade construction and operation are described in the Appendix).

Daily rainfall, temperature, wind speed, humidity and total solar radiation during the experiments were calculated from logged hourly data using two automated weather stations (Delta T, Cambridge), one located centrally within the area of the experiment, and one within a main-plot designated for shading. Preliminary studies before the experiments began showed that the shading devices occluded 0·79 of photosynthetically active radiation, with minimal effects on spectral distribution in the visible range. Variation in the effect on total solar radiation over the shaded area was from 0·76 at the edge to 0·84 in the centre. The average effect on total solar radiation on bright days (> 20 MJ/m²) was 0·69 and the effect over all shading treatment periods over all three seasons was 0·60. The reduction due to shading in daily mean air temperatures, averaged over all growth phases, was 0·5°C, the largest reduction being 1·7°C during 6 days from GS55–61 in 1996. Analysis of daily data shows no significant effect on relative humidity, although shading reduced mean daily wind-speed by 0·8 m/s (41 %) on the most shaded days. Under manual operation in 1994, total rainfall was reduced by about 8 %, due mainly to showers during bright days, but under automated operation in 1995 and 1996, rainfalls were unaffected.

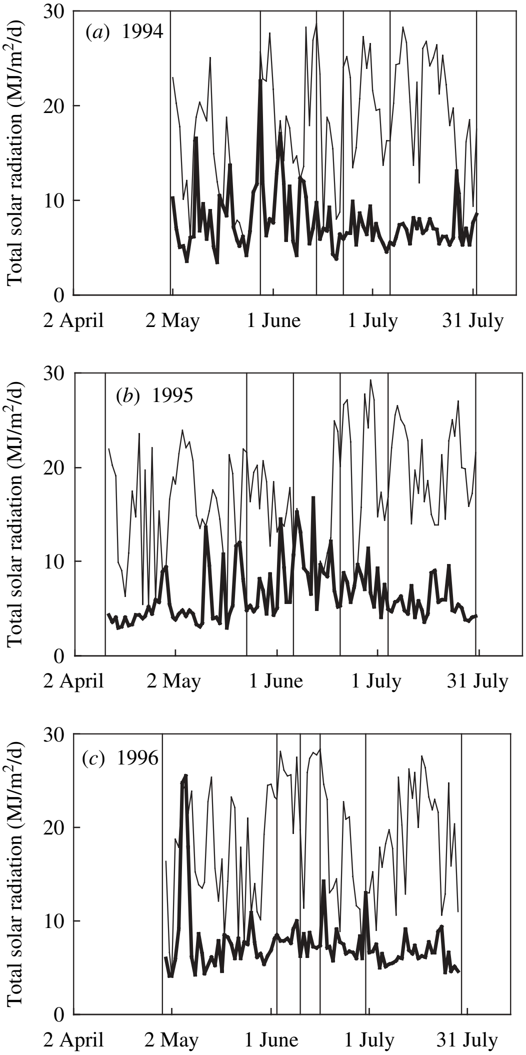

Fig. 1. Daily total solar radiation without (fine lines) and with (bold lines) shading at ADAS Terrington in 1994, 1995 and 1996. Vertical lines indicate divisions between shading periods.

Crop measurements

Adjacent areas were allocated for crop sampling and combine-harvesting within each sub-plot. Growth stages were recorded weekly on all subplots (Tottman 1987). At GS31, leaves on the mainshoots of 10 plants in each shading treatment were tagged and leaf emergence was recorded weekly until GS39 so that the relation of visible leaves to the flag leaf could be identified in retrospect. The length and width of each culm leaf blade were measured on five shoots from each subplot each week from GS31 until canopy

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death and individual leaf areas were calculated using a form factor of 0·83 (Bryson *et al.* 1997).

At the start and end of each shading treatment period, shoot number, dry weight, green area and nitrogen (N) content were measured (on all subplots in 1994 and subplots in three of the six blocks in 1995 and 1996) by taking all above-ground material from a quadrat (0·5 m^2 or more) placed diagonally to the rows and storing this in sealed bags at 4–6°C prior to analysis. On one 0·1 subsample live, dying and dead shoots were counted and the live shoots were separated into green leaf, green stem (subsequently referred to as 'stem', but note that leaf sheaths remained attached), and green ear and passed through a leaf area meter (Delta-T, Cambridge). Green area index (GAI) was expressed as the ratio of total projected green areas of leaves, stems and ears to ground area. Green tissues were recombined with their respective dead and dying tissues, and lamina, stem and ear components were dried at 80°C and weighed. Another 0·15–0·20 subsample was separated into ears (unemerged ears were extracted from the flag-leaf sheath in 1995 at GS55, and in 1996 at GS39 and GS55) and 'rest', dried at 80°C for 16 h, weighed, ground and analysed for total N by a combustion method, using a Leco FP-228 determinator (Leco Corporation, St. Joseph, Michigan).

Total radiation intercepted in each period was estimated from incident radiation and GAI (assuming linear changes between sampling dates), according to Beer's Law (Gallagher & Biscoe 1978), assuming extinction coefficients of 0·45 for GS31–39, 0·50 for GS39–55, 0·55 for GS55–61, 0·60 for GS61–71 and 0·65 for GS71–87. Interception of solar radiation was estimated, rather than measured, on the basis that, when extinction coefficients were estimated from incident and transmitted radiation logged over periods of several days, Thorne *et al.* (1988) found little variation for a single variety grown in a range of conditions. Extinction coefficient was assumed to increase during crop development because of evidence that bias occurs in assessing green tissue areas (or the interception for which this is responsible) and that these biases increase as senescent and dead tissues accumulate during development (D. T. Stokes, personal communication). The effects of this adjustment on radiation intercepted were usually small, since green areas were almost always sufficient for interception of 0·7.

On the day of each quadrat-sampling, adjacent shoots were taken for analysis of soluble carbohydrate in stem material: within an hour of mid-day, six shoots were cut at ground level, placed immediately in a sealed bag, transported within an hour in a cool box to the laboratory where leaf blades and ears were discarded, and stems were dried at 102°C in a forced-draught oven for 2 h, weighed and subsequently analysed for water-soluble carbohydrate (MAFF 1986). Amounts of soluble carbohydrate in stem material (g/m^2) were calculated by multiplying the concentration (dry basis) by total stem weight of the quadrat sample.

Within a day prior to harvest, more than 100 shoots were cut at ground level from several positions within all subplots, weighed, threshed, the chaff being retained with the straw, reweighed as grain and 'rest', dried at 80°C to constant weight and the weights recorded. The 'rest' was analysed for N by Leco; the grain was analysed for N by near-infrared reflectance (NIR systems model 6500, using Infrasoft International software for calibration and correction; Barnes *et al.* 1989), and a 100 g subsample was counted. Components of crop performance at harvest were then calculated on a per shoot basis. Shoots/m^2 were not determined at harvest. To express harvest results, including grain yield, on an area basis and to maximize precision and consistency with previous measurements, values/shoot were multiplied by the shoot numbers/unit area, averaged from the four samplings between GS55 and GS87. There was no significant change after GS55.

Grain yields were also determined by combine harvesting a strip of at least 10 m^2 from each subplot. As is common (Bloom 1985), these estimates showed a negative bias compared with those from hand-sampling: the mean biases were −15%, 0% and −17% in 1994, 1995 and 1996, respectively.

RESULTS

Seasonal growing conditions

The three summers in which the experiments took place were well suited to a study of light, in that ambient total solar radiation from May to July in each year exceeded the local 8-year average of 17·6 MJ/m^2 per day (Table 2). Rainfalls were small (Table 2), but all three fields had soil with at least 170 mm/m available water to at least 2 m depth (Hall *et al.* 1977), i.e. >250 mm, so even with the maximum soil moisture deficit of 157 mm in July 1995 (calculated by MORECS; Thompson *et al.* 1981), only occasional symptoms of drought were seen. Drought was thus unlikely to have affected growth significantly.

The autumn of 1993 was cold and wet, and plant establishment was poor. Subsequent crop growth was slow, and there were only 595 shoots/m^2 with a GAI of 1·4 when stem extension began (GS31) on 2 May 1994. By contrast, drilling was achieved in satisfactory conditions on 24 and 30 September in the 2 following years, plant establishment was good, and over-winter growth was more successful. It was warm from sowing until February 1995 and there were 805 shoots/m^2 and a GAI of 2·1 when stem extension started on 12 April 1995.

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Table 2. *Mean daily temperature, total rainfall and solar radiation for the three growing seasons in which shading experiments were conducted, and long-term means for 1961–1990 at ADAS Terrington. Average annual total solar radiation was taken from Denver, Norfolk for 1986–1993*

	Total Rainfall mm	Mean temperature °C	Total radiation MJ/m² per d
		Sep–Aug	
Long-term mean	585	9·4	9·8
1993/94	696	9·9	9·7
1994/95	485	10·6	10·5
1995/96	475	9·4	10·1
		May–Jul	
Long-term mean	150	13·7	17·6
1993/94	100	15·1	17·8
1994/95	51	14·8	17·7
1995/96	78	13·4	18·5

Table 3. *Total incident solar radiation, with (+) and without (−) shading, for successive phases of wheat development in three seasons at ADAS Terrington*

Season	1993/94		1994/95		1995/96	
Shade	−	+	−	+	−	+
Development phase	*Solar radiation (MJ/m²)*					
Canopy expansion (GS31–39)	376	222	652	226	590	282
Ear emergence (GS39–55)	334	160	226	99	172	57
Pre-flowering (GS55–61)	124	50	187	131	149	46
Grain expansion (GS61–71)	283	95	281	104	219	112
Grain filling (GS71–87)	518	180	526	143	530	179

Despite uniform management in 1995, parts of the 1995/96 experiment showed distinct patchiness in spring, before treatments were applied. Aerial photographs showed that patches related clearly to cropping in the same field 2 years previously. Land that had been bare in 1994 (affecting 15 subplots) produced a mean of 1227 shoots/m² and a GAI of 4·5 containing 132 kg N/ha by the start of stem extension in 1996, whereas land which had been cropped in 1994 (21 subplots) had 1017 shoots/m² and a GAI of 2·8 containing 75 kg N/ha. Associated differences in crop growth occurred throughout the summer of 1996. A study of potential covariates, including ground cover in 1994 and measurements taken before treatments were applied in 1996, determined that crop N (kg N/ha) at GS31 was most effective in reducing residual variation in the statistical analyses of growth measurements made from GS31 to GS87. Therefore this covariate was used in the statistical analyses.

Crop husbandry practices in 1994 and 1996 prevented any visible nutrient deficiencies, weed or pest infestations, and there was no lodging in any year. However, windy weather in May 1995 caused an intended fungicide application to be postponed from flag leaf emergence (GS39) until the onset of ear emergence (GS51) and an epidemic of yellow rust (causal organism *Puccinia striiformis*) subsequently developed which reached maximum severities of 32%, 31% and 17% on the flag leaf, leaf 2 and leaf 3 (counting from the flag) respectively. This epidemic substantially reduced canopy size after GS39 and is relevant to consideration of crop growth.

Development stages were reached early in 1995 and late in 1994, with 1996 being intermediate, and the durations of the phases of development differed between seasons (Table 1). The shading treatments did not affect development, except for the first shaded period in 1995 when emergence of each of the last three leaves and the ear was delayed by about 1 week, and (even though there were no noticeable symptoms when shading stopped on 21 May) the subsequent yellow rust epidemic was also reduced (see below). This delay was reduced to about 2 days by the time of flowering. The durations of shading treatments were held to coincide with the development of the unshaded crop. Thus in 1995, shading was not applied during the final week of flag emergence. Differences in phase duration were more significant for the receipt of solar radiation within each phase than were seasonal differences in the intensity of solar radiation. The cumulative solar radiation during each development phase, and the effects of shading on this are shown in Table 3. The reduction in solar radiation due to shading varied between periods depending on the proportion of sunny days; overall the shading treatments reduced radiation levels to 41% of ambient, reductions ranging from 56 MJ/m² pre-flowering in 1995 to 426 MJ/m² during canopy expansion in 1995.

The patterns of incident solar radiation (Fig. 1) generally exemplified the contrasts that occur in incident light during any growth period under temperate conditions; total solar radiation during the five phases in the 3 years ranged from 0·76–1·41 of long-term average (Tables 2 and 3). For instance, in the pre-anthesis periods (GS39–55 and GS55–61) in 1995, solar radiation was only 0·60 of that in the same periods in 1996. Thus, although some shading effects in these experiments were large (−0·27 to −0·70 of

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Table 4. *Effects of shade during canopy expansion (GS31–39) on maximum total areas of culm leaf laminae of winter wheat cv. Slejpner in three seasons at ADAS Terrington. Maximums were taken as the greatest mean area over three consecutive weeks, calculated from weekly measurements of leaf length and width, using a form factor of 0·83 (Bryson* et al. *1997)*

Season	1993/94		1994/95		1995/96	
Shading	−	+	−	+	−	+
	Area per leaf (*mm*^{2})					
Flag leaf	2901	3666	2487	3400	2437	2620
Leaf 2	2570	2980	3172	3490	2650	2644
Leaf 3	1769	2088	2890	2894	2341	2261
Leaf 4	1627	1617	2364	2565	1810	1706

ambient incident radiation), they were in keeping with the variable pattern of incident light in the UK.

Effects of shading on microclimate were small, treatment periods were relatively short and effects on development were slight. Apparent leaf extension effects (Table 4) indicate that leaf temperatures were more affected than air temperatures, but even a difference of a few degrees is unlikely to have affected photosynthetic rates at these light intensities (Baker *et al.* 1988).

Canopy expansion (*GS31–39*)

Immediate effects on shoot numbers, green leaf areas, total dry weights and its component weights of stems and leaves will be considered first, followed by any lasting effects on yield formation.

In all seasons, numbers of shoots decreased during stem extension. The decrease was largest in 1996 when the initial shoot number was 1070/m^2, and smallest in 1994 when the initial shoot number was 610/m^2. Nevertheless, ultimate fertile shoot numbers were most in 1996 at 620/m^2, least in 1994 at 440/m^2, with 550/m^2 in 1995. There were no statistically significant effects of treatments on shoot numbers on any occasion, although average shoot numbers over the period during which they remained stable (GS55 to GS87) showed reductions of 26, 31 and 44/m^2 due to the first shading period in the three seasons, respectively. Slafer *et al.* (1994) concluded that small shading effects on shoot numbers such as these generally occur in crops with few tillers/plant, often due to dense plant establishment. Plant numbers were not observed directly in the present experiment, however, the small shading effects could only have supported the explanation suggested by Slafer *et al.* (1994) if establishment of seeds sown had been very high: 0·90, 0·85 and 1·00 in each season, respectively. These levels are more than could have occurred in 1994 when establishment was poor, and also in 1996 when emergence was $< 1·00$.

Stem extension was concurrent with emergence of the last three leaves. Maximum area of a leaf was reached within 2 weeks of its emergence in 1994 and 1995 but, in the cool conditions of 1996, leaf expansion continued gradually until early June (6, 4 and 2 weeks after emergence of leaves 3, 2 and the flag respectively). Final leaf size generally increased from leaf 4 to leaf 2, but the flag leaf was smaller than leaf 2 in 1995 and 1996. Culm leaf areas varied considerably between seasons (Table 4).

GAIs increased during this phase (Fig. 2) and were still increasing as it ended due to emergence of stem and ear and some further leaf expansion. The early decrease in GAI following GS39 in 1995 was due to disease. Maximum GAI was not large in any year, and was particularly small in 1994 (4·9). The effects of shade during canopy expansion were to increase the maximum total area of the top two leaves from 5500 to 6700 mm^2 in 1994, from 5700 to 6900 mm^2 in 1995, and from 5100 to 5200 mm^2 in 1996 (Table 4), and to prolong leaf expansion in 1995. However, these differences in leaf area were countered by the small reductions in shoot number, so that there were no significant effects of shading on GAI (Fig. 2) in any year. In 1995, the yellow rust epidemic was not measurable until after flag leaf emergence. Individual leaf measurements show that shading during canopy expansion decreased the tissue area subsequently showing symptoms by about 4 cm^2/shoot. This contribution to the +20 cm^2/shoot net effect of early shading on green area per shoot was also insufficient to cause a significant effect on GAI at any stage.

The small initial canopy in 1994 was estimated to have resulted in only 0·63 light interception during canopy expansion. Canopies in other years were sufficiently large to have intercepted more than 0·8 of incident light during this phase. Growth in total shoot dry weight during canopy expansion during the dull conditions of 1994 was small at 209 g/m^2, compared with 726 in 1995 and 665 in 1996 (Fig. 3). Over all seasons, this growth was partitioned 0·11–0·34 to leaf, 0·43–0·46 to structural stem and 0·22–0·34 to soluble stem (Table 5).

There was no statistically significant effect of shading on DM growth in 1994, but shading reduced growth by 411 g/m^2 in 1995 and 292 g/m^2 in 1996. The effects of shading on leaves were relatively small, whereas soluble stem weights were affected disproportionately more. Mean specific leaf weights were significantly less after shading at GS39 (38 g/m^2 compared with 42 g/m^2) in both 1995 and 1996, an effect which was just visible in the field, the leaves being paler, more lax in posture and shiny.

In summary, the effect of shading during stem extension and canopy expansion was to leave shoot

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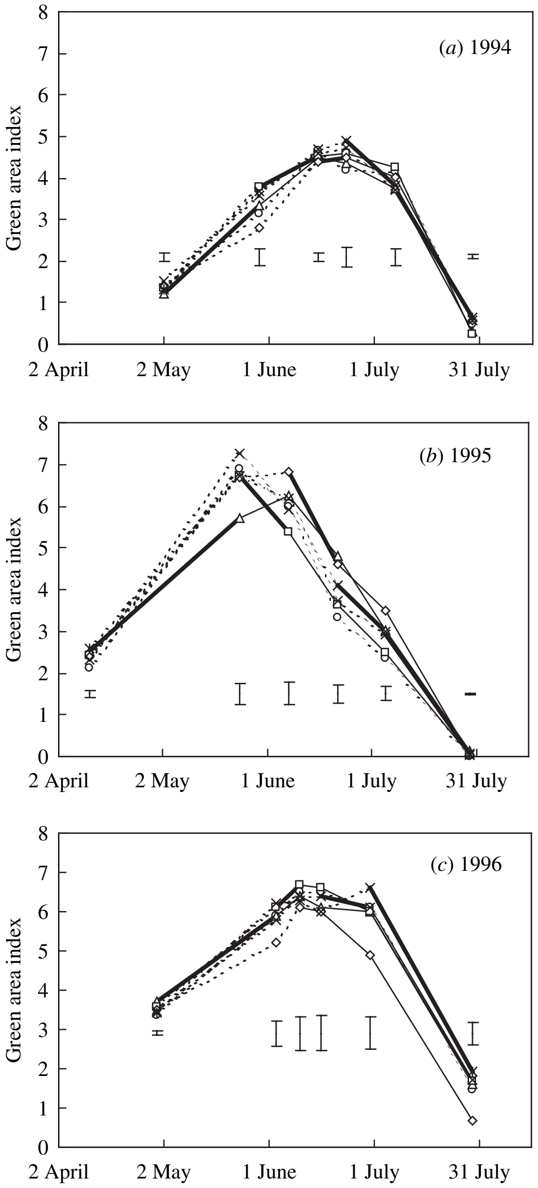

Fig. 2. Green Area Index for an unshaded control (○) and five treatments shaded in successive phases of wheat's development (GS31–39 Δ, GS39–55 □, GS55–61 ◇, GS61–71 × and GS71–87 ⋇) in three seasons at ADAS Terrington. The shaded period of each treatment is shown by a bold line. Vertical bars indicate one S.E.D.

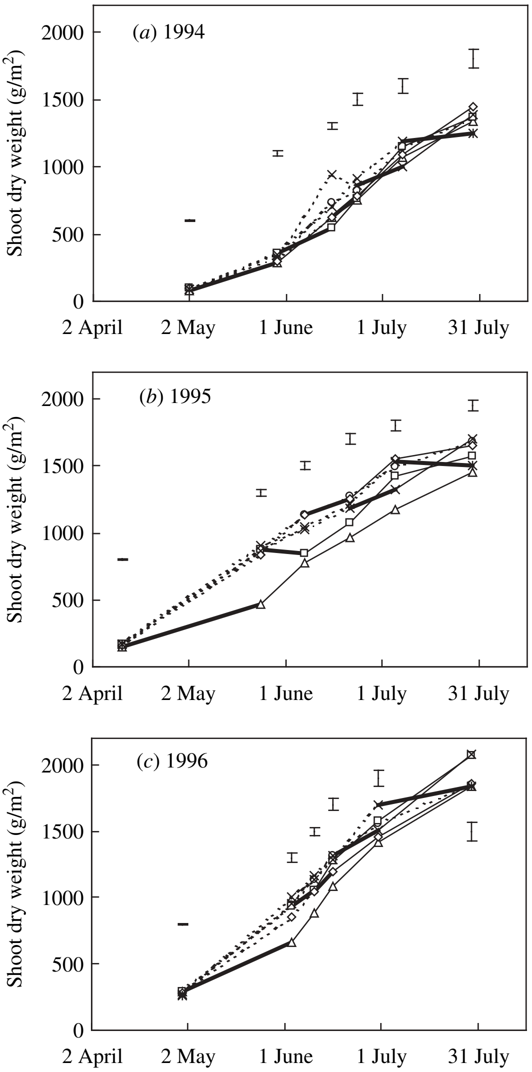

Fig. 3. Total shoot dry weight for an unshaded control and five treatments shaded in successive phases of wheat's development in three seasons at ADAS Terrington. Symbols as in Fig. 2. The shaded period of each treatment is shown by a bold line. Vertical bars indicate one S.E.D.

number and photosynthetic capacity relatively unaffected, but shoot dry weight substantially reduced. The reductions in dry weight persisted through to grain filling in 1995 and to flowering in 1996; by the end of grain filling, differences from the control were only statistically significant for 1995 at 227 g/m^2. Recovery from the treatment effect was most noticeable in the soluble stem component, but specific leaf weight and the weight of structural stem recovered in part (Fig. 4 and Table 5).

At harvest in 1994, there were no significant effects of shading from GS31 to GS39, but grain yield was significantly reduced by about 1·0 t/ha in 1995 and 1·1 t/ha in 1996 (Table 6). Although none of the differences in components of yield was significant in 1995, the main contributor to the reduction in yield

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Table 5. *Changes in dry weight* (g/m^2) *for shoot components of winter wheat cv. Slejpner during each shading period in three seasons at ADAS Terrington. 'Structural stem' refers to the difference between total stem and soluble stem material. Before full ear emergence in 1995 and 1996, ears were extracted from sheaths* (*ND: not determined*)

Season	1993/94			1994/95			1995/96		
Shading	−	+	S.E.D.	−	+	S.E.D.	−	+	S.E.D.
GS31 to GS39					(g/m^2)				
Leaf lamina	71	76	14	146	99	20	81	44	28
Structural stem	91	94	14	332	156	21	295	219	41
Soluble stem	47	40	7	248	60	20	194	72	19
Ear	ND	ND		ND	ND		95	38	9
Total	209	208	31	726	315	41	665	373	80
GS39 to GS55									
Leaf lamina	28	−10	18	−6	−52	26	22	8	34
Structural stem	243	151	37	121	51	36	99	96	23
Soluble stem	155	40	17	−19	−112	22	−18	−54	19
Ear	ND	ND		161	87	12	94	71	17
Total	431	190	55	257	−26	67	196	121	52
GS55 to GS61									
Leaf lamina	−14	4	20	−14	−44	23	−10	−7	40
Structural stem	−33	12	53	69	75	42	30	76	29
Soluble stem	−40	−17	24	20	7	30	80	29	18
Ear	179	163	28	66	83	17	73	53	15
Total	92	162	101	141	121	80	173	152	52
GS61 to GS71									
Leaf lamina	13	−1	14	−26	3	33	5	9	27
Structural stem	−7	9	27	−48	−2	53	−13	8	35
Soluble stem	61	−37	21	13	−50	27	46	−25	28
Ear	255	166	37	281	185	26	207	197	30
Total	320	137	77	221	137	102	244	189	89
GS71 to GS87									
Leaf lamina	−58	−44	21	−68	−87	33	−76	−90	27
Structural stem	−41	−11	37	−22	−95	54	−69	−52	37
Soluble stem	−191	−199	30	−241	−161	22	−281	−307	20
Ear	506	315	111	517	304	59	724	587	113
Total	218	60	159	187	−39	116	299	138	156

appeared to be the number of grains per ear. In 1996, grains/ear was reduced significantly from 49 to 42 whilst weight/grain was increased significantly from 40 to 43 mg (Table 6).

Ear expansion (*GS39–55*) *and pre-flowering* (*GS55–61*)

The phase between emergence of the flag leaf and the ear (GS39–55) lasted from 7 to 17 d (Table 1); cumulative total solar radiation and the effects of shading on this were considerably less than during stem extension (Table 3), but unshaded growth during this period was significant at 431, 257 and 196 g/m^2 in the three successive seasons. There were no significant effects on shoot numbers, leaf areas or GAI, but growth in total shoot dry weight was decreased, roughly in line with the reductions in solar radiation, by 241, 283 and 75 g/m^2 in the three seasons. The decreases in 1994 and 1995 were attributable mainly to effects on stems, particularly their soluble components (Fig. 4), on ear weight (Table 5), and specific leaf weight was reduced by 3 g/m^2. After shading ceased at GS55 there was a particularly rapid accumulation of soluble stem components compared with other treatments (Fig. 4). This shading period decreased ear weight at flowering by 39, 65 and 31 g/m^2, and grain number/ear determined at harvest by 8, 9 and 7 respectively (Table 6). The effects on grain yield in the three seasons related more closely to the earlier effects on dry weight than to the effects on grain number.

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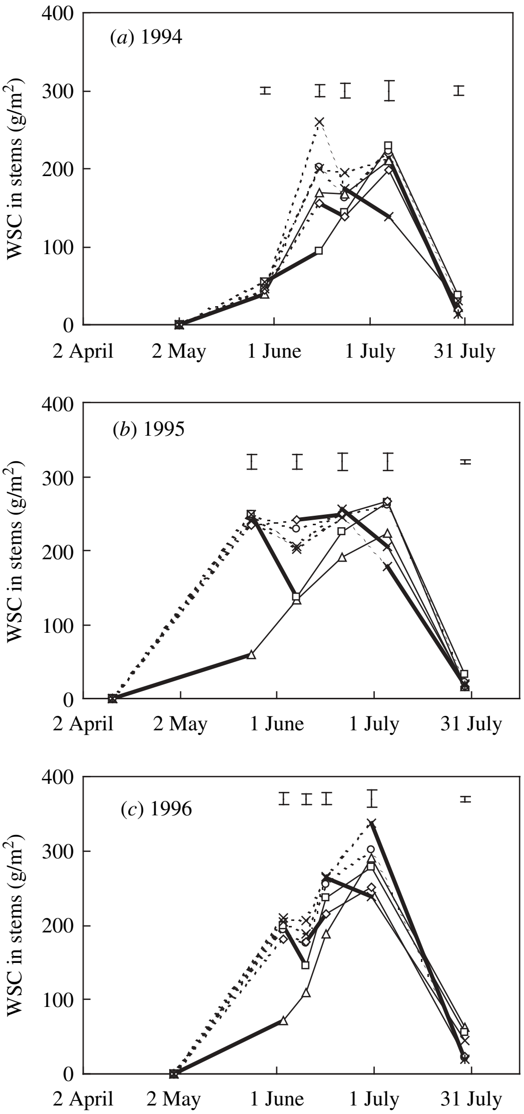

Fig. 4. Water-soluble carbohydrate (WSC) of stems and sheaths for an unshaded control and five treatments shaded in successive phases of wheat's development in three seasons at ADAS Terrington. Symbols as in Fig. 2. The shaded period of each treatment is shown by a bold line. Vertical bars indicate one S.E.D.

Growth during the short phase from ear emergence to flowering (GS55–61) was 135 g/m^2 on average, most of which was due to ears, but included some stem growth in 1996 (Table 5). There were no statistically significant effects of shading at the end of the period; surprisingly, even soluble stem components were unaffected. At harvest, shading from GS55–61 decreased grain yield by 0·14, 0·40 and 1·65 t/ha in the three seasons, and although the changes were too small to be accounted for by yield analysis, the most consistent impact appeared to be on grains/ear which decreased by a mean of 2·5 (Table 6).

Grain expansion (*GS61–71*)

The phase from flowering to the watery ripe (GS61–71) lasted 2 weeks in all three seasons. Unshaded growth in total shoot dry weight was 320, 221 and 244 g/m^2 and was mainly due to ear growth, however, a further 13–61 g/m^2 of soluble stem was also accumulated. Shading from GS61–71 reduced total growth by 183, 84 and 55 g/m^2 in the three seasons; this was due to depletion of stem carbohydrates by 98, 63 and 71 g/m^2 and, in 1994 and 1995, to reducing ear growth by 89 and 96 g/m^2, respectively. At harvest, shading from GS61–71 decreased grain yield by 1·35, 1·12 and 0·48 t/ha in the three seasons; there was a decrease in weight per grain of 3 mg in 1995, but the more consistently affected yield component was grains/ear, with 10, 1 and 2·5 less in the three seasons respectively (Table 6).

Grain filling (*GS71–87*)

The canopy senesced rapidly from watery-ripe to hard dough stage (GS71–87; Fig. 2). The patterns of canopy senescence in the three seasons were quite different, particularly due to the yellow rust epidemic in 1995. Effects of shading on senescence were not evident from GAI measurements but individual leaf data indicate delays in senescence due to early shading in 1995 and late shading in 1994. In each year, the unshaded treatment was the first to lose all green area.

Only ear dry weight increased during this phase; leaves and stems decreased in weight, particularly the soluble component of the stem (Table 5). In all 3 years, this apparent redistribution of dry weight exceeded new growth. Shading decreased total growth by 158, 226 and 161 g/m^2 in 1994, 1995 and 1996, mainly due to effects on ear growth. Soluble stem components decreased to almost zero during this phase, whatever their treatment history (Fig. 4), so there was no evidence for an increase in redistribution of stem material as a result of shading. At harvest, shading from GS71–87 decreased grain yield by more than any other shading treatment, the effects being 2·49, 2·66 and 3·06 t/ha for the three seasons (Table 6). This was largely due to a decrease of about 10 mg in weight per grain in each season. Harvest index was affected in each year, by −0·08, −0·07 and −0·07 respectively (Table 6).

Other post-anthesis shading studies have also normally shown the majority of the effect on dry weight to be accounted for by the grain, such that harvest index decreases markedly (Willington & Biscoe 1985, −0·11; Martinez-Carrasco & Thorne 1979, −0·11;

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Table 6. *Effects of shade on crop performance at harvest in three seasons at ADAS Terrington. Ear numbers are averages of quadrat samples taken between GS55 and GS87 (ND: not determined; S.E.D.: standard error of difference)*

Season Shading	Grain DM t/ha	Shoot DM g/m²	Harvest index	Ear DM g/ear	Chaff DM g/ear	Ears/m²	Grains/ear	Grains/m²	Grain DM mg/grain	Grain N mg/g	Grain N g/m²
1994											
none	9·2	1537	0·60	2·6	0·45	434	54	23 299	40	ND	ND
GS31 to 39	8·5	1456	0·58	2·5	0·45	415	54	22 581	38	ND	ND
GS39 to 55	8·6	1480	0·58	2·4	0·41	433	46	19 764	43	ND	ND
GS55 to 61	9·1	1548	0·59	2·5	0·44	437	53	23 201	39	ND	ND
GS61 to 71	7·9	1393	0·57	2·1	0·39	458	44	20 174	39	ND	ND
GS71 to 87	6·7	1286	0·52	1·9	0·43	448	53	23 642	28	ND	ND
S.E.D.	*0·93*	*156*	*0·011*	*0·17*	*0·026*	*35*	*3·3*	*2443*	*1·0*		
1995											
none	9·0	1858	0·49	2·0	0·41	562	42	23 574	38	20·8	18·7
GS31 to 39	8·1	1659	0·49	1·9	0·39	523	39	20 625	39	23·3	18·8
GS39 to 55	7·7	1715	0·45	1·8	0·38	540	33	17 804	43	22·7	17·5
GS55 to 61	8·7	1820	0·48	1·9	0·39	569	37	21 281	41	21·5	18·6
GS61 to 71	7·9	1720	0·46	1·8	0·40	543	41	22 309	35	22·2	17·5
GS71 to 87	6·3	1511	0·42	1·5	0·40	552	41	22 457	28	26·4	16·8
S.E.D.	*0·35*	*57*	*0·016*	*0·06*	*0·026*	*17*	*1·3*	*902*	*0·7*	*0·52*	*0·82*
1996											
none	12·3	2105	0·58	2·4	0·41	629	49	30 797	40	20·1	24·7
GS31 to 39	10·7	1853	0·58	2·2	0·36	583	42	24 763	43	20·6	22·0
GS39 to 55	12·2	2115	0·58	2·2	0·34	667	42	27 714	44	20·7	25·3
GS55 to 61	10·9	1882	0·58	2·2	0·38	584	47	27 203	40	19·9	21·6
GS61 to 71	11·9	2057	0·58	2·3	0·40	634	46	29 453	40	20·3	24·2
GS71 to 87	8·9	1763	0·51	1·8	0·38	625	47	29 544	30	22·9	20·5
S.E.D.	*0·94*	*176*	*0·013*	*0·13*	*0·018*	*69*	*2·4*	*3,072*	*0·9*	*0·52*	*2·04*
Mean											
none	10·2	1833	0·55	2·3	0·42	541	48	26 109	39	20·4	21·7
GS31 to 39	9·1	1656	0·55	2·2	0·40	507	45	23 039	40	21·9	20·4
GS39 to 55	9·5	1770	0·54	2·1	0·37	546	40	21 897	44	21·7	21·4
GS55 to 61	9·5	1750	0·55	2·2	0·40	530	46	24 215	40	20·7	20·1
GS61 to 71	9·2	1723	0·53	2·1	0·40	545	44	23 906	38	21·2	20·8
GS71 to 87	7·3	1520	0·48	1·8	0·40	542	47	25 412	29	24·7	18·6

Table 7. *Calculated mean proportion of solar radiation intercepted by green tissues of wheat cv. Slejpner at ADAS Terrington during five treatment periods in three growing seasons. Results for 1995 were corrected for interception by diseased tissues*

	Treatment period					
Season	GS31–39	GS39–55	GS55–61	GS61–71	GS71–87	Grain fill GS61–87
1994	0·63	0·86	0·92	0·92	0·73	0·80
1995	0·85	0·93	0·85	0·77	0·49	0·59
1996	0·87	0·95	0·97	0·97	0·87	0·90

Savin & Slafer 1991, −0·05; Pararajasingham & Hunt 1991, −0·10). In fact, the effects of shading from GS71–87 on grain yield here were larger than the effects on total dry weight; Martinez-Carrasco & Thorne (1979) also showed this effect. This implies that late shading causes either some reduction in dry matter redistribution or a large reduction in respiratory losses (Pearman *et al.* 1981; Pararajasingham & Hunt 1991).

Assimilates for grain filling

Assimilates available for grain filling were considered to arise from concurrent photosynthesis and redistributable reserves. Estimates of proportional radiation interception during each development phase are shown as means of all treatments (Table 7), given that canopy sizes were not affected significantly by shading (Fig. 2). Results were corrected for interception by diseased tissues during each of the five treatment periods, estimated as 0·003, 0·03, 0·09, 0·12 and 0·13, respectively, from weekly assessments of green and total leaf areas by leaf layer. The different mean interception after anthesis of approximately 0·8, 0·6 and 0·9 in the three seasons respectively could largely be explained by canopy size and duration; relatively small canopies in 1994, advanced senescence due to disease in 1995 and delayed senescence in 1996. When combined with incident radiation, radiation intercepted during grain filling in unshaded treatments was 640, 470 and 670 MJ/m² in 1994, 1995 and 1996 respectively.

There was a reasonable relationship between dry matter growth and estimates of radiation intercepted (Fig. 5); the slope for unshaded treatments indicated a radiation use efficiency (RUE) of 1·2 g/MJ ($R^2 = 0·79$). Whilst the precision of RUE estimates for individual growth phases was limited (being the ratio of two differences), there was little evidence that unshaded RUE changed through the different development phases. There was a tendency for RUE to increase during shading, although this did not always apply, e.g. during GS71–87. Where intercepted radiation in the period following shading was relatively small (<200 MJ/m²) RUE also tended to be large, but with greater levels of intercepted radiation the converse tended to occur (Fig. 5).

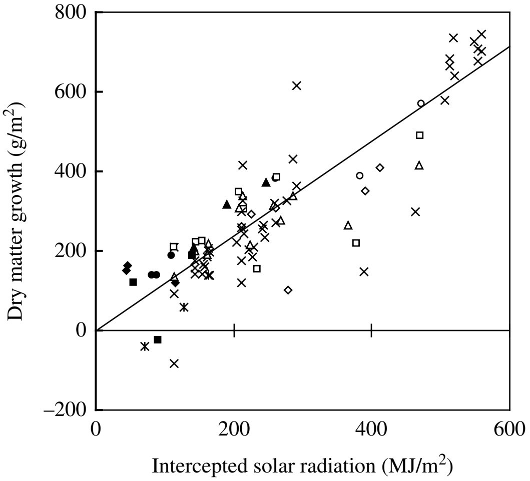

Fig. 5. Relationship between changes in shoot DM and radiation intercepted during each shading period (GS31–39 Δ, GS39–55 □, GS55–61 ◇, GS61–71 ○ and GS71–87 ⚹) at ADAS Terrington in 1994, 1995 and 1996; closed symbols show treatments during shading and open symbols indicate treatments which were previously shaded. The regression line is fitted with no intercept to the unshaded treatments (×; $y = 1·192x$, $R^2 = 0·79$).

The patterns of soluble carbohydrates in stems over time (Fig. 4) conformed with the notion that these provided an assimilate source during grain filling (Judel & Mengel 1982; Kiniry 1993). However, they also provided a temporary reserve of assimilate before anthesis, particularly when shading was applied during ear formation (GS39–55). This reserve could have moderated effects of pre-anthesis shading on grain number and specific leaf weight.

Net loss of assimilate from stems and leaves did not start until GS71, except where shading was applied from GS61–71. Soluble carbohydrate in stems at GS61 or GS71 made up about 0·25 of total non-ear

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dry matter. Subsequent decreases in soluble carbohydrate ranged from 0·19–0·45 g/shoot and accounted almost in full for decreases in total stem weight (y = 0·95x; $R^2 = 0{\cdot}81$); soluble carbohydrates remaining at GS87 were always small (maximum 0·11 g/shoot; 63 g/m^2) but were significantly less (0·03 g/shoot) following shading between GS71 and GS87 in 1994 and 1996. In 1995, amounts were similarly small (0·04 ± 0·011 g/shoot) across all shading treatments, probably due to disease. Concurrent with grain filling, there was a small decrease in lamina dry matter (0·04–0·14 g/shoot), unaffected by shading and unrelated to soluble carbohydrate, but greater in 1995 than 1994 or 1996. Much of this may have been associated with protein redistribution to grain because decreases in straw N to GS87 indicated similar dry matter losses (N × 6·25). Analysing over seasons, soluble carbohydrate in stems at GS61 underestimated apparent redistribution or loss of dry matter (change in the non-ear fraction) to grain (y = 1·17x) in an imprecise relationship ($R^2 = 0{\cdot}20$).

DISCUSSION

The aim of the present study was to assess whether yield variation for high yielding, dull, moist conditions (such as those in north-west Europe), could be accurately and precisely explained in terms of sink, source, or both, and then to consider implications for predictability of wheat yield. The detail incorporated into any explanation must necessarily be constrained (Passioura 1996) by the moderate level of precision of growth measurements. Possibly it is this difficulty that has persuaded many workers to resort to analyses in relative terms, whereby errors common across treatments or sampling occasions can be ignored. However, doing so loses essential elements of predictability.

Explaining grain yield

Considering the evidence for sink limitation first, several findings were supportive. Firstly, all three pre-anthesis treatments significantly reduced grain number and grain yield. Secondly, both current and previous shading treatments tended to increase RUE, indicating possible feedback from constraining sinks. Thirdly, and most convincingly, although neither ears/m^2 ($R^2 = 0{\cdot}38$) nor grains/ear ($R^2 = 0{\cdot}02$) correlated well with yield, grains/m^2 ($R^2 = 0{\cdot}56$) showed a good relationship, particularly if the final shading treatment was omitted ($R^2 = 0{\cdot}88$). Slopes of regressions between grain yield and grains/m^2 (constrained through the origin) were 38·2 and 40·3 mg/grain with and without the final treatment respectively. However, if the sink estimates were based on grains/m^2 and a potential of 44 mg/grain, the maximum treatment mean observed in each season, total grain sinks (g/m^2) would have exceeded observed grain yields, on average by 9% (15% without the last shading).

Although there were significant treatment effects on mean dry weight per grain, it is possible that differences may not have arisen directly through changes in post-anthesis assimilate supply per grain, but indirectly through changes in the number of distal grains with small sink capacity (Miralles & Slafer 1996; Chanda & Singh 2002). Because no shading was applied before spikelet number would have been determined, grain numbers/ear can be taken to indicate that there were up to nine distal grains whose presence was affected by pre-anthesis treatments and, assuming about 20 spikelets/ear, these were largely in the third rather than fourth position. However, if these were to account for all of the differences in mean grain weight, distal grains would have had to be unrealistically small: 12 mg on average, and about 30 mg less than the proximal grains. Miralles & Slafer (1996) show grains in floret positions 3 and 4 to be 5 mg and 14 mg less, respectively, than those in positions 1 and 2. Thus, pre-anthesis shading effects on weight/grain almost certainly included other effects, of which the most likely is a difference in post-anthesis assimilate supply/grain.

Evidence for source determination of grain yield can also be seen in the findings reported in the present paper. Soluble stem carbohydrate was almost depleted after grain filling. Shading from GS71–87 reduced yield more than any other treatment. Grain yield related significantly to post-anthesis shoot growth (y = 325 + 0·93x; $R^2 = 0{\cdot}59$) and to total shoot dry weight at harvest (y = 0·53x, $R^2 = 0{\cdot}69$). Furthermore, if all soluble carbohydrate present at anthesis and all post-anthesis photosynthate (estimated from intercepted radiation, and assuming RUE was the mean for unshaded treatments: 1·2 g/MJ) were considered to constitute the total source for grain filling, the relative changes in weight per grain were largely similar to the relative changes in assimilate for grain filling (Fig. 6).

Data plotted on similar axes have been used previously (Slafer & Savin 1994; Borras *et al.* 2004) as evidence of sink limitation in wheat. However, previous work estimated source entirely on the basis of post-anthesis green area duration, and excluded soluble stem carbohydrates. Intercepted radiation is preferred in the present paper because green area duration is not linearly related to source, and soluble stem carbohydrate is included because it clearly constitutes a source of assimilate for grain filling. In contrast to the previous work, the relationship in the present study appears to show most treatments to be compatible with source determination; the only treatments with evidence for sink determination were from 1995 when presence of disease probably caused slight over-estimation of total source. The same graph

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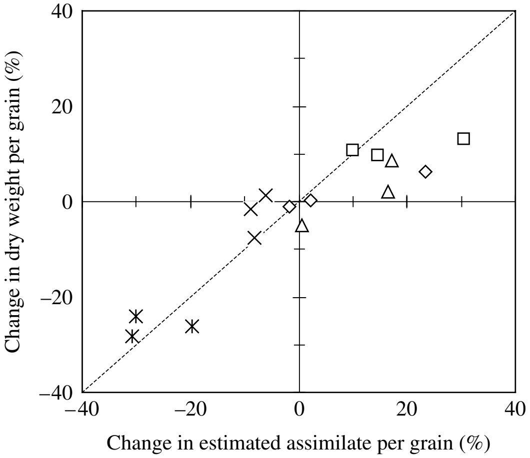

Fig. 6. Relationship between changes, relative to the control, in estimated assimilate available per grain (including all soluble stem carbohydrate at anthesis and assuming that post-anthesis RUE was 1·2 g/MJ) and weight per grain. Symbols as in Fig. 2. $R^2 = 0{\cdot}77$.

plotted with absolute rather than relative scales (mg/grain; not shown) reveals a similarly good relationship ($R^2 = 0{\cdot}72$) but also that the mean estimate of source was slightly (~2 mg/grain) smaller than the recorded weight per grain. This under-estimation of source should probably be attributed to slightly greater DM redistribution from straw in the more source-limited treatments.

Except for the final shading treatment, which clearly caused source-limitation, it appears that both sink- and source-based explanations of yield variation could be applied satisfactorily in this study. There follows a consideration about which of the sink- and source-based explanations of yield might offer better predictability.

Predicting determinants of grain yield

The grain sink can be taken as the product of fertile florets/m^2 and potential weight per grain (PWG; Evans & Wardlaw 1996). Fischer and others (see Fischer 1985), working mainly with spring wheats in the warm and largely cloudless conditions of Mexico, New South Wales, or the Canberra phytotron, showed that floret survival was dependent on a 30-day period before anthesis. They quoted an average response to intercepted radiation of about 20 grains/MJ, but did not clarify whether their relationship showed an intercept. The data in the present paper, except the treatment shaded from GS61–71 (which reduced grain number probably by interfering with fertilization), showed responses to intercepted radiation with a greater slope and a significant intercept. An intercept could arise through buffering by stem reserves, such that a minimum number of grains would be formed, even if the effective period was extremely dull. However, such buffering is not supported by the work of McMaster *et al.* (1987) and others (see Fischer 1985) who did not show changes in partitioning due to shading during this period.

The relationship between grains formed and radiation intercepted can be separated into a radiation use efficiency (RUE), a proportion of DM partitioned to ears, and a DM requirement per fertile floret. Fischer's (1985) analysis of grain numbers indicated a DM requirement for floret formation of about 10 mg, based on the ratio of chaff weight to grain number (or 100 grains/g as expressed by Abbate *et al.* 1998). The ratios found in the present paper were similar between treatments but differed between seasons, with 8·5, 10·2 and 8·3 mg/grain in 1994, 1995 and 1996 respectively. The larger requirements in 1995 (when the crop was affected by disease) may have arisen indirectly, through decreased grain filling and an increase in irretrievable grains at harvest. A value of 8·5 mg/floret is consistent with data of Whaley *et al.* (2000). The data are commensurate with partitioning of about 0·40 to the ear in the 375 °Cd centred on ear emergence.

The practical value of the sink concept depends also on predictability of PWG; which is best studied on crops which are clearly sink-limited, hence evidence here cannot help. Calderini *et al.* (2001) found that shading just before anthesis influenced individual grain weight. More usually, variation in PWG has been attributed to events just after anthesis, with significant effects shown from shading (Brocklehurst *et al.* 1978; Singh & Jenner 1984; Wang *et al.* 2003), thinning (Fischer & Laing 1976), grain removal (Radley 1978; Fischer & HilleRisLambers 1978) and spikelet removal (Brocklehurst 1977); the mechanism being variation in endosperm cell number (Brocklehurst 1977) which is determined in a discrete period soon after anthesis (Gao *et al.* 1992). An assimilate effect at this stage is somewhat surprising since assimilate availability is high, and must usually be well in excess of requirements for cell division: soluble stem carbohydrate is close to its maximum, incident radiation is maximal, senescence has yet to reduce full radiation interception, and the main phase of starch deposition has yet to start. The detailed work of Singh & Jenner (1984) failed to show relationships between intra-ear substrate levels and cell numbers.

The uncertain physiological determination of PWG makes prediction problematic. Perhaps the best approach is that adopted by Moreno-Sotomayor & Weiss (2004) who assume a maximum growth rate per grain, determined empirically for each variety. Considering predictability of sink overall, it appears that, despite a general consensus that this is the most

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common constraint on yield (Borras *et al.* 2004; Shearman *et al.* 2005), there is not yet any satisfactory means for its prediction. Responses of fertile florets/m^2 to radiation intercepted before anthesis are insufficiently robust, and no good predictor of PWG is known. Even if in-crop observations were feasible, the best measure would be ear weight/m^2 at anthesis, which would only have sufficient precision and accuracy to indicate gross differences in grain yield. It is therefore worth considering the predictability of total source for grain filling; particularly as this has been the approach used in most crop models.

Taking canopy area as the product of shoot number/m^2 and green area/shoot, it appears that shoot numbers in these crops were not primarily dependent on supplies of photosynthate after the start of stem extension. This contrasts with most previous tests of shading during canopy expansion (Willey & Holliday 1971; Fischer 1975; Kemp & Whingwiri 1980; Willington & Biscoe 1985). The discrepancy may be accounted for by the less severe shading technique used here. Small, nonsignificant decreases in shoot survival due to shading in all seasons were counteracted by small significant increases in final leaf size, such that maximum GAI was not significantly affected. Increased leaf size in dull conditions is a common response in many species (e.g. Givnish 1988), but does not appear to have been reported previously for field-grown wheat. The apparent interdependence between culm leaf expansion and shoot death may have arisen through internal competition for N. Uptake of N related well to canopy expansion here, as in parallel studies of N nutrition (Sylvester-Bradley *et al.* 1997; Grindlay *et al.* 1997); the ratio of shoot N to canopy size was held at about 3 g/m^2 through May and June, and was unaffected by shading. It is difficult to achieve satisfactory predictions of canopy size or N uptake for wheat (Gillett *et al.* 1999). However, in-crop observation of canopy size is feasible (Russell *et al.* 1998). Models which calculate N uptake or canopy expansion from DM growth (e.g. Greenwood *et al.* 1987; Lemaire *et al.* 1997) could not explain the effects of shading seen in the present study.

Amounts of soluble carbohydrate held by UK wheat vary genetically and due to growing conditions, but without significant interaction (Foulkes *et al.* 1998). Amounts for cv. Slejpner tend to be low in the range of contemporary varieties: 200–400 g/m^2. It appeared from the present results that the environmental component of variation in amounts at GS61 might be predictable from shoot numbers because, without previous shade, they were consistent across seasons at $0{\cdot}42 \pm 0{\cdot}031$ g/shoot. Amounts were best explained by there being a finite storage capacity per stem, a concept supported by the longer time it took to reach the maximum, when shoot numbers were greater: until GS55, GS39 and GS71 in the three seasons respectively. The delay in reaching capacity in 1994 can be explained by dull conditions during stem extension and by later canopy closure due to poor establishment. Previous studies of soluble stem storage have largely concerned moisture-stressed crops (e.g. Herwaarden *et al.* 1998) and do not appear to have identified a maximum capacity, or a means of predicting it.

Considering the ageing of leaves and the brighter conditions after anthesis, it is surprising that there was no detectable decrease in RUE during grain filling. However, the lack of substantial variation here is not unique (Sinclair & Muchow 1999) and the similarity with previous estimates for wheat argues that prediction of source could reasonably be based on a single value of RUE.

Senescence of the canopy during grain filling may be difficult to predict, but there are some useful indicators. The seasonal variation found here depended largely on canopy size at anthesis, which may be assessable and, in the case of 1995, on the presence of disease, which can be observed. Hence, post-anthesis radiation interception can be considered predictable to some extent.

Prospects for source- versus sink-based models are also affected by uncertainty about future weather. Source-based approaches are clearly more dependent on events after anthesis. This may not be such a disadvantage, even in the UK's variable conditions, because analysis of temperature and sunshine data shows that, due to the association between radiation and temperature, incident radiation during a thermal period of 690 °Cd during June and July has been relatively consistent (682 ± 60 MJ/m^2; A. Gay, personal communication).

Comparing the predictability of source and sink determinants at anthesis, it is probably easier and more convincing to observe (not predict) canopy size and shoot number (hence soluble stem carbohydrate), than it is to observe or predict grain number or ear weight/m^2. After anthesis, however, predictability becomes poor for both source and sink: there is uncertainty about rate and duration of senescence, but there is also at least equivalent uncertainty about PWG. If, as seems to be the case here, crops grown in light-limited conditions are finely balanced between source and sink limitation, it seems unlikely that current prediction methods can confidently identify the dominant limit.

We dedicate this paper to the memory of Keith Scott and Rob Clare, who worked with us to initiate this work, and whose vision and resolve inspired us. We are grateful to David Jacobs and the Hydrology Team of ADAS Boxworth who designed and built the shades, to A. Gay for solar radiation analyses and to the UK Department for Environment, Food and Rural Affairs for funding.

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APPENDIX

Construction and operation of the automated shades

Each shading device occupied 20 × 9 m land and was constructed of five galvanized steel hoops (McGregor Polytunnels, Hampshire) 3·2 m high, spaced 5 m apart, joined by galvanized steel ties, and covered with black, high density polyethylene, knitted cloth. Shades were open at each end, except that cloth extended downwards 1·1 m from the top and 2 m from the sides.

Each shade moved with 10 wheels on tracks running the length of each block (about 150 m), and mounted every 2 m on plates secured to the ground by three 0·75 m metal pins. The wheels were powered by 24 V, 100 Watt motors (Parvalux PM6 LIS), geared to reduce maximum motor speed from 2000 to 42 rpm. The central motor of the five on each side was equipped with a brake. The 24 V power supply was provided by two 12 V, 38 A h sealed lead-acid batteries, connected in series, and trickle charged by solar panels mounted at the southern end of the shade framework.

The shades were developed from manual operation in 1994 to full automatic operation in the latter part of 1995 and in 1996. When manually operated, the shades were moved into position at the start of days forecast to be bright, and were left in position all day. When automated, the shades were triggered to move from their park positions to their treatment positions by a radio signal from a central control 'mast' when the hourly mean total solar radiation sensed by a dome solarimeter and recorded on a datalogger (Campbell Scientific CR10) exceeded 250 J/s/m^2. On receiving the signal to move, an audible warning signal was triggered and, after a short delay, the shade began to move in a direction set by a switch on its control panel. The shade moved slowly until an opto-proximity reflector, mounted on the shade, passed a portable reflector mounted beside the rail and 2 m along from a reflector which defined the parking position of the shade. The shade then moved at full speed (about 1·5 m/s) until, at approximately 2 m before the shading position, a third reflector slowed its motion, and a fourth reflector caused it to stop. This sequence was repeated in reverse, so that the shades returned to their park positions when the hourly mean total solar radiation became less than 250 J/s/m^2.

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