Journal of Agricultural Science (2005), **143**, 503–518. © 2005 *Cambridge University Press*
doi:10.1017/S002185960500568X *Printed in the United Kingdom*

Fungicide and cultivar affect post-anthesis patterns of nitrogen uptake, remobilization and utilization efficiency in wheat

M. J. GOODING*, P. J. GREGORY, K. E. FORD AND S. PEPLER

School of Agriculture, Policy and Development, The University of Reading, Earley Gate, PO Box 237, Reading RG6 6AR, UK

(*Revised MS received 13 September 2005*)

SUMMARY

Three successive field experiments (2000/01–2002/03) assessed the effect of wheat cultivar (Consort, Hereward and Shamrock) and fungicide (epoxiconazole and azoxystrobin) applied at and after flag leaf emergence on the nitrogen in the above-ground crop (*Total N*) and grain (*Grain N*), net nitrogen remobilization from non-grain tissues (*Remobilized N*), grain dry matter (*Grain DM*), and nitrogen utilization efficiency ($NUtE_g = Grain\ DM/Total\ N$). Ordinary logistic curves were fitted to the accumulation of *Grain N*, *Grain DM* and *Remobilized N* against thermal time after anthesis and used to simultaneously derive fits for *Total N* and $NUtE_g$.

When disease was controlled, Consort achieved the greatest *Grain DM*, *Total N*, *Grain N* and $NUtE_g$; in each case due mostly to longer durations, rather than quicker rates, of accumulation. Fungicide application increased final *Grain DM*, *Grain N*, *Total N* and *Remobilized N*, also mostly through effects on duration rather than rate of accumulation. Completely senesced leaf laminas retained less nitrogen when fungicide had been applied compared with leaf laminas previously infected severely with brown rust (*Puccinia recondita*) and *Septoria tritici*, or with just *S. tritici*. Late movement of nitrogen out of fungicide-treated laminas contributed to extended duration of both nitrogen remobilization and grain N filling, and meant that increases in $NUtE_g$ could occur without simultaneous reductions in grain N concentration.

INTRODUCTION

The efficient use of nitrogen is important for the economic and environmental sustainability of wheat (*Triticum aestivum* L.) production (Foulkes *et al.* 1998). Improving nitrogen uptake and partitioning to the grain reduces the amount of nitrogen at risk of loss to the environment (Raun & Johnson 1999) and enhanced grain N recovery is important for maintaining protein concentrations (N × 5·7) in high yielding crops (Cox *et al.* 1986), and thus the marketability of wheat for a number of end-uses (Dimmock & Gooding 2002*a*).

However, high grain nitrogen concentrations may indicate that the crop is less efficient at producing grain dry matter per unit N accumulated (Foulkes *et al.* 1998). Improved nitrogen utilization efficiency to produce grain ($NUtE_g$), i.e. the ratio of grain dry matter to nitrogen in the above-ground crop (Moll *et al.* 1982; Ortiz-Monasterio *et al.* 1997; Kindred & Gooding 2004), could assist in maintaining yields with reduced nitrogen fertilizer applications and/or increasing the energy balance of the crop (White 1981; Murphy & Helal 1996; Rosenberger *et al.* 2001).

Extending canopy life with fungicide programmes can increase nitrogen recovery through improving both nitrogen uptake and remobilization (Ruske *et al.* 2003). These effects can be associated linearly with the green area duration of the flag leaf (Ruske *et al.* 2003) although clarification is required because associations vary with cultivar; green area duration, and hence possible retention of nitrogen in the canopy (Jamieson & Semenov 2000) can be extended beyond the end of grain filling (Pepler *et al.* 2005); and the amount of remobilization may vary with pathogen

* To whom all correspondence should be addressed. Email: m.j.gooding@reading.ac.uk.

Table 1. *Monthly mean air temperatures, rainfall, soil moisture deficit (SMD) and solar radiation receipts, Crops Research Unit, University of Reading*

Month	Air temperatures (°C, mean of daily max. and min.)			Total rainfall (mm)			Calculated SMD (mm, mean of values calculated daily)			Solar radiation receipts ($MJ/m^2/day$) monthly means		
	2000/2001	2001/2002	2002/2003	2000/2001	2001/2002	2002/2003	2000/2001	2001/2002	2002/2003	2000/2001	2001/2002	2002/2003
September	14·8	13·9	14·7	85	52	28	139·4	194·5	207·3	8·8	9·4	10·5
October	10·6	13·6	10·7	142	95	81	16·1	119·9	142·6	5·5	5·7	5·4
November	6·8	7·4	8·7	92	29	146	0	88·8	0	3·1	3·5	2·6
December	5·8	3·5	6·5	88	22	100	0	58·0	0·4	1·5	2·5	1·4
January	3·7	5·5	4·7	73	60	73	0	0·7	0	2·8	2·2	3·1
February	5·3	7·4	4·7	68	82	33	0	0·5	0	5·1	4·8	5·0
March	6·1	8·1	8·0	85	51	19	3·5	13·5	27·1	6·5	7·9	9·8
April	8·4	10·0	9·6	70	37	31	9·0	41·8	56·5	11·5	14·4	12·7
May	13·4	12·6	12·4	34	68	53	75·8	60·8	89·1	16·8	14·9	15·2
June	15·4	15·1	17·1	35	39	54	158·3	120·3	148·8	19·3	15·6	17·6
July	18·3	17·2	18·3	37	72	32	230·6	148·2	228·2	15·8	15·0	15·8
August	17·9	18·4	20·0	114	45	13	201·0	188·2	326·4	13·4	13·5	17·4

infection strategy, e.g. whether biotrophic or more necrotrophic (Dimmock & Gooding 2002*a*).

There is little information on the effect of different diseases and their control by fungicides on $NUtE_g$. Extending green area duration of the flag leaf by means of genetics, climate or disease control can be associated with increased grain dry matter yields (Dimmock & Gooding 2002*b*; Verma *et al.* 2004). Fungicide use can be associated with improved duration and rate of grain filling with dry matter (Dimmock & Gooding 2002*b*; Ruske *et al.* 2003), and similar effects achieved with heterosis (Kindred & Gooding 2004) have improved $NUtE_g$. Any effect of fungicide on grain dry matter must, however, depend on effects on nitrogen uptake after anthesis because if this does not meet grain N demand, photosynthesis in the flag leaves is suppressed or curtailed (Gregory *et al.* 1981), and green area may be sacrificed (Jamieson & Semenov 2000; Sylvester-Bradley *et al.* 2005).

In the present paper, an attempt is made to understand more clearly the effects of cultivar, and foliar diseases and their control with fungicides, on nitrogen uptake, remobilization and utilization efficiency in winter wheat. Quantities of nitrogen in different plant organs and grain dry matter are monitored during senescence and grain filling of cultivar × fungicide field experiments. The approach was to fit logistic curves to accumulation over thermal time of dry matter and nitrogen in grain (Giunta & Motzo 2005). This allowed rate and duration of accumulation to be separated from each other, and the treatment effects on rate and duration to be assessed over seasons. Similarly, a logistic curve was fitted to remobilized N (above-ground N at anthesis minus non-grain N at thermal time after anthesis) and combined with that for grain nitrogen to describe nitrogen in the above-ground biomass (above-ground N at anthesis + grain N − remobilized N), which was, in turn, combined with the grain dry matter curve to describe the development of $NUtE_g$.

MATERIALS AND METHODS

Site details

Field experiments on winter wheat were carried out at the Crops Research Unit, University of Reading (0°54′W, 51°29′N) over three seasons (2000/01, 2001/02 and 2002/03) on a free-draining sandy loam overlying coarse red-brown sand, from the Sonning series (Jarvis 1968). Weather data (Table 1) were recorded at an automated weather station at the site. In summary, low rainfall and high solar radiation receipts in 2000/01 and 2002/03 led to higher soil moisture deficits (SMD) in the summers of 2001 and 2003 compared with the summer of 2002. The 2001/02 season had lower solar radiation receipts

Table 2. *Dates of non-experimental crop husbandry and corresponding growth stages* (*GS, Zadoks* et al. *1974*)

	GS	2000/01	2001/02	2002/03
Indices before seed bed preparation (Anon 1994)				
pH		6·7	6·9	6·9
Phosphorus		3	3	3
Potassium		2	1	1
Magnesium		2	1	1
Drilling date		10.10.00	17.10.01	10.10.02
Seed rate (seeds/m^2)		400	400	400
Fertilizer (kg/ha)				
Sulphur	Seed bed	16	30	30
Potassium	Seed bed	33	62	62
Nitrogen	30	100	100	100
Nitrogen	32	100	100	100
Crop protection chemicals (active ingredient/ha)				
Autumn/winter herbicide	13–22	Bromoxynil 400 g Ioxynil 400 g	Isoproturon 2·5 kg	Isoproturon 2·5 kg
Spring fungicide	31	Epoxiconazole 63 g	Epoxiconazole 63 g	Epoxiconazole 63 g
Spring herbicide	31	Metsulfuron-methyl 5·25 g Thifensulfuron-methyl 51 g	Fluroxypyr 200 g	Metsulfuron-methyl 5·25g Thifensulfuron-methyl 51 g
Summer insecticide	70	Lambda-cyhalothrin 5 g		
Combine harvest date		14.8.01	14.8.02	7.8.03

and temperatures than the other seasons and was comparatively wet with particularly large rainfalls in May and July. Details of soil indices and crop management not part of the experimental treatments are shown in Table 2. Nitrogen recoveries in neighbouring experiments for treatments given no nitrogen fertilizer (Clarke 2002; Kindred & Gooding 2004), but otherwise similar husbandry to the experiments reported here, were 97, 106 and 46 kg N/ha in the above-ground crop biomass, and 63, 69 and 30 kg N/ha in the grain, for the harvests of 2001, 2002 and 2003 respectively.

The smallest experimental unit (subplot or subsubplot) measured 2×10 m, of which the central $1{\cdot}3 \times 10$ m strip was combine harvested. The treatment structure in each experiment was randomized in three complete blocks.

Experimental designs

The 2000/01 experiment involved two cultivars (Consort and Hereward) sown as main plots divided into five subplots receiving different fungicide treatments. Consort was chosen because it was a commercially popular cultivar for biscuit making in the UK and yield increases following fungicide use on this cultivar were often associated with reductions in grain concentrations of nitrogen (Dimmock & Gooding 2002*a*). In contrast, Hereward was a UK breadmaking cultivar that often exhibited a positive or nil response of grain nitrogen concentration to fungicide application (Dimmock & Gooding 2002*a*).

Table 3. *Fungicide treatments* (*g active ingredient/ha*) *applied at different growth stages* (*GS, Zadoks* et al. *1974*)

Treatment	GS 39 Epoxiconazole/ Azoxystrobin	GS 59 Epoxiconazole/ Azoxystrobin
1	0/0	0/0
2	63/125	0/0
3	63/125	63/0
4	63/125	0/125
5	63/125	63/125

The fungicides were delivered at 200–250 Pa pressure in 220 l/ha through air bubble jet nozzles (size 0·3, Billericay Farm Services) to produce a spray of medium droplet size (Matthews 2000). Treatment 1 (Table 3) had no fungicide applied at or after flag leaf emergence (although all plots had received fungicide at GS 31, Table 2). Treatments 2–5 all had epoxiconazole (as Opus, BASF, Cheadle Hume, UK) plus azoxystrobin (Amistar, Syngenta, Wittlesford, UK) applied at flag leaf emergence (Growth stage (GS) 39, Zadoks *et al.* 1974) and then the 2×2 factorial combination of with and without epoxiconazole, and with and without azoxystrobin at ear emergence (GS 59). The block structure for the analysis of variance (GenStat Version 6.1.0.200) was block/cultivar/treatment, and the treatment structure was nested i.e. cultivar × (GS39 spray/(GS59 epoxiconazole × GS59 azoxystrobin)).

The 2001/02 experiment was a split-plot design, but with three winter wheat cultivars (Consort, Hereward and Shamrock) as main plots. Shamrock was added as a second cultivar with breadmaking potential, but with greater susceptibility to brown rust (*Puccinia recondita*) compared to Hereward (Ruske *et al.* 2003). Cultivar main plots were divided into subplots (2×10 m) to receive one of two fungicide treatments (1 and 5; Table 3). Thus the block structure was block/cultivar/fungicide treatment, and the treatment structure was cultivar × fungicide.

In 2002/03 a split-split-plot factorial design was used where two irrigation treatments (main plots) comprised either no irrigation or trickle irrigation, applied twice weekly between 14 June and 18 July, to theoretical field capacity based on calculations from the meteorological data. This meant a total of 160 mm was applied during grain filling, in addition to rainfall. Main plots were divided into four subplots (6×10 m) receiving two replications of with and without fungicide (treatments 1 and 5; Table 3). The subplots were further split into three cultivar (Shamrock, Hereward and Consort) sub-subplots so the block structure was block/irrigation treatment/subplot/cultivar, and the treatment structure was irrigation × fungicide × cultivar.

Measurements

Visual assessments of the flag leaf were made weekly from anthesis until senescence. Ten leaves were selected at random from each sub- or sub-subplot and the percentage diseased area and green leaf area assessed by comparison with standard keys (Anon. 1976). Modified Gompertz curves (Eqn 1) were fitted to the green leaf area (*GLA*) decline over thermal time (t) for each sub- or sub-subplot. The Gompertz time (m) scalar is the fitted thermal time after anthesis for the flag leaf to senesce to 37% green leaf area.

$$GLA_{(t)} = 100 \times e^{-e^{-b(t-m)}}$$

(Eqn 1; Dimmock & Gooding 2002*b*)

Nitrogen content and partitioning during grain filling was assessed from 15 (2001 and 2003) or 30 (2002) randomly harvested ear-bearing stems every 7–10 days in each sub- or sub-subplot. Samples were separated into flag leaf laminas, penultimate leaf laminas, other leaf laminas, stems plus leaf sheaths, chaff and grain. The dry weights were determined gravimetrically after oven drying (80 °C for 48 h). The ears were separated into chaff and grain using a laboratory threshing machine (except for ears sampled in June which were threshed by hand). The grain and vegetative samples were milled with mills appropriate to the material: Perten Instruments 3100 for grain; and either Tema, Model T100 or Retsch, Model SM1 for vegetative components. The N concentration was determined with a VG602 mass spectrometer after first combusting the material in a linked Roboprep C and N analyser (Europa Scientific Ltd).

Data for *Grain DM*, and *Grain N* accumulation, and N loss from non-grain tissues (assumed to be *Remobilized N*), over thermal time (t) from anthesis were fitted with ordinary logistic models (i.e. constant omitted, Eqns 2–4).

$$Grain\ DM_{(t)} = \frac{C_{DM}}{1 + e^{-B_{DM}(t - M_{DM})}}$$

(Eqn 2; Zahedi & Jenner 2003)

$$Grain\ N_{(t)} = \frac{C_{GN}}{1 + e^{-B_{GN}(t - M_{GN})}}$$

(Eqn 3; Ruske *et al.* 2003)

$$Remobilized\ N_{(t)} = \frac{C_{RN}}{1 + e^{-B_{RN}(t - M_{RN})}} \qquad \text{(Eqn 4)}$$

The quantity of $Remobilized\ N_{(t)}$ is the amount of nitrogen in the above-ground crop at anthesis ($Total\ N_{(t=\mathbf{0})}$) minus the nitrogen in the non-grain tissues, i.e. $Remobilized\ N_{(t)} = Total\ N_{(t=\mathbf{0})} - Vegetative\ N_{(t)}$ (Cox *et al.* 1986). This is identical to $Remobilized\ N_{(t)} = Grain\ N_{(t)} - (Total\ N_{(t)} - Total\ N_{(t=\mathbf{0})})$ (Barbottin *et al.* 2005) because $Vegetative\ N_{(t)} = Total\ N_{(t)} - Grain\ N_{(t)}$. Both expressions assume that the net amount of nitrogen lost from the above-ground non-grain tissues after anthesis that does not reach the grain is insignificant. Therefore $Total\ N_{(t)}$ can be fitted with Eqn 5, which in turn can be used in Eqn 6 to fit $NUtE_g$.

$$Total\ N_{(t)} = Total\ N_{t=\mathbf{0}} + [Eqn\ 3] - [Eqn\ 4] \qquad \text{(Eqn 5)}$$

$$NUtE_{g(t)} = \frac{[Eqn\ 2]}{[Eqn\ 5]} \qquad \text{(Eqn 6)}$$

Equations 2–6 were fitted simultaneously after the data had been scaled such that the maximum for each dependent variable was the same. Curves were fitted with the FITNONLINEAR directive in GenStat.

Fits were made for each sub- or sub-subplot such that the fitted value on the last date of assessment (*FV*), duration of accumulation (taken time to reach 95% of *FV*), and maximum rates of accumulation could be determined for each experimental unit. These variables can be determined directly from the fitted logistic curves (Eqns 2–4): Duration is

$$\frac{(B \times M - \ln((C(FV \times 0{\cdot}95)) - 1)}{B} \qquad \text{(Eqn 7)}$$

and maximum rate of accumulation is $B \times C/4$. Final values, maximum rates and durations for Eqns 5 and 6 were determined numerically after calculating fitted values at 5 °Cd intervals. Sub- and sub-subplot values for calculated rates, durations and final values were

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

Table 4. *Effect of wheat cultivar on the accumulation of grain dry matter (DM), nitrogen in the above-ground crop biomass (Total N) and grain nitrogen (Grain N); net nitrogen remobilization from non-grain tissues (Remobilized N); and the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$). Values are derived from Eqns 2–6: Rate = maximum rate, Duration = thermal time to 95% of final value, Final = fitted value on last assessment date. Values are means of 3 years for plots receiving fungicide treatment 5 (see Table 3)*

	Shamrock	Consort	Hereward	S.E. (D.F. = 13)
Grain DM				
Rate ($g/m^2/°Cd$)	2·39	2·05	1·94	0·139
Duration (°Cd)	673	821	756	23·7
Final (g/m^2)	821	953	830	18·8
Total N				
Rate ($mg/m^2/°Cd$)	17·1	17·4	15·9	1·34
Duration (°Cd)	577	731	660	34·1
Final (g/m^2)	21·1	22·9	22·1	0·35
Grain N				
Rate ($mg/m^2/°Cd$)	32·5	31·9	29·7	1·61
Duration (°Cd)	771	895	859	21·6
Final (g/m^2)	16·5	18·4	17·7	0·36
Final conc. (g/kg DM)	20·1	19·4	21·4	0·11
Remobilized N				
Rate ($mg/m^2/°Cd$)	20·9	18·3	23·2	1·99
Duration (°Cd)	794	873	767	30·1
Final (g/m^2)	11·3	11·5	11·5	0·19
Final (% anthesis N)	70·8	71·9	72·2	1·16
Final contribution to grain N (%)	70·3	63·8	65·7	1·39
Final nitrogen harvest index	78·0	80·3	80·0	0·84
$NUtE_g$				
Rate ($g\ DM/g\ N/m^2/°Cd$)	0·13	0·10	0·10	0·009
Duration (°Cd)	676	722	636	17·8
Final (g DM/g N)	38·9	41·6	37·5	0·49

subjected to appropriate factorial split-plot analyses of variance. In addition, final values were calculated for: grain nitrogen concentration (*%GNC*, Eqn 8); remobilized nitrogen as a percentage of N in the canopy at anthesis (*%remob*, Eqn 9); apparent contribution of *Remobilized N* to *Grain N* (*%cont*, Eqn 10); and nitrogen harvest index (*%NHI*, Eqn 11).

$$\%GNC = \frac{100 \times Grain\ N_{FV}}{Grain\ DM_{FV}} \quad \text{(Eqn 8)}$$

$$\%remob = \frac{100 \times Remobilized\ N_{FV}}{Total\ N_{t=0}} \quad \text{(Eqn 9)}$$

$$\%cont = \frac{100 \times Remobilized\ N_{FV}}{Grain\ N_{FV}} \quad \text{(Eqn 10)}$$

$$\%NHI = \frac{100 \times Grain\ N_{FV}}{Total\ N_{FV}} \quad \text{(Eqn 11)}$$

Parameter values generated by the curve fitting were combined over years in further analyses of variance. Firstly, data for treatment 5 in all 3 years were combined to assess cultivar effects when least affected by disease. Cultivar values in the 2002/03 experiment were averaged over subplot and irrigation treatment within blocks, to provide three cultivar means per block, balanced with the 2 previous years. Shamrock data for 2000/01 were input as missing values to allow a block structure of year (3 levels)/block (9)/cultivar (3). Similarly, the main effect of fungicide over years was assessed by using fungicide means per block for treatments 1 and 5 to allow a block structure of year (3)/block (9)/fungicide (2).

RESULTS

The simultaneous fitting of Eqns 2–6 appeared adequate to describe the pattern of *Grain DM*, *Total N*, *Grain N*, *Remobilized N* and $NUtE_g$ over thermal time, accounting for between 0·978 (2001) and 0·998 (2002) of the variation ($R^2_{adj.}$) in the grand means over thermal time.

Mean effects of cultivar and fungicide over years

On average, duration of *Grain N* accumulation was estimated as being longer than for *Grain DM*, in part supported by similarly late net remobilization of N from vegetative tissues (Table 4). In contrast,

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

$NUtE_g$ was defined earlier in grain filling than dry matter accumulation as late increases in *Grain DM* were at least partially matched by late increases in *Total N* (Table 4).

When disease was controlled with the most robust fungicide programme (treatment 5) cv. Consort achieved the greatest *Grain DM*, *Total N*, *Grain N* and $NUtE_g$ ($P<0{\cdot}01$ for cv. effect in each case); due to greater durations ($P\leqslant 0{\cdot}02$ in each case), rather than rates, of accumulation (Table 4). When disease was controlled, all cultivars remobilized a similar proportion of N, averaging 0·716 for treatment 5 over the 3 years. Shamrock had the lowest final *Grain N* so *Remobilized N* accounted for a higher proportion of *Grain N* in this cultivar. Nitrogen harvest index was similar for all cultivars when disease was controlled. Final grain nitrogen concentration was highest in Hereward and least in Consort.

Fungicide application increased final *Grain DM* ($P<0{\cdot}01$) and *Grain N* ($P<0{\cdot}01$) such that when averaged over all experiments and cultivars, fungicide treatment had no effect on grain nitrogen concentration (Table 5). Increases in grain accrual of dry matter and nitrogen were due to significant increases in duration ($P\leqslant 0{\cdot}04$), rather than rate of accumulation. *Grain N* supply was supported by greater accumulation of nitrogen in the above-ground canopy ($P=0{\cdot}01$), and also by greater N remobilization from vegetative tissues ($P<0{\cdot}01$) when disease had been controlled, again due to increases in duration rather than rate. The fungicide-mediated increase in post anthesis N uptake and N remobilization was reflected in an increased nitrogen harvest index ($P<0{\cdot}01$). Fungicide effects on N uptake were greater than on N remobilization such that disease control was associated with a reduction in the proportion of *Grain N* that appeared to derive from net remobilization ($P<0{\cdot}05$). Fungicide treatment significantly improved $NUtE_g$ ($P<0{\cdot}01$).

Table 5. *Effect of fungicide on the accumulation of grain dry matter (DM), nitrogen in the above-ground crop biomass (Total N) and grain nitrogen (Grain N); net nitrogen remobilization from non-grain tissues (Remobilized N); and the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$). Values are derived from Eqns 2–6: Rate = maximum rate, Duration = thermal time to 95% of final value, Final = fitted value on last assessment date. Values are means of 3 years and three cultivars*

Fungicide treatment (Table 3)	1	5	S.E. (D.F. = 8)
Grain DM			
Rate (g/m²/°Cd)	2·5	2·1	0·31
Duration (°Cd)	706	763	16·8
Final (g/m²)	764	876	12·0
Total N			
Rate (mg/m²/°Cd)	18·7	16·7	1·33
Duration (°Cd)	566	669	33·1
Final (g/m²)	20·7	22·2	0·34
Grain N			
Rate (mg/m²/°Cd)	32·2	31·2	1·00
Duration (°Cd)	800	853	11·7
Final (g/m²)	15·5	17·7	0·25
Final conc. (g/kg DM)	20·3	20·3	0·17
Remobilized N			
Rate (mg/m²/°Cd)	21·8	20·8	1·21
Duration (°Cd)	753	815	14·9
Final (g/m²)	10·8	11·4	0·12
Final (% anthesis N)	67·5	71·8	0·74
Final contribution to grain N (%)	70·7	66·0	1·43
Final nitrogen harvest index	74·8	79·7	0·35
$NUtE_g$			
Rate (g DM/g N/m²/°Cd)	0·14	0·11	0·016
Duration (°Cd)	645	679	21·2
Final (g DM/g N)	37·0	39·4	0·43

Fungicide × cultivar effects within years

Fungicide application had significant effects on nitrogen recovery, accumulation, efficiency and remobilization, but this depended on cultivar and season.

2001

Mixed infections of brown rust and *S. tritici* developed on untreated flag leaves, particularly of Consort, on which brown rust was dominant (Fig. 1*a–d*). All fungicide treatments gave good control of brown rust (Fig. 1*c–d*). The greater disease severity on the untreated flag leaves of Consort was associated with premature senescence, with green leaf area reaching 37% (Gompertz time scalar, *m*) 541 °Cd after anthesis (S.E. = 49·1). Consort flag leaves receiving fungicide treatment 5 did not senesce to this level until 725 °Cd (i.e. 10 days after the untreated plots, S.E. = 1·2). In contrast, untreated Hereward leaves did not senesce until 666 °Cd, and green area duration was not significantly extended by fungicide application ($P<0{\cdot}05$ for the cv. × fungicide interaction). There were also cv. × fungicide effects on final estimates of *Grain DM*, *Total N* and *Grain N* where effects of fungicide were larger on Consort than on Hereward (Table 6). In each case the effects of cv. × GS39 spray × GS59 azoxystrobin were significant ($P=0{\cdot}008$, 0·039 and 0·029 respectively; Table 6, Fig. 2*a–c*), i.e. on Consort, there were benefits of adding azoxystrobin at GS 59, which were not reflected in the green leaf area data. Benefits of fungicide for final *Grain DM* derived through effects on duration of grain filling, whereas effects on final *Total N* and *Grain N* arose through effects on both rate and duration. Fungicide effects on final *Grain N*

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

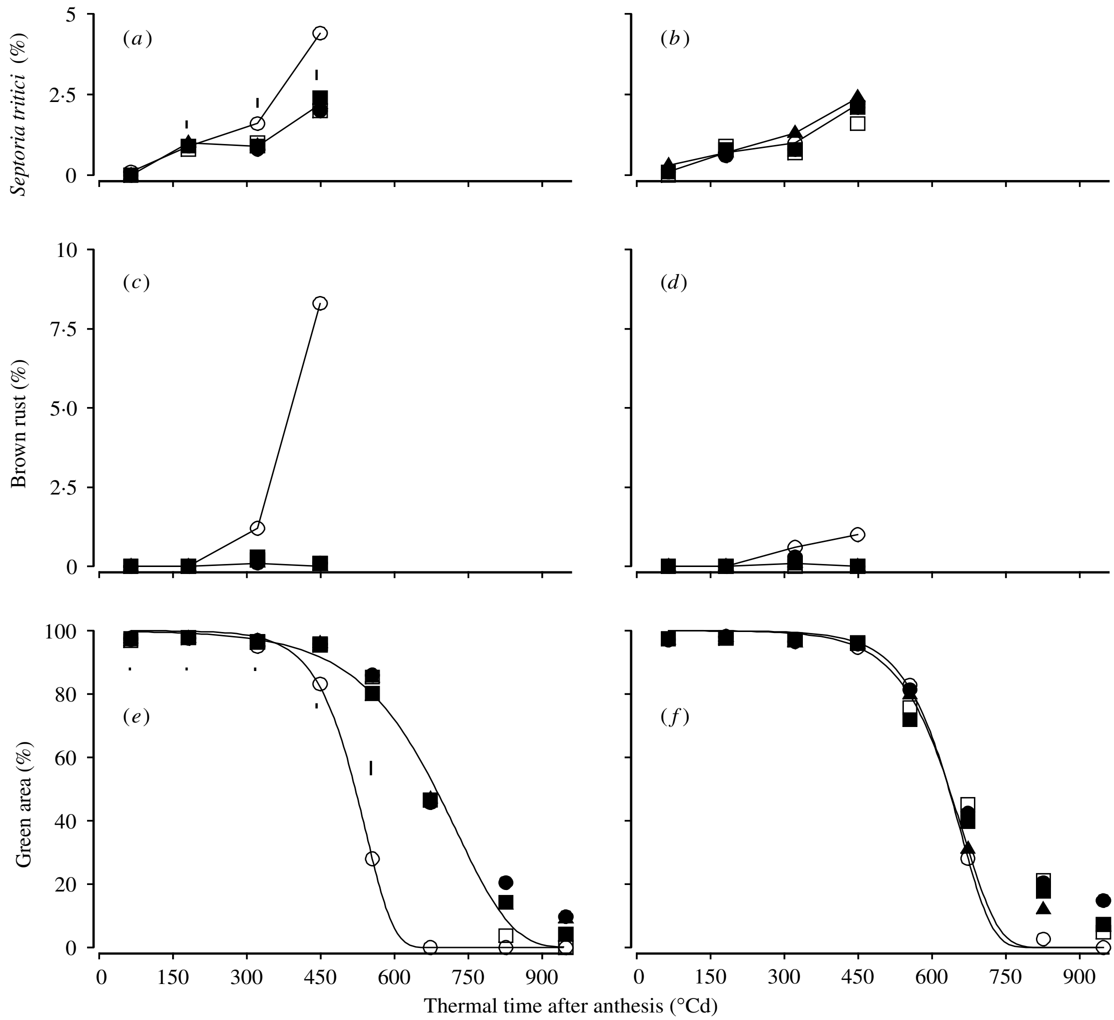

Fig. 1. Effect of fungicide treatment on the areas of green and disease on the flag leaves of Consort (left) and Hereward (right) winter wheat in 2001. Fungicide treatments 1 to 5 (Table 3) represented by ○, □, ●, ■ and ▲ respectively. Lines only fitted to treatments 1 and 5; Modified Gompertz (Eqn 1) in *e* and *f*. Vertical bars are S.E. (D.F. = 16) for comparing means within a cultivar.

and final *Grain DM* were broadly similar such that there was no significant fungicide effect on grain nitrogen concentration. There was certainly no indication that nitrogen had been diluted (Table 6).

Fungicide effects on *Remobilized N* were small (Fig. 2*d*) but, when both cultivars were considered there was still a benefit for adding azoxystrobin at GS 59 (Table 6; $P = 0{\cdot}049$ for GS39 spray × GS59 azoxystrobin effect). On Consort, fungicide appeared to slightly reduce the rate but increase the duration of nitrogen remobilization (Fig. 2*d*). The basis of this effect was clarified by considering nitrogen in different plant organs. Nitrogen quantities in the leaf laminas were often significantly higher shortly after anthesis when disease had been controlled (e.g. Fig. 2*h*). By complete senescence, however, nitrogen quantities were always significantly less in laminas of Consort previously sprayed with fungicide than in leaves prematurely senesced with disease (Fig. 2*g–i*). This increased loss of nitrogen from leaf laminas previously sprayed with fungicide was not evident until late into grain filling, certainly after 95% of final *Grain DM* had been accumulated. Although fungicide increased final remobilization from all leaf laminas, the effects on remobilization from the whole crop were still small because the quantity of net

Table 6. *Effect of wheat cultivar and fungicide treatment in 2001 on the accumulation of grain dry matter (DM), nitrogen in the above-ground crop biomass (Total N) and grain nitrogen (Grain N); net nitrogen remobilization from non-grain tissues (Remobilized N); and the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$). Values are derived from Eqns 2–6: Rate = maximum rate, Duration = thermal time to 95% of final value, Final = fitted value on last assessment date (925 °Cd after anthesis)*

Cv.	Consort			Hereward				
Fungicide*	Nil	Flag	Flag + azoxy.	Nil	Flag	Flag + azoxy.	S.E.a†	S.E.b†
Grain DM								
Rate (g/m²/°Cd)	2·39	2·33	2·38	2·41	2·30	2·30	0·200	0·141
Duration (°Cd)	580	650	680	540	600	570	35	25
Final (g/m²)	823	949	1007	872	918	878	22·9	16·2
Total N								
Rate (mg/m²/°Cd)	14·5	20·7	21·1	22·0	24·8	21·5	2·71	1·91
Duration (°Cd)	520	570	650	570	660	620	76	53
Final (g/m²)	20·6	22·6	23·8	22·8	24·6	23·0	0·87	0·62
Grain N								
Rate (mg/m²/°Cd)	30·7	35·7	35·6	37·4	39·5	36·8	2·20	1·56
Duration (°Cd)	710	730	770	680	700	690	36	25
Final (g/m²)	15·7	18·0	19·4	18·3	19·6	18·6	0·73	0·51
Final conc. (g/kg DM)	19·1	19·0	19·3	20·9	21·3	21·1	0·51	0·36
Remobilized N								
Rate (mg/m²/°Cd)	19·8	15·7	15·4	25·4	25·5	31·8	6·79	4·80
Duration (°Cd)	700	790	790	600	560	570	55	39
Final (g/m²)	9·8	10·1	10·3	10·1	9·7	10·2	0·24	0·17
Final (% anthesis N)	66·7	68·6	70·1	68·9	66·3	69·7	1·69	1·19
Final contribution to grain N (%)	62·4	56·5	53·3	56·2	49·8	55·2	3·11	2·20
Final nitrogen harvest index	76·3	79·7	81·6	80·1	79·8	80·7	0·75	0·53
$NUtE_g$								
Rate (g DM/g N/m²/°Cd)	0·14	0·11	0·11	0·13	0·12	0·13	0·015	0·010
Duration (°Cd)	500	600	580	450	400	410	45	32
Final (g DM/g N)	40·0	42·2	42·4	38·5	37·4	38·2	1·09	0·77

* See Table 3, Nil = treatment 1, Flag = mean of treatments 2 and 3, Flag + axozy. = mean of treatments 4 and 5.
† Standard errors (D.F. = 16) for comparing means within a cultivar with nil fungicide (S.E.a) or between fungicide means (S.E.b).

remobilization from the stem + leaf sheaths + chaff was large in comparison, and not increased by fungicide (Fig. 2 *f*, *j*). Indeed, fungicide reduced the proportion of *Grain N* that was from remobilized N because fungicide effects on *Total N* were greater.

The beneficial effect of fungicide on *Total N* uptake after anthesis, and on *Remobilized N* was reflected in improved final nitrogen harvest index ($P = 0{\cdot}015$ for GS39 spray × GS59 azoxystrobin), particularly on Consort ($P = 0{\cdot}002$ for cv. × GS39 spray). There was no significant effect of fungicide on $NUtE_g$ in 2001.

2002

Mixed infections of powdery mildew, brown rust and *S. tritici* developed on the untreated flag leaves of cv. Shamrock (Fig. 3 *a*, *d*, *g*). In contrast, only *S. tritici* was recorded on Consort (Fig. 3 *b*) and Hereward (Fig. 3 *c*). *S. tritici* was most severe on Consort and was associated with the earlier senescence of the untreated flag leaves on this cultivar (time to 37% green leaf area, Gompertz m, = 560 °Cd, S.E. = 13·9), compared with the untreated flag leaves of Shamrock ($m = 617$ °Cd) and Hereward ($m = 640$ °Cd). With fungicide applied, flag leaf senescence of the cultivars was more coincident ($m = 866$, 836 and 829 °Cd for Consort, Shamrock and Hereward respectively), contributing to a significant ($P < 0{\cdot}05$) cv. × fungicide interaction.

Fungicide significantly increased final *Grain DM*, *Total N*, *Grain N*, *Remobilized N*, nitrogen harvest index and $NUtE_g$ (Table 7, $P < 0{\cdot}001$, $= 0{\cdot}003$, $< 0{\cdot}001$, $= 0{\cdot}014$, $< 0{\cdot}001$ and $< 0{\cdot}001$ respectively). For most of these measures it at least appeared that fungicide effects were greatest on Consort with $P = 0{\cdot}008$, 0·46, 0·098, 0·078, 0·046 and 0·001 for the

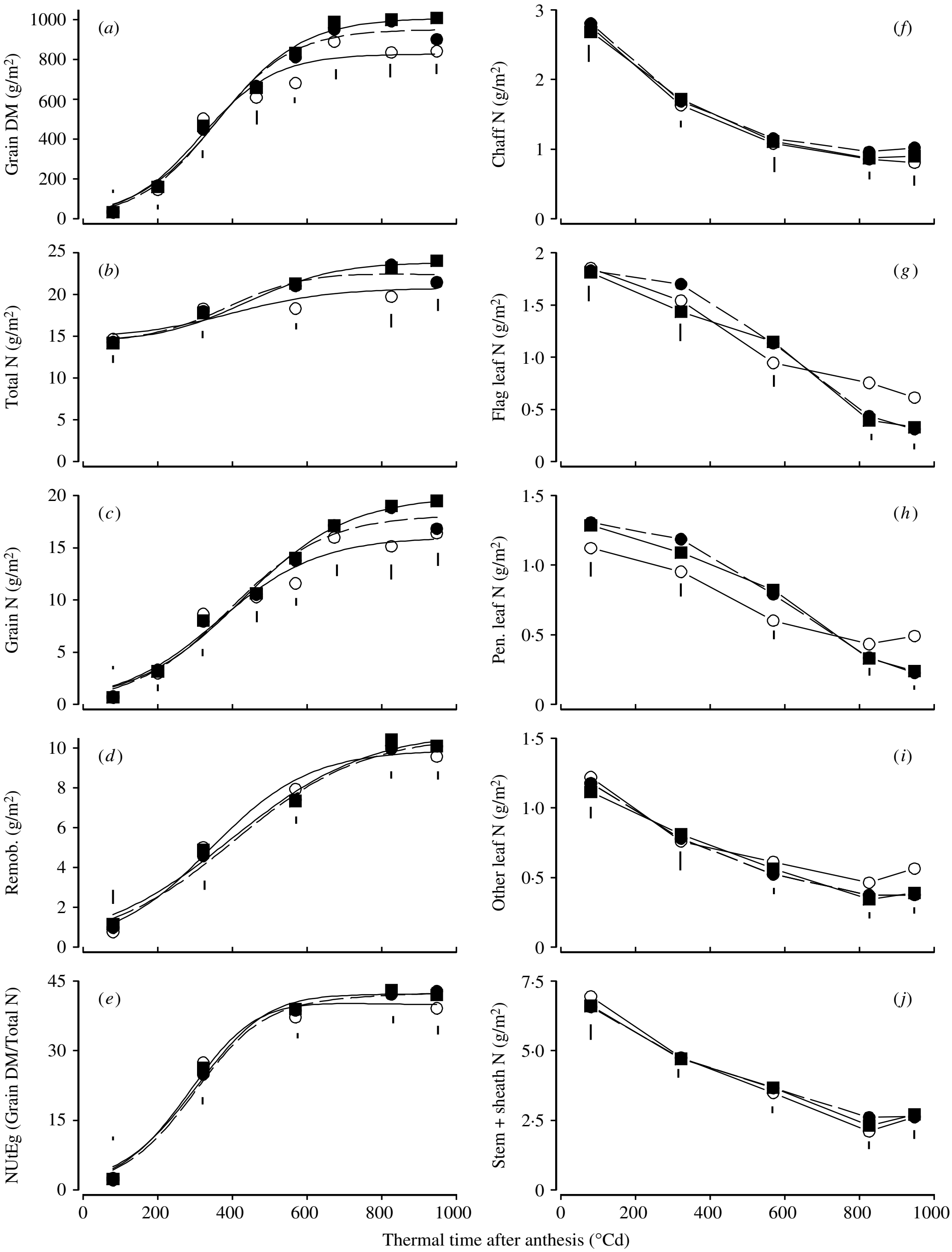

Fig. 2. Effect of fungicide applications to Consort winter wheat in 2001 on: accumulation of (*a*) grain dry matter (DM), (*b*) nitrogen in the above-ground crop biomass (Total N) and (*c*) grain nitrogen; (*d*) net nitrogen remobilization from non-grain tissues; (*e*) the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$); (*f*) nitrogen in the non-grain ear tissue (chaff); nitrogen in the lamina of the (*g*) flag leaf, (*h*) penultimate leaf and (*i*) leaves below the penultimate leaf; and (*j*) nitrogen in the stem and leaf sheaths. Symbols ○, ● and ■ correspond to fungicide treatment 1, mean of treatments 2 and 3, and mean of treatments 4 and 5 respectively (Table 3). Fitted lines in a–e are from Eqns 2–6. Vertical bars are maximum S.E. (D.F. = 16), i.e. for comparisons with ○.

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

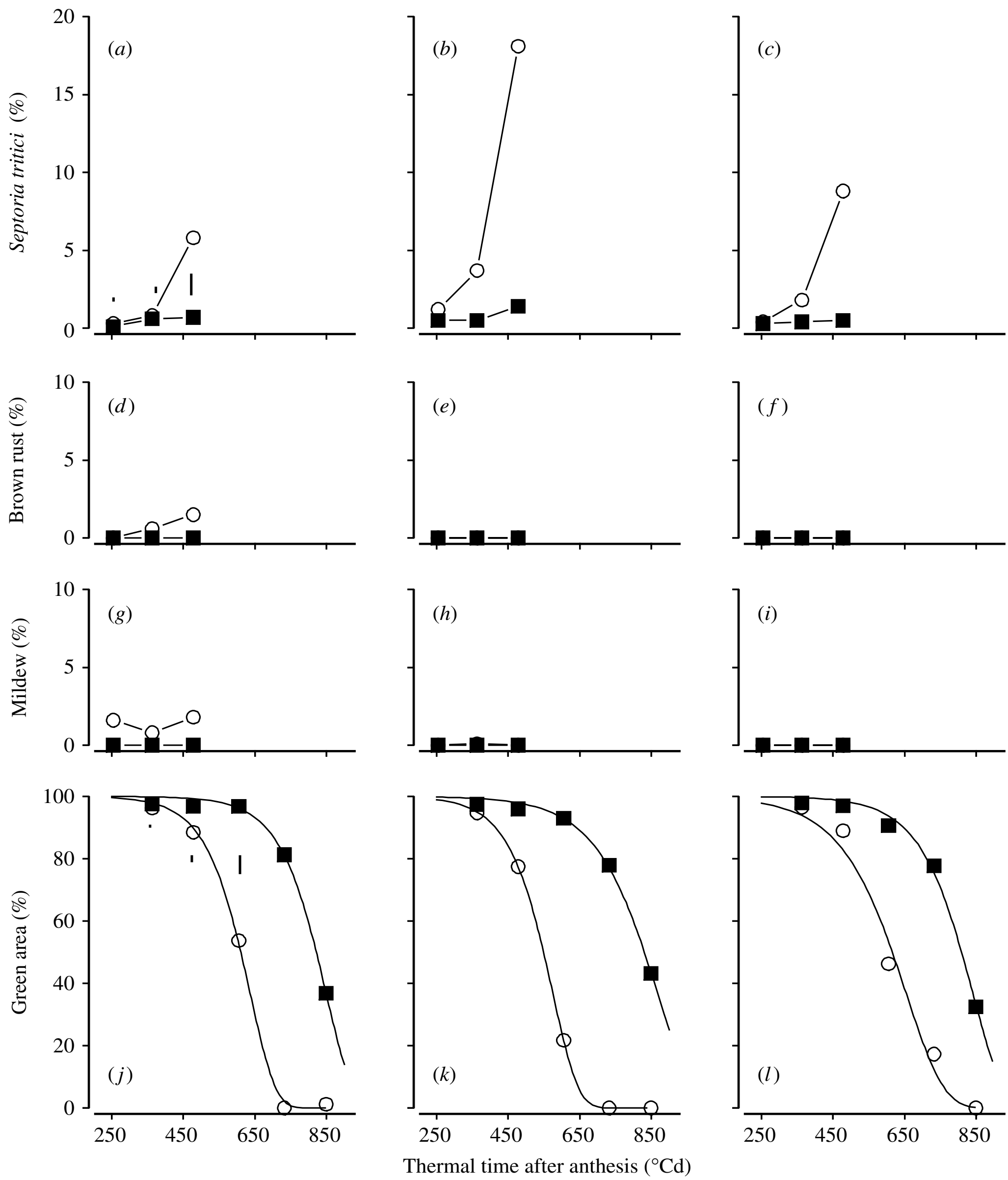

Fig. 3. Effect of fungicide treatment on the areas of green and disease on the flag leaves of Shamrock (left), Consort (centre) and Hereward (right) winter wheat in 2002. Fungicide treatments 1 and 5 (Table 3) represented by ○ and ■ respectively. Fitted lines in *j*, *k* and *l* are modified Gompertz (Eqn 1). Vertical bars are S.E. (D.F. = 6) for comparing fungicide treatment means within a cultivar.

respective cv. × fungicide effects. On Consort, fungicide effects on *Grain DM* and *Grain N* appeared mostly associated with improved rates of accumulation (Fig. 4*a*, *c*). As in 2001, fungicide appeared to reduce rate, but increase duration of N remobilization, again associated with disease control resulting in less nitrogen remaining in senesced leaf laminas (Fig. 4 *f*–*g*). In contrast to 2001, fungicide application also resulted in less N remaining in the Stem + leaf sheath + chaff on the final assessment date, contributing to the greater final amount of *Remobilized N*. Despite the increased *Remobilized N*, fungicide effects were still greater on *Total N* accumulated, such that the proportion of *Grain N* that appeared to derive

Table 7. *Effect of wheat cultivar and fungicide treatment in 2002 on the accumulation of grain dry matter (DM), nitrogen in the above-ground crop biomass (Total N) and grain nitrogen; net nitrogen remobilization from non grain tissues (Remobilized N); and the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$). Values are derived from Eqns 2–6: Rate = maximum rate, Duration = thermal time to 95% of final value, Final = fitted value on last assessment date (1186 °Cd after anthesis)*

Cv.	Shamrock		Consort		Hereward		
Fungicide*	−	+	−	+	−	+	S.E.† (D.F. = 6)
Grain DM							
Rate (g/m²/°Cd)	1·4	1·3	1·1	1·6	1·4	1·5	0·17
Duration (°Cd)	860	890	950	1000	840	900	63
Final (g/m²)	762	864	770	1068	812	887	25·0
Total N							
Rate (mg/m²/°Cd)	12·2	10·0	10·2	12·5	11·0	11·1	1·75
Duration (°Cd)	570	720	930	940	600	770	108
Final (g/m²)	20·8	22·3	21·6	24·4	21·4	23·1	0·50
Grain N							
Rate (mg/m²/°Cd)	25·7	22·8	20·5	26·6	26·2	26·9	3·67
Duration (°Cd)	890	950	1020	1060	880	970	68
Final (g/m²)	14·7	16·7	15·6	19·8	16·2	18·1	0·49
Final conc. (g/kg DM)	19·3	19·4	20·4	18·6	19·9	20·4	0·29
Remobilized N							
Rate (mg/m²/°Cd)	24·1	21·2	24·3	18·4	19·0	18·7	2·41
Duration (°Cd)	780	880	820	990	920	930	56
Final (g/m²)	10·9	11·4	11·0	12·4	11·8	12·0	0·24
Final (% anthesis N)	64·2	67·1	64·5	73·0	69·5	70·3	1·40
Final contribution to grain N (%)	74·2	68·6	70·8	62·8	74·0	66·5	2·49
Final nitrogen harvest index	70·8	74·8	72·1	81·3	75·7	78·1	1·09
$NUtE_g$							
Rate (DM/N/m²/°Cd)	0·076	0·068	0·068	0·073	0·066	0·069	0·0083
Duration (°Cd)	750	760	760	850	850	790	52
Final (DM/N)	36·7	38·7	35·6	43·9	38·1	38·3	0·58

* See Table 3 −, + = treatments 1 and 5 respectively.
† Standard error for comparing means within a cultivar.

from net remobilization was reduced by fungicide application (Table 7; $P = 0·014$).

Effects of fungicide on *Grain N* were more consistent over cultivar than were effects on *Grain DM* such that there was a significant cv. × fungicide interaction on grain nitrogen concentration ($P = 0·016$), arising because dilution of N in Consort grain contrasted with slight increases in concentration in the other cultivars (Table 7).

2003

There were no significant cv. × irrigation or fungicide × irrigation interactions so all data are presented as means of with and without irrigation.

As in the previous year, the dominant late season foliar pathogen was *S. tritici*, reaching 3, 8 and 5% of flag leaf areas of Shamrock, Consort and Hereward respectively by 580 °Cd after anthesis. Levels on the fungicide-treated plots at the same time were 0·5, 0·9 and 0·9% respectively. Brown rust was only seen at trace levels and then only on untreated flag leaves of Consort, reaching 0·8% of leaf area. Untreated flag leaves of Consort senesced first ($m = 574$ °Cd, S.E. = 10), followed by Hereward (645 °Cd) and Shamrock (662 °Cd) (Fig. 5*a–c*). Again, fungicide treatment delayed senescence, and reduced the differences between cultivars ($m = 752$ °Cd, 723 °Cd and 712 °Cd for Consort, Hereward and Shamrock respectively) resulting in a significant cv. × fungicide effect ($P < 0·001$).

As in the 2 previous years, final *Grain DM* and *Grain N* were increased by fungicide application (Table 8), particularly on Consort ($P = 0·016$ and 0·05 for cv. × fungicide effect). There was a similar interaction apparent ($P = 0·082$) on *Total N*. Fungicide treatment increased final *Remobilized N* of all cultivars ($P = 0·002$ for fungicide effect), and also reduced the amount of nitrogen in all flag leaves when fully

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

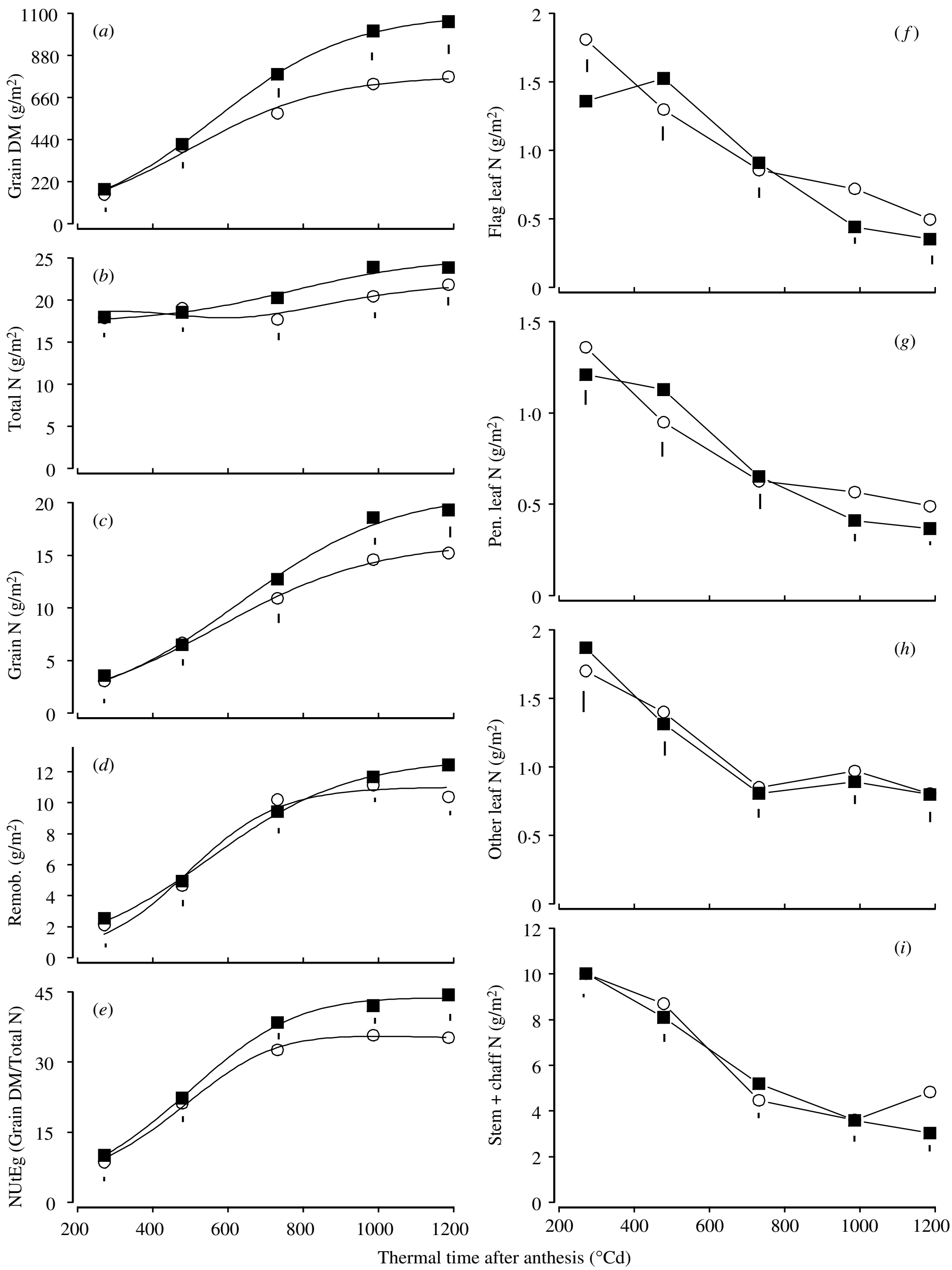

Fig. 4. Effect of fungicide applications to Consort winter wheat in 2002 on: accumulation of (*a*) grain dry matter (DM), (*b*) nitrogen in the above-ground crop biomass (Total N) and (*c*) grain nitrogen; (*d*) net nitrogen remobilization from non-grain tissues; (*e*) the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$); nitrogen in the lamina of the (*f*) flag leaf, (*g*) penultimate leaf and (*h*) leaves below the penultimate leaf; and (*i*) nitrogen in the stem, leaf sheaths and chaff. Symbols ○ and ■ correspond to fungicide treatments 1 and 5 respectively (Table 3). Fitted lines in *a*–*e* are from Eqns 2–6. Vertical bars are S.E. (D.F. = 6).

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

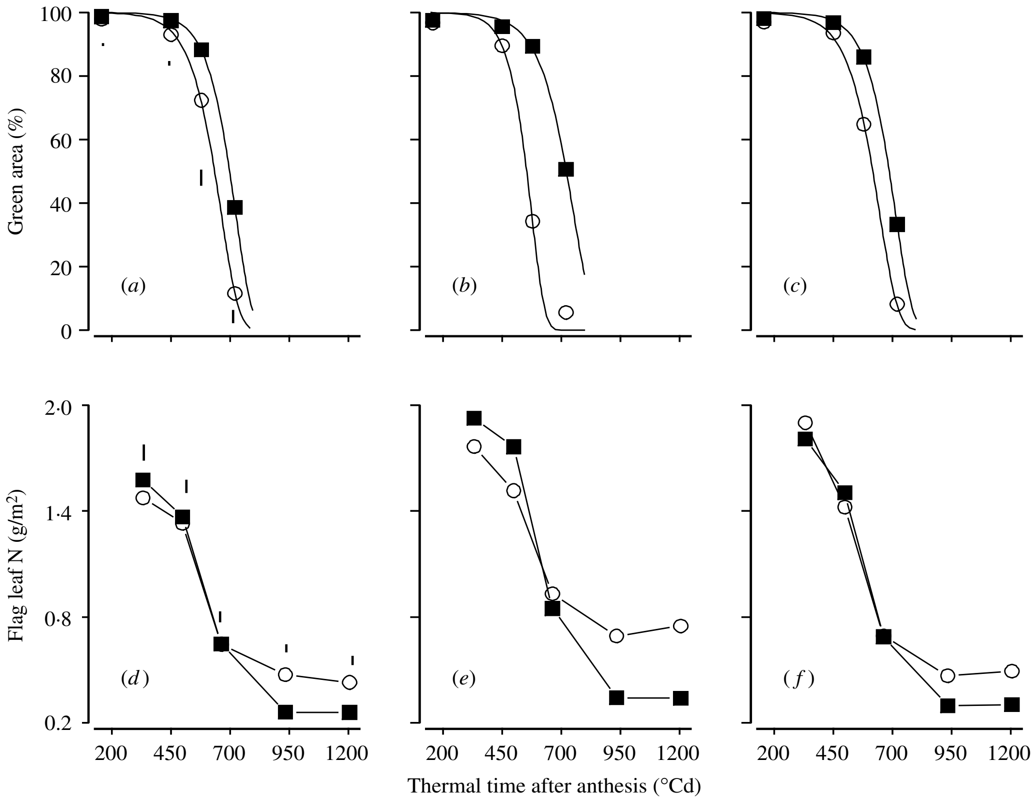

Fig. 5. Effect of fungicide treatment on the green area and nitrogen content of flag leaves of Shamrock (left), Consort (centre) and Hereward (right) winter wheat in 2003. Fungicide treatments 1 and 5 (Table 3) represented by ○ and ■ respectively. Fitted lines in *a–c* are modified Gompertz (Eqn 1). Vertical bars are S.E. for comparing fungicide treatment means within a cultivar.

senesced (Fig. 5*d–f*). Fungicide reduced the apparent contribution of remobilized N to *Grain N* in Consort, but not in the other two cultivars ($P=0{\cdot}042$ for the cv. × fungicide interaction). Fungicide increased the nitrogen harvest index of all cultivars ($P<0{\cdot}001$ for main effect) as it did for $NUtE_g$ ($P=0{\cdot}039$).

DISCUSSION

The data from neighbouring plots with no nitrogen fertilizer (0 N) applied, combined with the average final values for fungicide treatment 5 presented here, suggest that apparent N fertilizer recovery in the above-ground crop (($Total\ N-Total\ N_{0N}$)/fertilizer N) and grain averaged 69 and 61%, respectively. Similarly, apparent recovery of all available N (fertilizer N + $Total\ N_{0N}$) in the grain was 62% and the efficiency with which the crop produced grain dry matter from all available N was 30 g grain DM/g available N. All these ratios are similar to those obtained for other UK winter wheat crops on sandy soils (King *et al.* 2001; Kindred & Gooding 2004). The average net nitrogen remobilization from non-grain tissues for fungicide treatment 5 of 72% was comparable to previous estimates of 70 and 76% (Barbottin *et al.* 2002, 2005) for wheat growing without significant drought stress and with robust disease control.

The present paper confirms that wheat cultivars vary in nitrogen recovery and $NUtE_g$ (Ortiz-Monasterio *et al.* 1997; Foulkes *et al.* 1998). For N recovery, the difference between fungicide-treated Consort and Shamrock of 18 kg N/ha was large but not unprecedented for elite lines of similar age, given large amounts of N fertilizer (Ortiz-Monasterio *et al.* 1997). A similar comment can be made for the difference of 2 g DM/g N in $NUtE_g$ between the two cultivars (Ortiz-Monasterio *et al.* 1997). In both cases, Consort achieved the higher values and the present paper demonstrates that this was mostly due to extended duration of nitrogen uptake and grain filling. It is unclear from previous work how widespread this mechanism is, although cultivars with the 1BL/1RS rye translocation, thought to

Table 8. *Effect of wheat cultivar and fungicide treatment in 2003 on the accumulation of grain dry matter (DM), nitrogen in the above-ground crop biomass (Total N) and grain nitrogen; net nitrogen remobilization from non-grain tissues (Remobilized N); and the ratio of grain DM/Total N (Nitrogen utilization efficiency, $NUtE_g$). Values are derived from models in Eqns 2–6: Rate = maximum rate, Duration = thermal time to 95% of final value, Final = fitted value on last assessment date (1205 °Cd after anthesis)*

Cv.	Shamrock		Consort		Hereward		
Fungicide*	–	+	–	+	–	+	S.E.† (D.F.)
Grain DM							
Rate (g/m²/°Cd)	3·8	3·3	3·4	2·4	5·8	2·2	1·25 (20)
Duration (°Cd)	608	579	634	737	681	773	74·5 (17)
Final (g/m²)	654	701	623	737	688	720	29·0 (17)
Total N							
Rate (mg/m²/°Cd)	36·0	20·5	19·5	19·1	26·6	16·4	5·92 (28)
Duration (°Cd)	380	444	486	537	331	571	96·8 (23)
Final (g/m²)	18·8	18·5	17·8	19·5	20·2	20·1	0·71 (21)
Grain N							
Rate (mg/m²/°Cd)	48·1	38·0	31·3	33·5	39·7	27·7	6·81 (24)
Duration (°Cd)	691	712	768	823	796	895	68·5 (20)
Final (g/m²)	13·7	14·7	12·6	15·1	15·3	16·2	0·60 (19)
Final conc. (g/kg DM)	21·0	21·0	20·3	20·4	22·5	22·6	0·44 (35)
Remobilized N							
Rate (mg/m²/°Cd)	17·3	19·0	14·6	20·5	26·0	22·1	2·70 (39)
Duration (°Cd)	790	858	869	849	724	810	34·1 (37)
Final (g/m²)	11·0	12·4	11·0	11·7	11·3	12·2	0·26 (33)
Final (% anthesis N)	68·4	76·7	68·0	72·8	70·0	75·8	1·63 (33)
Final contribution to grain N (%)	81·2	86·2	88·8	80·0	74·9	77·0	4·12 (12)
Final nitrogen harvest index	72·8	79·7	71·0	77·6	76·1	80·7	1·12 (28)
$NUtE_g$							
Rate (DM/N/m²/°Cd)	0·209	0·180	0·188	0·139	0·323	0·123	0·0652 (21)
Duration (°Cd)	677	723	738	728	612	695	46·0 (38)
Final (DM/N)	34·8	38·1	35·5	38·1	34·4	35·9	0·97 (27)

* See Table 3 –, + = treatments 1 and 5 respectively.
† Standard errors for comparing means within a cultivar.

confer increased canopy persistence, often have high nitrogen uptakes and utilization efficiencies (Foulkes *et al.* 1998). Nitrogen uptake after anthesis must depend on nitrogen availability this late into the season. In the UK, even wheat crops not given nitrogen fertilizer (Sylvester-Bradley *et al.* 2001), or crops given nitrogen before the end of April (Sylvester-Bradley & Stokes 2001) can maintain an average rate of N uptake of about 1 kg N/ha/day during grain filling. The average temperature during grain filling of the experiments reported here was 17 °C, and average *Total* $N_{t=0}$ was 16 g/m², so the equivalent rate of *Total N* accumulation from anthesis to 95% of final grain weight was 1·4 kg N/ha/day. This value is certainly within the range reported for commercial wheat crops (Sylvester-Bradley & Stokes 2001), not withstanding differences arising from fitting logistic rather than linear models to describe grain filling. Access to more nitrogen would not appear to explain Consort's ability to maintain grain filling and nitrogen uptake. The cultivars did not vary in *Total* $N_{t=0}$ and Shamrock had higher root length and weight densities than Consort in the 2001/02 experiment during grain filling, significantly so below the plough layer (Gregory *et al.* 2005).

The present paper confirms that late-season foliar disease, and associated premature senescence of the flag leaf, can be associated with reduced final *Grain DM*, *Total N*, *Grain N*, *Remobilized N* and *NHI* (Ruske *et al.* 2003). Greater fungicide effects on these attributes for Consort can, therefore, be accounted for by its greater susceptibility to brown rust in 2001, and *S. tritici* in 2002 and 2003. It is also confirmed that increasing grain yield with fungicide use is not necessarily accompanied by dilution of grain protein concentration, as exemplified by the average effect

https://doi.org/10.1017/S002185960500568X Published online by Cambridge University Press

of fungicide increasing grain yield by 1·3 t at 85% DM/ha but having no effect on grain N concentration, i.e. it appears that diseases can be just as damaging to nitrogen accumulation and partitioning as they are for accumulation and partitioning of dry matter. As with cultivar, most of the effect of fungicide on nitrogen recovery was due to increased duration of N uptake, also associated with extended grain filling. The present authors demonstrate that fully senesced laminas, previously infected with brown rust or *S. tritici*, have retained more nitrogen than fully senesced leaves where disease had been controlled with fungicide. This effect has been previously documented for rusts (Dimmock & Gooding 2002*a*) but not, apparently, for *S. tritici*. When disease is controlled it seems nitrogen can be moved from the foliage to the grain very late in grain filling, thus contributing to late increases in grain nitrogen concentration. Although fungicide effects on remobilized N was only a relatively small component of the increase in *Grain N* following disease control, it did mean that it was possible to increase $NUtE_g$ without necessarily reducing grain nitrogen concentration, something that was not possible using the genotypic effects presented here or elsewhere (Kindred & Gooding 2004).

Extending the grain filling period by ensuring late-N availability and good disease control is proposed as a major component for future yield increases in UK wheat (Sylvester-Bradley *et al*. 2005). Both the genotypic and fungicide effects presented in the present paper suggest that significant improvements in nitrogen recovery, and dry matter produced per unit of available nitrogen, can be increased by extending or maintaining the grain-filling period, associated with extended nitrogen uptake into the above-ground crop, nitrogen accumulation by the grain, and in the case of fungicides, improved remobilization from vegetative tissues.

This work was part of Project 2422 funded by the Home Grown Cereals Authority of the UK. The authors also thank Dr S. A. Jones for technical assistance.

REFERENCES

Anon. (1976). *Manual of Plant Growth Stages and Disease Assessment Keys*. London: Ministry of Agriculture, Fisheries and Food (Publications).

Anon. (1994) *Fertiliser Recommendations for Agricultural and Horticultural Crops*. MAFF Reference Book 209 6th edn. LONDON: HMSO.

Barbottin, A., Jeuffroy, M. H. & Bouchard, C. (2002). Genotypic variability of nitrogen remobilisation in wheat. *Proceedings of the VII Congress of the European Society of Agronomy, Cordoba, Spain* (Eds F. J. Villalobos & L. Testi), pp. 665–666. Seville: European Society of Agronomy.

Barbottin, A., Lecomte, C., Bouchard, C. & Jeuffroy, M. H. (2005). Nitrogen remobilization during grain filling in wheat: genotypic and environmental effects. *Crop Science* **45**, 1141–1150.

Clarke, M. P. (2002). *Irrigation effects on growth, yield and quality of winter wheat as predicted by models and observed in field experiments*. PhD thesis, The University of Reading.

Cox, M. C., Qualset, C. O. & Rains, D. W. (1986). Genetic-variation for nitrogen assimilation and translocation in wheat. 3. Nitrogen translocation in relation to grain-yield and protein. *Crop Science* **26**, 737–740.

Dimmock, J. P. R. E. & Gooding, M. J. (2002*a*). The influence of foliar diseases, and their control by fungicides, on the protein concentration in wheat grain: a review. *Journal of Agricultural Science, Cambridge* **138**, 349–366.

Dimmock, J. P. R. E. & Gooding, M. J. (2002*b*). The effects of fungicides on rate and duration of grain filling in winter wheat in relation to maintenance of flag leaf green area. *Journal of Agricultural Science, Cambridge* **138**, 1–16.

Foulkes, M. J., Sylvester-Bradley, R. & Scott, R. K. (1998). Evidence for differences between wheat cultivars in acquisition of soil mineral nitrogen and uptake and utilization of applied fertilizer nitrogen. *Journal of Agricultural Science, Cambridge* **130**, 29–44.

Giunta, F. & Motzo, R. (2005). Grain yield, dry matter, and nitrogen accumulation in the grains of durum wheat and spring triticale cultivars grown in a Mediterranean environment. *Australian Journal of Agricultural Research* **56**, 25–32.

Gregory, P. J., Marshall, B. & Biscoe, P. V. (1981). Nutrient relations of winter-wheat. 3. Nitrogen uptake, photosynthesis of flag leaves and translocation of nitrogen to grain. *Journal of Agricultural Science, Cambridge* **96**, 539–547.

Gregory, P. J., Gooding, M. J., Ford, K. E., Clarke, M. P. & Pepler, S. (2005). *Managing Roots, Nitrogen and Fungicide to Improve Yield and Quality of Wheat. Project Report No. 359*. London: Home-Grown Cereals Authority.

Jamieson, P. D. & Semenov, M. A. (2000). Modelling nitrogen uptake and redistribution in wheat. *Field Crops Research* **68**, 21–29.

Jarvis, R. A. (1968). *Soils of the Reading District*. Harpenden: Rothamsted Experimental Station.

Kindred, D. R. & Gooding, M. J. (2004). Heterotic and seed rate effects on nitrogen efficiencies in wheat. *Journal of Agricultural Science, Cambridge* **142**, 639–657.

King, J. A., Sylvester-Bradley, R. & Rochford, A. D. H. (2001). Availability of nitrogen after fertilizer applications to cereals. *Journal of Agricultural Science, Cambridge* **136**, 141–157.

Matthews, G. A. (2000). *Pesticide Application Methods*, 3rd edn. Oxford: Blackwell Science.

Moll, R. H., Kamprath, E. J. & Jackson, W. A. (1982). Analysis and interpretation of factors which contribute to efficiency of nitrogen-utilization. *Agronomy Journal* **74**, 562–564.

MURPHY, D. P. L. & HELAL, H. M. (1996). Farming for energy – agronomic principles and environmental impacts. In *Energy from Crops*. (Eds D. P. L. Murphy, A. Bramm & K. C. Walker), pp. 41–110. Cambridge, UK: Semundo Ltd.

ORTIZ-MONASTERIO, J. I., SAYRE, K. D., RAJARAM, S. & MCMAHON, M. (1997). Genetic progress in wheat yield and nitrogen-use efficiency under four nitrogen rates. *Crop Science* **37**, 898–904.

PEPLER, S., GOODING M. J., FORD, K. E., ELLIS, R. H. & JONES, S. A. (2005). Delaying senescence of wheat with fungicides has interacting effects with cultivar on grain sulphur concentration but not with sulphur yield or nitrogen: sulphur ratios. *European Journal of Agronomy* **22**, 405–416.

RAUN, W. R. & JOHNSON, G. V. (1999). Improving nitrogen use efficiency for cereal production. *Agronomy Journal* **91**, 357–363.

ROSENBERGER, A., KAUL, H. P., SENN, T. & AUFHAMMER, W. (2001). Improving the energy balance of bioethanol production from winter cereals: the effect of crop production intensity. *Applied Energy* **68**, 51–67.

RUSKE, R. E., GOODING, M. J. & JONES, S. A. (2003). The effects of triazole and strobilurin fungicide programmes on nitrogen uptake, partitioning, remobilization and grain N accumulation in winter wheat cultivars. *Journal of Agricultural Science, Cambridge* **140**, 395–407.

SYLVESTER-BRADLEY, R. & STOKES, D. T. (2001). Fertilizer strategies to control the uptake and distribution of nitrogen in winter wheat. *Aspects of Applied Biology* **64**, *Wheat Quality*, pp. 185–186.

SYLVESTER-BRADLEY, R., STOKES, D. T. & SCOTT, R. K. (2001). Dynamics of nitrogen capture without fertilizer: the baseline for fertilizing winter wheat in the UK. *Journal of Agricultural Science, Cambridge* **136**, 15–33.

SYLVESTER-BRADLEY, R., FOULKES, J. & REYNOLDS, M. (2005). Future wheat yields: evidence, theory and conjecture. In *Yields of Farmed Species: Constraints and Opportunities in the 21st Century* (Eds R. Sylvester-Bradley & J. Wiseman), pp. 233–260. Nottingham: Nottingham University Press.

VERMA, V., FOULKES, M. J., WORLAND, A. J., SYLVESTER-BRADLEY, R., CALIGARI, P. D. S. & SNAPE, J. W. (2004). Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica* **135**, 255–263.

WHITE, D. J. (1981). Energy in agriculture. *Proceedings of the Fertiliser Society No. 203*. London: Fertiliser Society.

ZADOKS, J. C., CHANG, T. T. & KONZAK, C. F. (1974). A decimal code for the growth stages of cereals. *Weed Research* **14**, 415–421.

ZAHEDI, M. & JENNER, C. F. (2003). Analysis of effects in wheat of high temperature on grain filling attributes estimated from mathematical models of grain filling. *Journal of Agricultural Science, Cambridge* **141**, 203–212.