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Describing and understanding barley growth and development through the use of benchmarks

by

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ABSTRACT

Plots of winter barley, *cv* Pearl, were grown to a standard protocol at six sites across the UK, and in three seasons (2001to 2004). A detailed programme of assessments was conducted to provide a quantitative understanding of the yield-forming process, to indicate where the yield-limiting steps exist in barley, and provide benchmarks for crop growth. Benchmark dates for key growth stages (GS) were identified, with southern sites (Rosemaund, King's Lynn and Sutton Bonington) consistently reaching these key stages around 5 to 12 days before the northern sites (Edinburgh, Aberdeen and High Mowthorpe). The leaf emergence rate (phyllochron), as with wheat, was linearly related to temperature, and on average taking 108 ºC days for each leaf to emerge.

High yields were associated with good overwinter growth and early spring N uptake. Poor overwinter growth did not appear due to low N availability but other factors, such as cool autumn temperatures, slow germination and establishment. Across all sites and seasons, average grain yield was 8.8t ha^{-1} @ 85%DM. On average, there were 775 ears m^{-2}, with 24 grains ear^{-1}, at a grain weight of 46 mg. These and other benchmarks have been published in The Barley Growth Guide (HGCA, 2006). They provide a valuable reference point against which growers can assess the growth and development of their own crops. Yield appeared to be limited by the storage capacity of the grains (the number of grains produced and their potential size), rather than the ability of the crop to supply photosynthates for grain filling. Analysis of the yield forming process has shown that the number of grains m^{-2} (ears m^{-2} x grains ear^{-1}) accounted for 83% of the variation in yield between sites and years. High numbers of grains m^{-2} were associated with high levels of pre-anthesis biomass accumulation and it is suggested that a target for future crop impovement is to extend the period between the start of stem elongation and flowering to increase grain numbers further. A quantitative assessment of the amount of photosynthates potentially available for grain filling has shown that they exceeded the storage capacity of the grain in 16 of the 17 site/years analysed, but that the scale of the excess differed greatly. The results also show that the potential size of the grain is determined by both pre- and early post-flowering growth conditions. The amount of light intercepted by the crop per unit grain number during the period of early grain development appears to be particularly important in determining the final grain size (average grain weight). Crop management, therefore, may need to focus on protecting the canopy and ears during this critical early post-flowering phase.

Low grain N% was found to be associated with high average grain weights. Thus, where low grain N% is required, it is important that agronomic treatments designed to increase yield by increasing the number of grains m^{-2}, do not lead to a corresponding decrease in average grain weight. Our results, based on the variation that occurred in crop growth between sites, suggest that there is scope for increasing grain numbers without significantly reducing average grain weight and increasing grain N%.

SUMMARY

Introduction

For UK winter barley production to be economically sustainable, crops must achieve an acceptable output in terms of yield and quality, with the minimum of inputs.

Much detailed research has been conducted in barley, detailing apical development and vernalisation (Kirby and Appleyard 1980; Chun 1993), tillering (Kirby and Faris 1972: Kirby *et al.,* 1985b), grain filling and dry matter accumulation (Scott *et al.,*1983; Ellis and Kirby 1980), and yield formation and its components (Gallagher *et al.,* 1975; Hay 1995). Whereas this work has been useful in understanding certain specific aspects of crop development and growth, it has not been sufficient to keep pace with the yield increases that have been observed in winter wheat. Average yields of both wheat and barley were similar in the late 1940s, at about 2.5t ha^{-1}, however since then the yield of wheat/has risen to an average of over 8t ha^{-1} and barley to only 6t ha^{-1}.

To narrow the gap between the two crops, this project aims to provide a quantitative understanding of the yield-forming process in winter barley, to indicate where the yield-limiting steps exist, and provide benchmarks for crop growth.

The benefits of using an understanding of the physiology of yield formation in conjunction with 'benchmarks' for crop growth have been clearly demonstrated for wheat (Spink *et al.,* 2000). Due to the apparent physical similarities between wheat and barley it is attractive to assume that they are physiologically very similar. Whilst there is currently little information on resource capture or physiology of winter barley in the UK, a review of existing information and the results of a pilot study funded by HGCA indicated that wheat and barley are developmentally, and possibly physiologically quite different (Bingham *et al.,* 2000). As such the pathway to improving crop performance may be different in the two crops. Barley has been identified as having potentially greater tiller production, a smaller flag leaf, leaf 2 and leaf 3, and a lower vernalisation requirement. Barley, despite being indeterminate, may also be more limited by grain storage capacity, due to barley having only one grain per spikelet (wheat can have several).

Objective

This project aims to provide an underpinning understanding of barley growth, development, and yield formation, and establish benchmarks for crop progress to produce a growth guide. This should provide the necessary physiological understanding on which decisions to rationalise inputs of pesticides and fertilisers can be made, as well as identifying targets for crop improvement.

Methods

Crops of the two-row winter barley *cv* Pearl were grown to a standard protocol at six sites across the UK, and in three seasons (2001/02, 2002/03 and 2003/04). Sites were chosen to represent the major UK winter barley growing regions, and soil types (Table 1).

Crops were managed to be free of weed competition, pests and diseases throughout the season, and a full plant growth regulator (PGR) programme was used to avoid lodging. Crops were fertilised as for a standard crop of feed barley, following RB209 fertiliser recommendations.

Sites and sowing dates

Table 1 Site locations and area represented (sites will later be referred to by the highlighted abbreviation)

Site	Region (s) represented	% of winter barley crop represented
ADAS Rosemaund, Hereford	W. Mids and South West	21
East Anglia (near King’s Lynn)	Eastern England	21
Sutton Bonington, Leicestershire	E. Midlands	13
ADAS High Mowthorpe, N. Yorks	Yorkshire and the Humber	15
SAC Edinburgh	Scotland	10
SAC Aberdeen	Scotland	10

Sites were selected so that variation in soil characteristics within the field was as small as possible. Serious weed problems were avoided, particularly wild oats, black grass and rye grass. Sites were in a standard barley rotational position, e.g. in England after a first wheat crop. Sites were drilled between 15 September and 9 October in each season. Seed rates were selected to achieve plant populations of 250 to 300 plants m^{-2}, based on thousand grain weight (TGW) and expected establishment.

Assessments

A detailed programme of assessments was conducted at all sites and in all seasons, from sowing through to harvest (Appendix 1). This included destructive harvests to determine biomass and partitioning between plant parts as well green area index (GAI) and non-destructive measurements of light interception, tiller and leaf production. The timing of growth assessments was weighted towards the main period of growth in spring and summer, with assessments being conducted monthly through the winter, every fortnight in early spring, and every week in late spring and summer. Dry matter samples were submitted for N% determination at alternate samplings to quantify the pattern N uptake through the season.

Results

Crop development benchmarks

Yield components such as ears m^{-2}, grain per ear, and grain weight are all affected by the length of key developmental phases. Broadly, ears m^{-2}, being influenced by leaf emergence, tillering and tiller survival up to GS59 (Tottman 1987), grains per ear primarily by ear formation between GS39 and GS59, and grain weight by assimilate production between GS59 and GS87. As the first step in improving the understanding of yield formation in barley, it was necessary to determine when these key growth stages occur. Across the six sites and three years the key growth stages were identified and benchmark dates established by taking the median date for all sites and years for each stage.

Table 2. Key Growth stages and established benchmark dates

Growth Stage	Definition	Median Date
GS21	Onset of tillering, main shoot + 1 tiller	13 Nov
GS30	Start of stem elongation. ear at 1cm	2 Apr
GS31	First internode detectable	16 Apr
GS39	Flag leaf emerged, ligule visible	6 May
GS59	Inflorescence completely emerged	26 May
GS71	Early grain development, watery ripe	8 Jun
GS87	End of grain filling, hard dough	5 Jul

Differences between sites and years were evident, with southern sites (Rosemaund, King's Lynn and Sutton Bonington) consistently reaching these key stages between 5 to 12 days before the northern sites (Edinburgh, Aberdeen and High Mowthorpe). The differences were smaller at the earlier growth stages but at physiological maturity (GS87), cooler days in the north had slowed plant development and extended the grain filling period (GS59 to 87) on average by 12 days compared to southern sites (Appendices 2 and 5).

Leaf emergence and tillering

Tiller production and tiller survival influence the final number of fertile shoots or ears m^{-2}, which is usually determined by GS59 (ear emergence). Tillers emerge from the axil between a leaf and its subtending leaf sheath. As a result the rate of tiller appearance tends to follow the rate of leaf emergence. Tiller emergence generally ceases with the onset of rapid mainstem elongation. Typically, tiller numbers increased during the vegetative phase, reached a peak before onset of stem elongation and then declined to a stable ear number of between 500 to 1000m^{-2}. The rate of leaf emergence and tillering was recorded at all sites. The leaf emergence interval (phyllochron) was shown, as with wheat, to be linearly related to temperature, on average taking 108 ºC days for each successive leaf to emerge. Differences between sites were apparent, though clear latitude effects were not evident. In total southern sites produced on average 15 leaves per main stem whereas in the cooler north, main stems had 13 leaves. This was probably due to a shorter thermal duration from sowing to floral initiation (at which point the shoot apex switches from initiating leaf to spikelet primordia) at northern sites. It is possible that in the cooler northern conditions the vernalization requirement was fulfilled earlier and this led to a reduction in the thermal time for leaf primordia initiation.

The small differences in final leaf number across sites appeared to have little or no effect on tillering, and final ear number. Autumn tillering was generally a feature of all sites, with the highest rates of production in calendar time occurring in December, extending into January for southern sites (Fig. 1) where warmer weather conditions were favourable. Tiller abortion generally started in February for southern sites, with final shoot numbers being 34% lower than the February maximum. For northern sites tiller emergence tended to continue for longer, with maximum tiller number being reached in April and the start of tiller abortion delayed until May. Final tiller numbers showed that a similar percentage of tillers had aborted in northern and southern sites. By the end of the season final shoot numbers across all sites averaged 775 m^{-2} (Fig. 1).

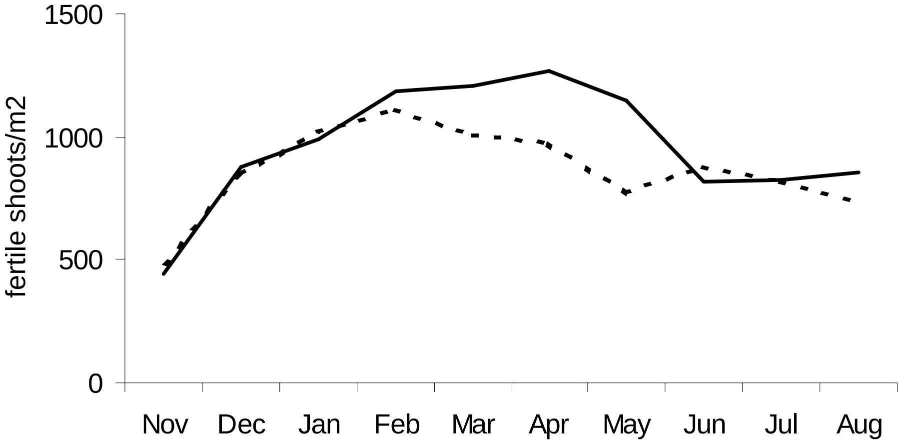


Fig. 1. Average shoot numbers (2002-2004) for northern (solid line) and southern (dotted line) sites.

Pattern of N uptake

Nitrogen and dry matter accumulation in plants are clearly related and an underlying sigmoidal pattern of N uptake was present, despite considerable variation between site and season. Through the late autumn and winter, N uptake was generally slow. Rates of uptake increased in March/April as longer photoperiods stimulated mainstem elongation and warmer temperatures stimulated canopy expansion through more rapid leaf emergence and expansion. On average between GS31 and GS39 in late April, N uptake was at its most rapid. Between GS39 and GS59, N uptake slowed, and N uptake was generally low after GS59 (Fig. 2).

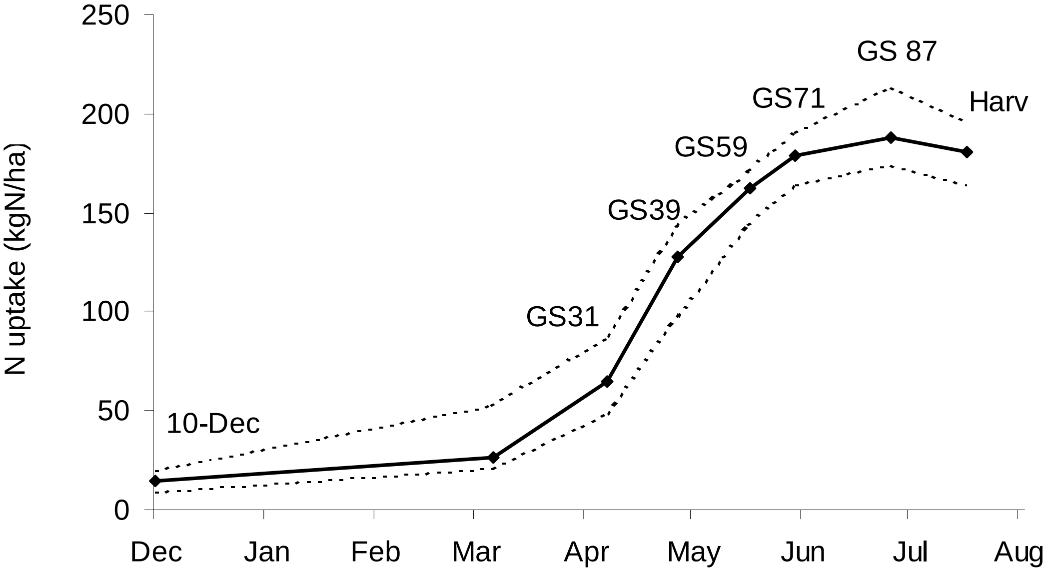


Fig. 2: Average pattern of N uptake, across all sites and seasons, dotted lines represent the interquartile range.

Green area index and N uptake

There was a close relationship at all sites between green area index and N uptake. Over all sampling dates, the median amount of N uptake for each unit of green area was 27.6 kgN ha^{-1}, with a range between 20.1 and 42.4 kgN ha^{-1} (Table 3)

Table 3: Nitrogen uptake for each unit of green area index (in kgN ha^{-1} GAI^{-1}), at all sites and years

Sites	2002	2003	2004	2002-2004
Aberdeen	25.0	27.5	32.1	28.2
Edinburgh	25.5	27.5	26.5	26.5
High Mowthorpe	29.9	22.9	23.7	25.5
King's Lynn	32.4	42.4	23.1	32.6
Rosemaund	20.1	20.7	22.6	21.2
Sutton Bonington	25.8	40.3	28.7	31.6
Mean	26.5	30.2	26.1	27.6

Crop N uptake over winter

Between sowing (late September/early October) and mid February, N uptake by most crops was between 10 and 40 kgN ha^{-1}, although early sowing and favourable autumn conditions at Rosemaund 2002 and Edinburgh 2004 resulted in crops taking up 75 and 58 kgN ha^{-1}, respectively.

A clear linear relationship ($R^2 = 0.97$) between N uptake and green area index was evident in February, indicating that on average 25.1kgN is required to form each unit of green area index (Fig. 3).

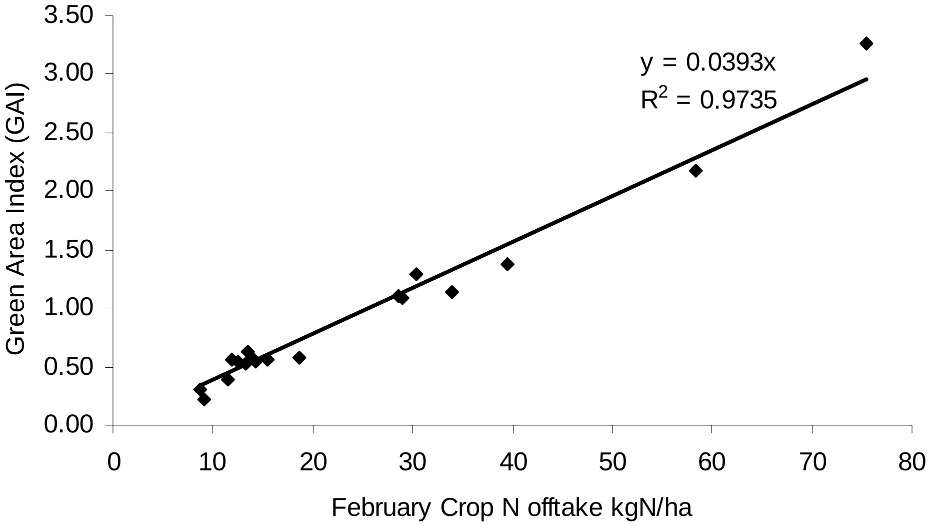


Fig. 3: Canopy size (GAI) v February N offtakes all site seasons.

Crops with a large green area over winter, although taking up more N overall, generally had a marginally lower N uptake (kgN ha^{-1}) per unit of GAI than smaller crops.

Despite some sites only achieving 10 to 20 kgN ha^{-1} uptake by mid February, other sites managed to take up 75 kgN ha^{-1} and this high early N uptake was associated with high yields (Fig. 4). However, where total N uptake by mid February was low, this did not appear to be due to the lack of N availability during this period. Assessments of crop N uptake and canopy size in early February (Fig. 5) and at GS39 (Fig. 6) showed negative correlations between N uptake and the amount of N per unit of GAI, indicating that where a lower total N offtake occurred, the amount of N per unit of GAI in the canopy was higher. This implies that slow growing crops, as observed at several sites including King’s Lynn in 2003, Sutton Bonington 2003, and Aberdeen 2004 may not have been restricted by low N availability but by other factors and that the low total N uptake observed was a symptom rather than the cause of poor growth at these sites. It is likely that weather and soil conditions in September and October influenced overwinter growth at these three sites. In all cases, dry soil conditions at planting and until the 2nd week of October, slowed germination and establishment, followed by below average October temperatures.

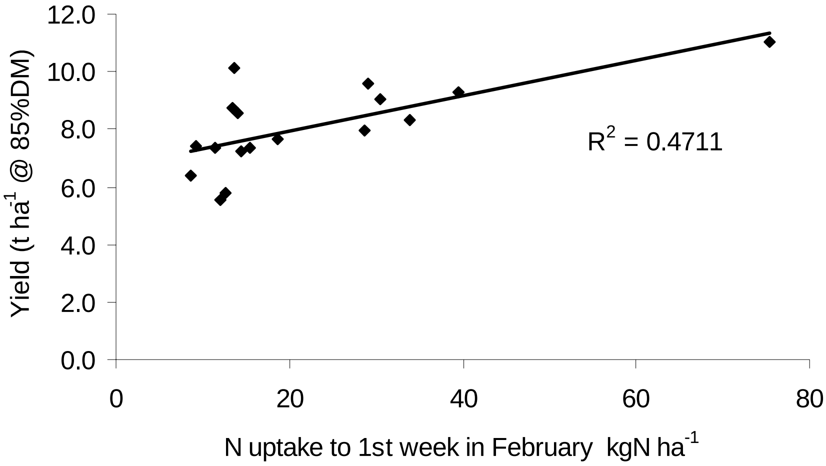


Fig. 4: Relationship between N uptake to the first week of February, and yield (t ha^{-1} @ 85%DM) at all sites and seasons.

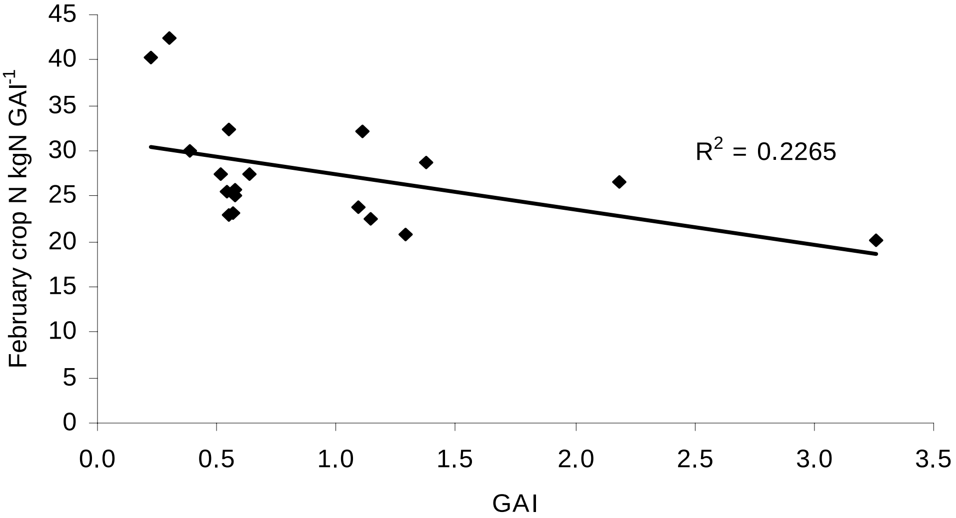


Fig. 5: Effect of Canopy size (GAI) in February with N uptake per unit of GAI, for all sites and seasons.

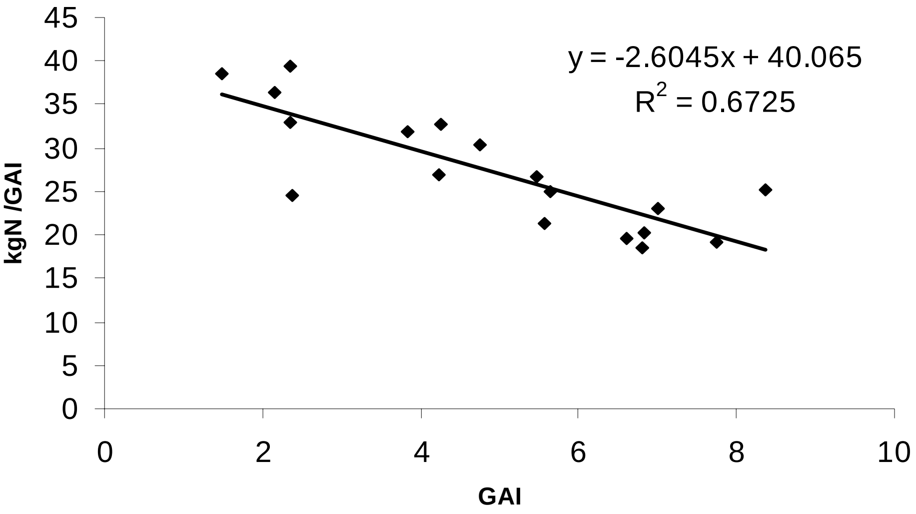


Fig. 6: Effect of canopy size (GAI) at GS39 with N uptake per unit of GAI, for all sites and seasons.

Components of yield

Yield can be considered in terms of the contribution of each of the yield components:
Final grain yield = Ears m^{-2} x Grains ear^{-1} x Average (mean) grain weight

In barley, previous work has shown that grain yield is generally more strongly related to grain number than grain size, with individual grain weight usually being the most stable component of yield (Gallagher *et al.,* 1975). The positive relationship between grain number and grain size and the general stability of individual grain weight suggests that grain sink size limits yield (Hay 1995). Grain number is controlled by number of ears m^{-2} and the number of grains ear^{-1}, and so is determined prior to anthesis.

Across all sites and seasons average grain yield was 8.8t ha^{-1} @ 85%DM, consisting, on average, of 775 ears m^{-2}, with 24 grains ear^{-1}, at a grain weight of 46 mg. Across all site seasons grains m^{-2} (ears m^{-2} x grains ear^{-1}) accounted for 83% of the variation in yield (Fig. 7).

High numbers of grains m^{-2} were associated with high level of biomass accumulation between GS31 and GS59, which was itself related to the amount of radiation interception during this period. As such it seems reasonable to hypothesise that increasing light interception between GS31 and GS59 will increase both the number of grains m^{-2}, and yield

Project results confirmed that greater biomass accumulation in the period up to GS59 was positively associated with grain numbers m^{-2} ($R^2 = 0.54$), with larger crops having both more ears m^{-2} and more grains ear^{-1}. Greater GS31 to GS59 biomass was associated with greater Photosynthetically Active Radiation (PAR) interception, although there was also a smaller contribution from Radiation Use Efficiency (RUE). There was a strong positive correlation between biomass accumulation from GS31 to GS59 and the duration of the GS31 to GS59 period. It can be concluded that the duration of this phenophase is critical in determining pre-anthesis growth. Therefore manipulating the duration of this phenophase must be a principal target for barley breeders in future years. Greater GS31to GS59 biomass was also associated with greater RUE in the present study. Recent work in wheat has found genetic gains in yield potential to be positively associated with pre-anthesis RUE linked to increased flag-leaf specific weight (thicker leaves). Selection for this trait may offer scope for genetic improvement in pre-anthesis RUE in barley. Alongside this, it will be important for agronomists to minimise any pre-anthesis stresses due, for example, to poor rooting affecting water and/or nutrient uptake, so depressing biomass productivity through effects on RUE.

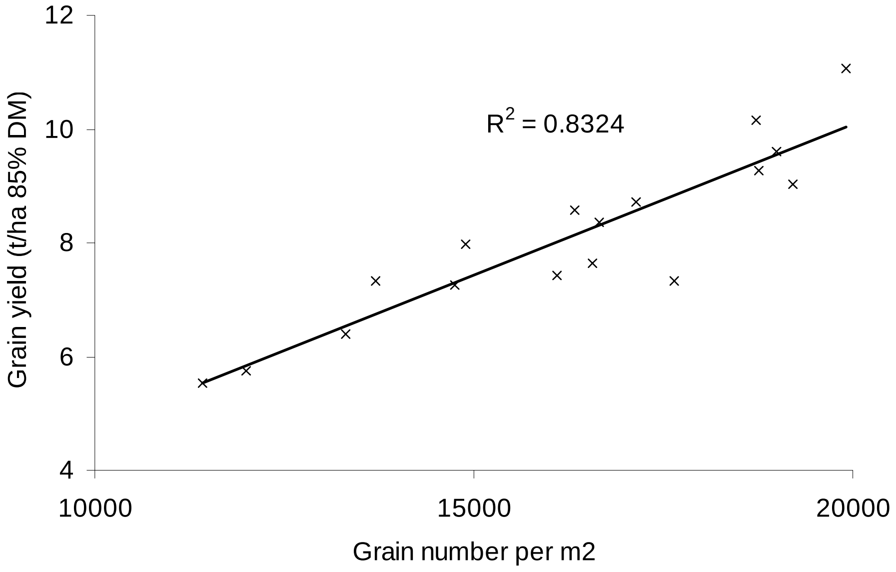


Fig. 7. Effect of grain number m^{-2} on grain yield (t ha^{-1} @85% DM)

As individual components, both grain number ear^{-1} and ear number m^{-2} were considered to be broadly of equal importance in determining grain number m^{-2}.

Mean grain weight by contrast was only weakly related to yield ($p=0.074$) and accounted for less than 20% of the variation in yield between sites and years (Fig. 8). Nevertheless, mean grain weight is an important aspect of quality as it is a measure of grain size and relates to the percentage of screenings and potential malt extract.

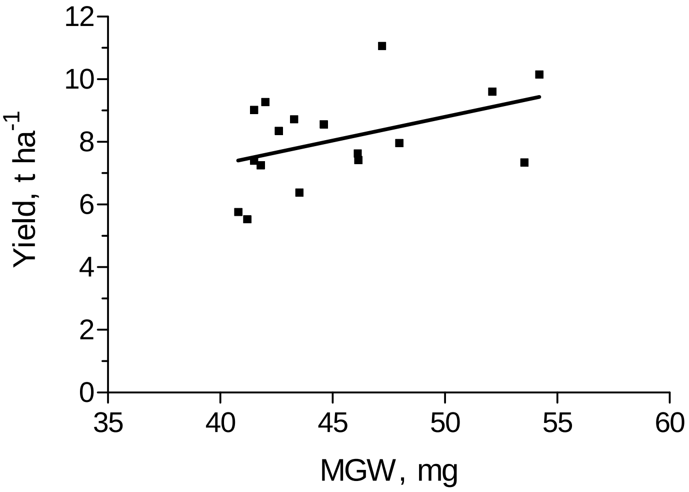


Fig. 8. Relationship between mean grain weight (MGW) (@ 85% DM) and grain yield (t ha^{-1} @85% DM) for 17 site/years. Line fitted by least squares regression $y = 0.151x + 1.25$; $P = 0.074$; $R^2 = 0.198$.

An explanation for the variation in MGW between sites and years was sought in terms of source or sink limitation of grain filling. Analysis of radiation interception and radiation use efficiency (RUE) during the post-anthesis period revealed that the pattern of RUE during grain filling differed between site/years. RUE was calculated as the slope of the relationship between cumulative light interception and above-ground biomass gain. For some the relationship was linear and RUE constant, for others the relationship was non-linear and RUE declined towards the end of grain filling. The extent and statistical significance of non-linearity was determined from the quadratic term of fitted 2nd order polynomials. Non-linearity could not be explained in terms of the shedding of leaf tissue during canopy senescence. There were weak associations ($R^2 < 0.3$) between the extent of non-linearity and GAI, above-ground biomass and leaf N concentration at GS59. A much stronger relationship was found between the green area per unit grain number (a index of the source:sink ratio) at GS59 and the decline in RUE ($R^2=0.63$). These results suggest that a major factor leading to the reduction in RUE during the second half of grain filling at some sites was some form of feedback inhibition from a limited sink capacity. This conclusion is supported by a reasonably strong relationship between non-linearity of RUE and the apparent contribution of stem carbohydrate reserves to grain yield ($R^2=0.47$). These findings also suggest that during the latter stages of grain filling stem reserves are utilised in preference to concurrently produced photosynthates.

The potential assimilate supply for grain filling was estimated as:
(max RUE x PAR interception) + WSC at flowering

Where RUE is the maximum during the post-anthesis period (i.e. before possible feedback limitation in those cases where RUE declines), PAR is the amount of photosynthetically active radiation intercepted by the crop and WSC is the amount of water soluble carbohydrate reserves accumulated pre-anthesis. The potential supply exceeded the measured grain yield at all sites except one, implying that crops were predominantly sink limited. The size of the excess, which is a measure of the relative source-sink balance during grain filling, differed widely between site/years. The sink limitation may arise from the number of grains per unit land area and/or their potential size.

The fact that the MGW varied between site/years, even when there was a potential excess of assimilate supply, implies that the potential grain weight must have differed. Further analysis was directed at investigating the control of potential grain weight. The variation in MGW between site/years was linked to differences in the mean rate and not the duration of grain filling. The fact that differences in rate could not be explained by differences in temperature, since they remained when the rate was expressed in units of thermal time (^oC days) rather than calendar time, is consistent with the view that the rate of grain filling was limited by some property of the grain itself.

MGW did not relate well to any measure of above ground growth or crop structure at ear emergence (GS59). There was a significant positive linear relationship between MGW and the amount of radiation (PAR) intercepted per unit grain number between ear emergence and the start of rapid grain filling (R^2=0.32, P=0.023), but not over the whole grain filling period. This is supports the conclusion that MGW is determined by potential grain size. A multiple regression model comprising five explanatory variables accounted for a much larger proportion of the total variation in MGW (R^2=0.72, P=0.013) than PAR interception on its own. There were significant positive associations of MGW with post-anthesis radiation use efficiency and PAR intercepted from GS59 to the start of rapid grain growth (RGG), and significant negative associations with the shoot number per plant, mean air temperature from GS39 to GS59 and mean daily rainfall from GS59-RGG. The results suggest that both pre and post-anthesis conditions operate in concert to determine the potential grain weight of barley in the UK. However, assimilate availability per grain during the period of early grain development when the number of endosperm cells is increasing appears to be central to setting the capacity of the grain for subsequent filling.

Differences between site/years in the amount of radiation intercepted per grain, and hence assimilation per grain, during this period were more closely related to the incident radiation than the number of grains m^{-2}. As such, there will be variation between sites in MGW over which we have no control. However, we suggest that at a particular site it will be important to try and maximise the amount of radiation intercepted per grain during the first two to three weeks following flowering in order to maximise MGW. This might involve avoiding the production of excessively dense canopies as these are associated with large grain number m^{-2} but little additional light interception above a GAI of 5 to 6. There may also be some scope to influence MGW through crop management by ensuring a high proportion of mainstems in the ear population (e.g. Naylor *et al.,* 1997), although its impact may be limited.

Source Sink balance

The control of grain filling can be considered in terms of the supply of photosynthate (source limitation) or the capacity of the grain to accumulate available carbohydrate (sink limitation). In this study at 16 of the 17 sites taken to harvest, the yield achieved was less than the potential yield, (based on potential supply of photoassimilates) (Table 4). This implies these crops were limited by the storage capacity of the ears (sink limited).

At the other site, Sutton Bonington in 2004, the potential was very close to the actual yield, indicating that this crop was either source limited or in balance (Table 4).

Table 4. Difference between potential photosynthate supply and grain yield, t ha^{-1} at 100% DM for each harvest year 2002-2004.

Site	Max RUE		
	2002	2003	2004
Aberdeen	1.84	0.62	1.53
Edinburgh	6.59	8.67	-
High Mowthorpe	3.03	0.64	3.21
King’s Lynn	2.88	1.28	3.78
Rosemaund	2.93	0.75	1.48
Sutton Bonington	3.82	2.99	-0.04

The conclusion that in the UK the yield of winter barley crops is largely sink limited is supported by the relationship found between grains m^{-2} and yield (Fig. 7). In a sink limited crop it would be expected that increasing both grains ear^{-1} and ears m^{-2} would improve the storage capacity of the crop and consequently yield.

Grain quality

Crops grown in this study were fertilised as for a standard feed wheat crop, as such it is perhaps surprising that grain N% was in many cases sufficiently low to meet the levels required for malting barley (<1.80%) (Table 5). This was most noticeable in 2003, where at all sites except Sutton Bonington, grain N% were well below this level. This was a season characterised by high thousand grain weights. When considered in terms of the effects of the yield components, grain N% appears to be most influenced by grain weight and not by ear number m^{-2} or grains ear^{-1} (Fig. 9).

Table 5. Grain N% across sites and seasons

Site	% grain N		
	2002	2003	2004
Aberdeen	1.92	1.46	1.75
Edinburgh	1.92	1.70	-
High Mowthorpe	1.77	1.33	1.50
King’s Lynn	1.94	1.68	1.87
Rosemaund	1.79	1.52	1.71
Sutton Bonington	1.88	1.85	1.88

Alleviating sink limitation through an increase in storage capacity of the crop (grains m^{-2} or potential grain weight), is likely to result in better utilisation of post anthesis radiation and improve yield. However, the above data suggest that if strategies to increase grains m^{-2} in turn reduce the average grain weight, it may actually result in a higher grain N% (Fig. 9), despite a higher overall yield. So to prevent an excessively high grain N%, strategies to improve yield must not adversely affect grain weight.

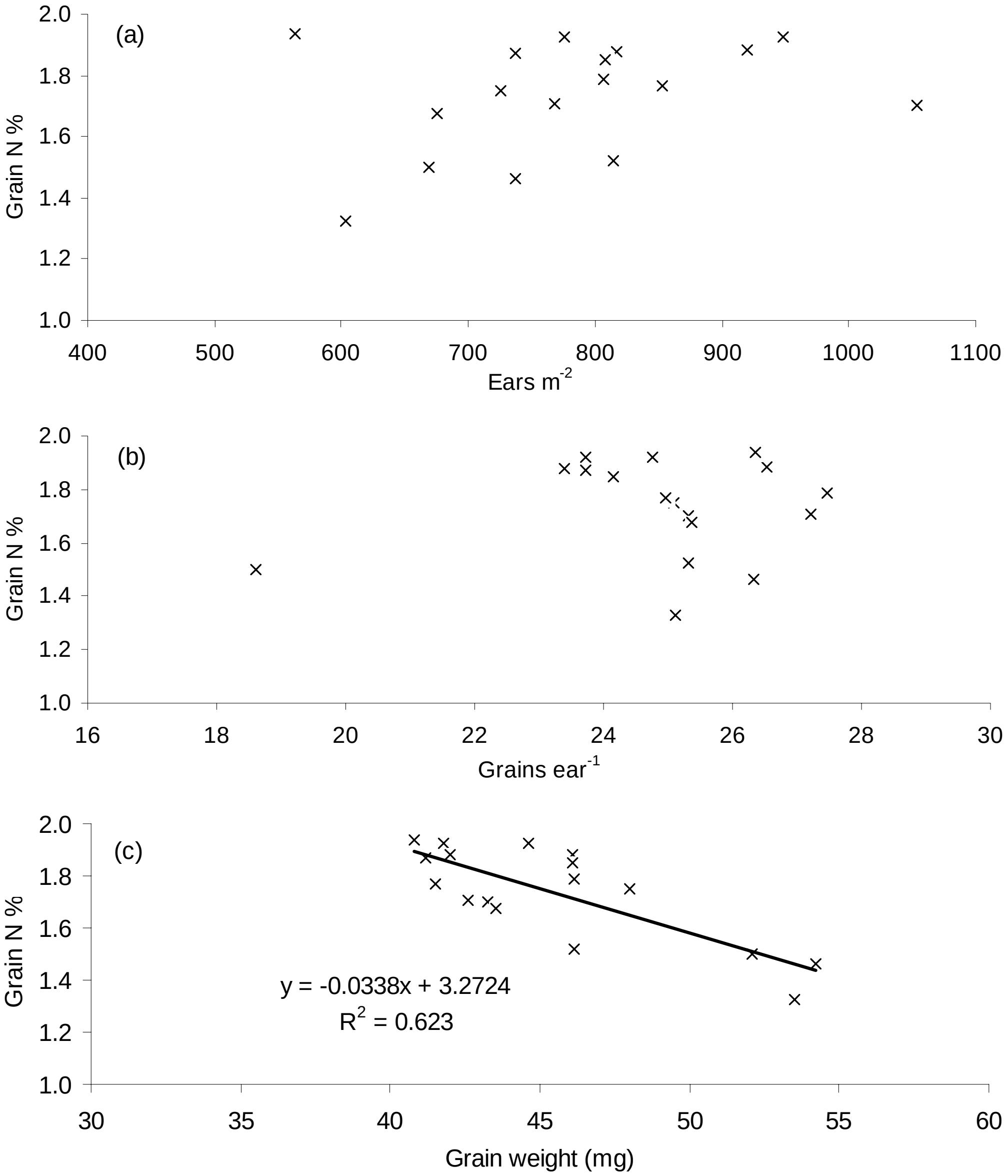


Fig. 9. Relationship of Grain N% with Grain weight, Grains ear^{-1} and Ears m^{-2} across all sites and seasons.

Conclusions

A primary objective of the current project was to produce detailed benchmarks for the growth and development of a winter barley crop, against which growers will be able to assess the performance of their own crops. The availability of benchmarks as a point of reference, will enable crop growth to be evaluated in a more quantitative way than was hitherto possible, providing a more objective basis for making management decisions. The benchmark data from the current project have been collated and published in The Barley Growth Guide (HGCA, 2006).

A second objective of the project was to undertake a comprehensive physiological analysis of the yield forming process in winter barley to highlight possible targets for crop improvement. The results show that in the UK yield is largley sink limited and thus improvements in yield should be possible by increasing the number of grains m^{-2}. Such increases might be achievable by lengthing the duration of the developmental period GS31 to GS59 and we recommend that this trait be given consideration by plant breeders. An inherent danger in increasing the sink capacity (grains m^{-2}) of the crop is that there is insufficient photosynthetic capacity during grain development and filling to meet the increased demand from a larger grain number. This could lead to a reduction in grain size (mean grain weight) and an increase in grain N%. However, the development and application of a novel technique for quantifying the extent of the source-sink imbalance in UK crops suggests that at most sites and in most years there is sufficient excess of potential assimilate to support an increase in grain number.

This project has also shown that mean grain weight is determined by the potential grain size, which is itself determined by pre- and early post-anthesis growth conditions. A key factor appears to be the amount of light intercepted per unit grain number during the period of early grain development (prior to the onset of rapid grain filling). An implication of these findings is that the effect of any future increase in grain number m^{-2} on grain quality (in particular mean grain weight and grain N%) is likely to be governed by its impact on the potential grain size, rather than total assimilate availability for grain filling. We, therefore, recommend that further physiological investigations be targetted at understanding the control of potential grain size.

Although in the current study most of the variation in light interception during the period of early grain development was associated with differences between sites and years in the amount of incident light and the duration of the slow period of grain development, we suggest that this period is likely to be a critical one for crop management to ensure that losses of green leaf area to disease or late season stress (e.g. drought) are minimal.

APPENDIX 1: GROWTH STUDY METHODS, ASSESSMENTS AND RECORDS

Overview

Plots of winter barley, *cv* Pearl, were grown to a standard protocol at six sites across the UK, and in three seasons (2001/02, 2002/03 and 2003/04). Sites were chosen to represent the major UK winter barley growing regions, and soil types.

Crops were managed to be free of weed competition, pests and diseases throughout the season, and a full plant growth regulator (PGR) programme was used to avoid lodging. Crops were fertilised as for a standard crop of feed barley, following RB209 fertiliser recommendations.

At each site 10 plots were used to monitor crop growth and development and to measure yield. Measurements were frequent and detailed, and were conducted concurrently at each site to ensure comparable data across sites.

Sites and Site Management

Plot layout and size

Replicated plots of winter barley, *cv* Pearl, were grown at six sites and in each of three seasons (2001/02, 2002/03 and 2003/04). There were 10 plots of barley at each site and in each season. These were arranged in a single row, with three plots used for destructive growth analysis, and four plots used for combine harvesting. The remaining three plots were spare sampling plots, used when additional plot area was required. Plots were of a minimum size of 4m x 21m.

Seed

Raxil Secur treated seed was supplied annually from one source.

Sites and sowing dates

Sites (Table 1.1) were selected to represent the main barley growing areas of the UK. Each site was located so as to have as little as possible variation in soil characteristics. Serious weed problems were avoided, particularly wild oats, black grass and rye grass. A standard barley rotational position, e.g. in England after a first wheat crop, was used in each case and were drilled between 15 September and 9 October in each season (Table 1.2). Seed rates were selected to achieve plant populations of 250 to 300 plants m^{-2}, based on thousand grain weight and expected establishment.

Table 1.1: Site locations and area represented (sites will later be referred to by the highlighted abbreviation)

Site	Region(s) represented	% of winter barley crop represented
SAC Aberdeen	Scotland	10
SAC Edinburgh	Scotland	10
ADAS High Mowthorpe, N. Yorks	Yorkshire and the Humber	15
East Anglia (near King's Lynn)	Eastern England	21
ADAS Rosemaund, Hereford	W. Midlands and S. West	21
Sutton Bonington, Leicestershire	E. Midlands	13

Table 1.2: Sowing dates for each site and season

Site	2001/02	2002/03	2003/04
Aberdeen	2-Oct	27-Sep	18-Sep
Edinburgh	9-Oct	17-Sep	16-Sep
High Mowthorpe	2-Oct	25-Sep	24-Sep
King's Lynn	22-Sep	29-Sep	17-Sep
Rosemaund	21-Sep	30-Sep	19-Sep
Sutton Bonington	3-Oct	30-Sep	15-Sep

Crop husbandry

Crops were managed to be free of weed competition, pests and diseases throughout the season; preventative measures such as herbicides, insecticides, slug pellets (pre-emergence) and full prophylactic fungicide programmes were used. To avoid aphid transmission of BYDV (in southern sites), synthetic pyrethroids were applied at full label rate in the autumn.

In order to avoid lodging, a full plant growth regulator (PGR) programme was used. Chlormequat (full rate) at GS30/GS31 (Tottman and Broad, 1987), followed by Terpal (half rate) at GS37 to GS39 were applied.

Autumn nitrogen was permitted if soil mineral nitrogen levels were expected to be low enough to restrict tillering. Spring nitrogen was applied as ammonium sulphate (21% N, 60% SO_3) at the start of rapid spring growth but before GS30 and ammonium nitrate at GS31 and GS32, as for feed barley. Soil mineral nitrogen in February was used to determine the amount of N to be applied based on the soil nitrogen supply (SNS) index according to Fertiliser Recommendations RB209 (MAFF 2000, 7th edition). In February, a total of six soil cores were taken, at 0-30cm, 30 to 60cm and 60 to 90cm horizons, from across the trial area, for soil mineral nitrogen analysis. Samples from each core were bulked for each soil horizon into three samples, one for each depth, and stored immediately in a chilled cool box, prior to being frozen and sent to Eurofins (formerly Direct Laboratories) at Wolverhampton, for analysis.

Plants were checked for manganese deficiency in February and at GS30 and GS31 and deficiency was treated with liquid manganese sulphate where necessary.

Assessments

Plant emergence

Starting one week after sowing, plant emergence was assessed every two days until first coleoptiles or leaf tips were observed above ground. Five lengths of row, each 1m in length, were marked out in three plots per site, and the number of emerged plants in each of these lengths of row was recorded, until full emergence, when a constant plant number was achieved. The date of 50% emergence was the date when half this number was recorded.

Soil sampling and analysis

Top soil (0 to 15cm depth) nutrient status analyses were conducted in September to test for P, K, pH and % organic matter. Twenty-five cores were taken from across each site, and bulked to produce one sample per site.

Crop health check

The crop was checked for any pests, diseases and weeds, by examining plants in the field and taking samples into the laboratory if necessary. This was done at each of the growth stage assessment dates and at each leaf/shoot number assessment date. Any pest attacks (e.g. grazing by rabbits or aphid infestation), winter damage (see next paragraph), mechanical damage (e.g. due to hail or trampling), lodging, or symptoms of nutrient deficiency, were recorded.

After crop damage by prolonged severe cold weather or after a sharp frost following a period of mild weather, the damage was scored, after allowing for a period of seven to eight days for symptoms to develop, using the following scale:

No damage.
Leaf tip damage
Severe leaf damage, up to 25% loss of leaf area.
Very severe leaf damage, up to 50% loss of leaf area.
Very severe leaf damage, up to 75% loss of leaf area.
Plant or all leaves dead.

The percentage of the crop in each category was recorded as well as the crop growth stage at time of assessment.

Stages of plant development (growth stages)

Stages of plant development, as detailed in the cereal growth stage decimal code (Tottman and Broad, 1987), were recorded at each sampling date and during shoot/leaf counting. As the crop approached key growth stages: GS31, GS39 and GS59, the frequency of crop visits was increased to three times a week (Monday, Wednesday and Friday), so that exact dates of these major stages of plant development were recorded. For the nodal stages (GS30 up to but not including GS37) a date for a growth stage was recorded when more than 50% of main shoots had reached the stage. From GS37, a plot was recorded as being at a specified stage when 50% of all shoots had reached this stage.

Leaf and shoot counts

Main stems of 10 plants were tagged before the onset of tillering (at GS12) in each of the three plots. Starting from GS12, the number of main stem leaves was recorded until flag leaf emergence (GS 39), at approximately 100 day ºC intervals. The total number of potentially fertile shoots per plant was recorded from GS12 until harvest.

Between GS39 and total leaf senescence, the number of green leaves (defined as having more than 50% area green), on each tagged main stem was recorded.

Growth analysis

Growth analysis measurements were carried out at monthly intervals, from approximately four weeks after emergence until early March; then at fortnightly intervals from mid-March to late April; then at weekly intervals from early May to physiological maturity.

At each growth analysis sampling event, plot samples were taken using quadrats (0.6m x 1.2m) placed in the field prior to the start of sampling, between emergence and GS12. Through the season these were harvested sequentially starting from the end of the plot. Each quadrat was orientated so that one row of crop passed through diagonal corners of the quadrat, with at least 0.5m separation between the parallel sides of adjacent quadrats, and at least 0.75m between quadrats and the ends and edges of plots and any tramlines.

Sampling and sample processing up to GS31

Plants within the quadrats were dug up or pulled out and placed into a plastic bag that was then sealed to prevent the leaves from drying out before leaf areas were measured. When immediate processing was not possible, samples were stored at 4°C for a maximum of two days. Where samples were contaminated with soil, they were washed and gently blotted dry after cold storage.

Processing the main sample

The total fresh weight of the quadrat sample was recorded.
Plant number was recorded.
The sample was divided into a 25% sub-sample (SS1) and a 75% sub-sample (SS2).
The number of plants in SS1 was recorded.
The potentially fertile shoots and the dead and dying shoots were recorded separately in SS1, before removing the roots.
Roots and below ground stem were then cut off (identified by a change in colour of the stem from white to green) and the fresh weights of the above-ground portions of SS1 and SS2 were recorded.
Samples for green area determination (SS1) were placed in plastic bags to prevent dehydration, and stored in a cold room at 4-6°C.

Measurements on sub-sample 1 (SS1)

The sub-sample was divided shoot by shoot into two categories: potentially fertile shoots and dead or dying shoots, as described below.

(a) A potentially fertile shoot was one where its newest leaf was green and showed no signs of dying back from the tip.
(b) A shoot was categorised as dead or dying when it had no green material or its newest expanding leaf had begun to turn yellow at the tip.

Potentially fertile shoots were separated into:

green lamina,
green true stem and sheath,
non-green stem and sheath,
dead material.

Yellowing parts of the leaves were classed as dead. If necrotic material was in isolated lesions a visual assessment of necrotic material was made and an equivalent portion removed from the end of the lamina. A leaf was classed as dead if it was yellow across the whole width of the base of the lamina.
The fresh weight of each fraction was recorded.

Green lamina and green stem projected area were recorded using a leaf area meter. All fractions were oven dried separately for at least 48 hours at 80°C and the dry weights of all fractions were recorded.
For the dead and dying shoot group, where the fresh weight was less than 5% of the total fresh weight of SS1, then the sample was dried for at least 48 hours at 80°C, and the total dry weight was recorded. Otherwise it was separated into the same fractions as the potentially fertile shoots and processed in the same way.

Measurements on sub-sample 2 (SS2)

Total fresh weight of SS2 and oven dry weight after drying at 80^{o}C for 48 hours were recorded. From December until GS31, the dried samples were analysed for nitrogen concentration using the Dumas method.

Sampling and sample processing after GS31 up to but not including the pre-harvest sample

Plants within the quadrats were cut off using sharp scissors, secateurs or a serrated knife, at the soil surface and placed into a plastic bag as soon as possible and sealed in order to prevent the leaves from drying out before leaf areas were measured.

From GS32, an additional sample of 10 randomly-selected potentially fertile shoots (WSC sample) was taken within each sampled plot from just outside the quadrats sampled. These samples were taken between 10.00h and 13.00h GMT (to avoid diurnal differences between sampling dates). Immediately after sampling, the 10 shoots were placed in a plastic bag, sealed and placed in a chilled cool-box. These were returned to the laboratory as quickly as possible, and then processed immediately.

Processing the main sample

The total fresh weight of the quadrat sample was recorded.
Dead and dying shoots were separated from fertile shoots, and fresh and dry weights were recorded.
The fertile shoots were counted into 10 equal piles and the total number of shoots was recorded. One pile was randomly selected (SS1) and the fresh weight was recorded.
A further two piles were taken (SS2), and the fresh weight recorded. If the fresh weight was less than 500g, further piles were added until the fresh weight was greater than 500g, and the fresh weight was re-recorded.

Measurements on sub-sample 1 (SS1)

In the potentially fertile shoot group, the material was separated into:

green lamina,
green true stem and sheath,
green ear and awn,
non-green stem and sheath,
non-green lamina,
non-green ear.

The fresh weight of each fraction was recorded.

Yellowing parts of the leaves were classed as dead. Where necrotic material was in isolated lesions, a visual assessment of necrotic material was made and an equivalent portion removed from the end of the lamina. A leaf was classed as dead if it was yellow across the whole width of the base of the lamina. Projected green areas for the green leaf, green stem and ear were recorded using a leaf area meter. All fractions were oven dried separately for at least 48 hours at 80°C and the dry weights of all fractions were recorded.

At alternate sampling times, any dried non-green material was mixed with the corresponding green sample, (e.g. non-green lamina with green lamina), and the dried lamina, stem and ear material were analysed for nitrogen concentration using the Dumas method.

Measurements on sub-sample 2 (SS2)

The fresh weight of the whole sub-sample was recorded before drying for at least 48 hours at 80°C.

Measurements on WSC sample

Water soluble carbohydrate concentration in the stem was assessed at each sampling time from GS32 onwards, and grain growth was assessed using these samples from GS71 onwards.

The fresh weight of 10 shoots was recorded.
The laminae of emerged leaves was removed at the ligule and discarded, along with any emerging leaves where they protruded from the leaf sheath.
The 10 stems were then re-weighed.
Stems were then immediately placed in a single layer in a gauze-based tray (cutting of stems was avoided because of potential sap loss) and “flash-dried” by placing in a pre-heated, forced-draught oven at 102°C for two hours.
After exactly two hours, the dry weight was recorded. The dried sample was then analysed for content.

To assess grain growth, individual grains were assessed weekly for dry matter growth and moisture content, from GS71 (grain watery ripe) to final harvest.

The fresh weight of the 10 ears was recorded.

Two grains from the centre of the ear were removed, and the two grains above them and two grains below them, giving six grains per ear, and 60 grains from the sample of 10 ears. Bulked fresh weights were recorded. The grains were dried at 102°C for at least 40 hours and bulked dry weights were recorded.

Sampling and sample processing pre-harvest

Pre-harvest samples were taken on the day of combine harvesting, or one day prior to combine harvesting. Plants within the quadrats were cut off using sharp scissors, secateurs or a serrated knife at the soil surface. An additional sample of 10 randomly selected, potentially fertile shoots (WSC, and grain growth sample), from just outside each quadrat sampled, was taken and processed as previously described.

Processing the main sample

The total fresh weight of the quadrat sample was recorded.
The shoots were counted into 5 equal piles and the total number of shoots recorded. One pile was randomly selected (SS1), and the fresh weight was recorded. A further two piles were selected (SS2).

Measurements on sub-sample 1 (SS1)

All the ears were cut off and counted, and the number was recorded. The fresh weights of ears and straw (including dead leaves) were recorded.

A representative sub-sample of at least 200g fresh weight of straw was taken and its fresh weight recorded, and then it was dried to constant weight (at least 40 hours at 80ºC). The ears were then immediately threshed and winnowed using a laboratory thresher and the grain and chaff were collected. The grain was then sieved over a 2mm sieve, and any remaining pieces of chaff, which passed through the sieve were added to the chaff fraction. The fresh weights of cleaned grain and chaff were recorded. Approximately 40g of cleaned grain was then used for grain weight determination, by counting the number of grains in the sample.

Measurements on sub-sample 2 (SS2)

The total fresh weight of SS2 was recorded, the whole sample was then oven dried at 102°C until a constant weight was reached, and the dry weight was recorded.

Crop height

Plant height was recorded by measuring from ground level to the uppermost leaf ligule or the ear collar (whichever was higher) of 10 randomly selected plants per plot, from GS30 until the ears started bending downwards.

Photosynthetically active radiation (PAR)

Measurements of PAR using hand-held ceptometers, were carried out at all growth analysis sampling times on three plots.

Two ceptometers were used to concomitantly measure PAR above the canopy and below the canopy at ground level, at 10 randomly selected locations per plot. This was repeated with one ceptometer above the canopy and the second also above the canopy but facing downwards. PAR readings were always taken between 10.00h and 14.00h GMT. These data were used to calculate incident, transmitted, intercepted and reflected PAR.

Potential root depth assessment and soil profile description

Assessment of the soil profile and potential root depth was carried out at anthesis on one replicate using an inspection pit.

A pit was dug at the edge of the study area, at least 0.5m from the edge of a plot and approximately half way along the length of the block of plots, unless some variability in soil profile was suspected (by sampling with a soil auger before selection of the site). If the profile was variable across the site, pits were dug at the extremities and their positions recorded accurately.

The bottom of the pit was below the plough layer and deep enough to identify any compaction. Factors that may have restricted rooting were recorded, such as impermeable underlying subsoils. Soil texture and topsoil depth were recorded.

Lodging

Where lodging occurred, assessments were made of the percent area of the plot (including the edges) which were either:

Leaning (stems at 5^o to 45^o from the vertical)
Lodged (stems at 45^o to 85^o from the vertical)
Lodged flat (85^o-90^o from vertical)
Brackled (buckling of straw a quarter or more up its length)

Total % area lodged = leaning + lodged + lodged flat + brackled

The proportions of the % area that were stem lodged or root lodged were also recorded.

Combine harvesting

At final harvest, the four plots designated for combine harvesting and not previously used for destructive sampling were harvested using a plot combine harvester, and grain yield was expressed at 85% dry matter. A sample of grains was also taken and assessed for screenings, specific weight, thousand grain weight and moisture content.

Meteorological records

Meteorological data including daily rainfall; daily maximum, minimum and mean air temperatures; total incident solar radiation (from a Kipp solarimeter), soil temperature at 10cm depth, and minimum grass temperature, were recorded.

APPENDIX 2: THE DETERMINANTS OF GRAIN NUMBER: CROP DEVELOPMENT, LEAF EMERGENCE, TILLERING AND PRE-ANTHESIS CROP GROWTH

Crop development and establishment of benchmark dates

Development can be defined as the changes in crop morphology or function that occur throughout the crops life cycle. It affects the way in which a crop adapts to a given environment, as well as playing a key role in determining final yield. Yield components are affected by factors influencing the length of key developmental phases. The Decimal Code for the Growth Stages of Cereals (Tottman, 1987) is recognised through the industry, identifying and describing the key stages in the life-cycle of cereal crops, in a way that is easily assessable in the field. The key was used to record crop growth stages on 20 separate occasions at each of the six sites, at regular intervals throughout the season, corresponding with the biomass assessment timings. A number of key growth stages were identified and benchmark dates were established by taking the median date for all sites and years for each stage (Table 2.1).

Table 2.1. Key growth stages and established benchmark dates

Growth stage	Definition	Median Date
GS 21	Onset of tillering. Main shoot + 1 tiller	13 Nov
GS 30	Start of stem elongation. Ear at 1 cm	2 Apr
GS 31	First internode detectable	16 Apr
GS 39	Flag leaf emerged, collar visible	6 May
GS 59	Inflorescence complete	26 May
GS 71	Start of grain development, watery ripe	8 Jun
GS 87	End of grain development, hard dough	5 Jul

With genetic and environmental factors having a profound effect on crop development, benchmarks were established using a single variety, Pearl, to remove the genetic variation. Tight controls on drill date, husbandry protocol and subsequent crop assessment were also imposed to help reduce environmental effects. Dates of key growth stages for all sites and all years are presented in Table 2.2. Wet conditions in the autumn of 2001 delayed drilling for more northern sites until early October. In the south, however, warm conditions resulted in rapid development, particularly at Rosemaund and King's Lynn. Crops were drilled from 15 to 24 September in the autumn of 2003, though dry conditions had a delaying effect on initial establishment, particularly where temperatures were highest. Southern sites tended to reach each of the key growth stages earlier than their northern counterparts.

Early growth

The appearance of the first tiller (GS21) was recorded in a one-month window from the third week in October to the third week in November, with a median date of 13 November. Conditions at establishment had a marked influence on how quickly crops reached this stage, moisture availability and temperature being the influential drivers. In the wet autumn of 2001, warmer temperatures favoured initial crop establishment, but in the very dry autumn of 2003 crop emergence was delayed. Stem extension started in late March, with GS30 being achieved by mid April at the latest. The ranges of dates at GS30 were greater than at any other growth stage. Effects of latitude became apparent with northern sites being a median of five days behind more southern sites.

Stem extension: GS31 to GS59

Southern crops produced more leaf primordia than northern crops, and had a longer interval between GS30 and GS31. Northern sites produced a maximum of 13 leaves on the main stem and southern sites a maximum of 15 leaves. A phyllochron of 108 ºC days separated the emergence of each leaf and was independent of latitude. GS31 was reached in a period spanning 5 April to 8 May with median dates of 12 April in the south and 17 April in the north. Emergence of the flag leaf (GS39) was complete by early May, southern sites being six days ahead of more northern sites. Emergence of the most important canopy leaves, on which subsequent growth would depend, took around three weeks. The ear was fully emerged by the end of May (GS 59).

Table 2.2. Recorded dates for growth stages at six sites (Ab=Aberdeen, Ed=Edinburgh, Mw=High Mowthorpe, SB=Sutton Bonington, Rm=Rosemaund and KL=King's Lynn), 2002 to 2004.

Growth		Northern Sites				Southern Sites			
Stage	Year	Ab	Ed	Mw	Median	SB	Rm	KL	Median
GS21	2002	19 Nov	28 Nov	12 Nov		12 Nov	19 Oct	30 Oct	
	2003	20 Nov	11 Nov	13 Nov		13 Nov	16 Nov	11 Nov	
	2004	13 Nov	17 Nov	31 Oct		13 Nov	17 Nov	17 Nov	
					13 Nov				13 Nov
GS30	2002	15 Apr	15 Apr	02 Apr		01 Apr	04 Mar	02 Apr	
	2003	04 Apr	14 Apr	06 Apr		14 Apr	22 Mar	31 Mar	
	2004	01 Apr	05 Apr	22 Mar		22 Mar	22 Mar	05 Apr	
					05 Apr				31 Mar
GS31	2003	22 Apr	24 Apr	17 Apr		12 Apr	15 Mar	17 Apr	
	2004	15 Apr	22 Apr	16 Apr		24 Apr	31 Mar	15 Apr	
	2005	10 Apr	19 Apr	14 Apr		05 Apr	05 Apr	10 Apr	
					17 Apr				12 Apr
GS39	2002	13 May	16 May	10 May		07 May	23 Apr	03 May	
	2003	14 May	09 May	01 May		03 May	30 Apr	06 May	
	2004	7 May	06 May	04May		30 Apr	08 May	08 May	
					09 May				3 May
GS59	2002	31 May	07 Jun	30 May		24 May	20 May	17 May	
	2003	31 May	29 May	25 May		27 May	20 May	15 May	
	2004	28 May	31 May	21 May		17 May	16 May	27 May	
					30 May				20 May
GS71	2002	19 Jun	21 Jun	17 Jun		05 Jun	31 May	07 Jun	
	2003	11 Jun	13 Jun	06 Jun		02 Jun	09 Jun	09 Jun	
	2004	09 Jun	10 Jun	07 Jun		24 May	01 Jun	07 Jun	
					11 Jun				5 Jun
GS87	2002	27 Jul	20 Jul	13 Jul		01 Jul	10 Jul	05 Jul	
	2003	17 Jul	18 Jul	05 Jul		30 Jun	26 Jun	03 Jul	
	2004	19 Jul	19 Jul	04 Jul		23 Jun	22 Jun	28 Jun	
					18 Jul				30 Jun

Grain development :GS71 to GS87

Grain maturity (GS87) was reached 45 days after full ear emergence (GS59). Only 7 days separated northern and southern sites over this whole period (GS59 to GS87), but the grain-filling phase (GS71 to GS87) was 12 days shorter for southern sites and was achieved by 30 June. GS87 was not reached until 18 July at northern sites.

Leaf emergence

The rate of leaf production is affected by genetic and environmental factors, with final leaf number and the time interval between the production of successive leaves (the phyllocron) being important components for determining the length of the period prior to ear emergence. Leaf production on the main tillers of 10 plants/plot was recorded by placing a tag around the newest fully expanded leaf at each assessment, generating data for calculating the rate of leaf production and total number of leaves produced. The phyllocron is strongly affected by temperature and was estimated in units of ºC days.

Phyllochron was expressed as thermal time (ºC days) and leaf emergence dates were calculated using the daily course of thermal time (Table 2.3).

Table 2.3: Leaf emergence dates for the 2001/02, 2002/03 and 2003/04 seasons for northern sites (Aberdeen, Edinburgh and High Mowthorpe) and southern sites (Sutton Bonington, King's Lynn and Rosemaund).

Emerged leaves	Northern	Southern
2	02-Nov	02-Nov
3	17-Nov	16-Nov
4	06-Dec	03-Dec
5	07-Jan	26-Dec
6	29-Jan	17-Jan
7	21-Feb	04-Feb
8	07-Mar	24-Feb
9	02-Apr	14-Mar
10	16-Apr	27-Mar
11	28-Apr	09-Apr
12	10-May	20-Apr
13	-	29-Apr
14	-	08-May

These calculated dates of leaf emergence correspond closely with the actual observed dates of final leaf emergence (GS39) (Table 2.3) re-affirming the strong relationship between thermal time and leaf emergence. The small differences may relate to the lesser effects of latitude and day length on leaf initiation and growth.

Leaf production started in the autumn with the emergence of the seedling. Fifty per cent emergence occurred approximately 15 days after drilling in mid/late September. The rate of leaf production was low throughout the winter months because of low temperatures, then increased as temperatures increased, as leaves were produced at successively shorter intervals. The final leaf (flag leaf) emergence date at GS39 was comparable between northern and southern sites, though southern sites produced, on average, an additional two leaves. All sites had a near-linear relationship between leaf number and accumulated thermal time above 0°C. Calculation of the phyllochron (ºC days/leaf) was established by plotting number of emerged leaves (on an average of 30 tagged plants/site) against thermal time from 50% emergence. The phyllochron was calculated as the reciprocal of the gradient of the fitted line (Figure 2.1).

The range of values recorded for the phyllochron was large, varying between sites and seasons (Table 2.4), though clear latitude differences were not apparent. The mean phyllochron value for barley was found to be 108°C, thus being the same as that observed in winter wheat (Whaley, 2001).

Table 2.4: Mean phyllochron (°C d) from 50% emergence to appearance of the flag leaf ligule for each site and season.

Site	2002	2003	2004	site average
Aberdeen	109.9	103.1	120.5	111.1
Edinburgh	117.6	119.0	*	118.3
High Mowthorpe	98.0	109.9	98.0	102.0
King’s Lynn	105.3	112.4	113.6	110.4
Rosemaund	105.3	107.5	109.9	107.6
Sutton Bonington	100.0	101.0	*	100.5
Season average	106.0	108.8	110.5	108.3

The maximum number of leaves on the main stem was 13 for northern sites and 15 for southern sites. As for wheat (Sylvester-Bradley *et al.,* 1998), it appears that final leaf number was affected by the date of emergence and latitude. Final leaf number is determined at the time of floral induction, the point at which the shoot apex switches from producing vegetative primordia to reproductive primordia (Miglietta 1988). As this occurred early in the spring in winter barley, at a time when considerable differences between sites was evident, it is perhaps not surprising that some differences in subsequent rate of leaf emergence were observed.

In conclusion, the overall pattern of leaf production across sites was comparable, with the differences between sites and seasons being in leaf production throughout the winter and early spring, and final leaf number. The early differences between northern and southern sites lessened as the season progressed such that, the appearance of the flag leaf was separated by only six calendar days in early May (9 May Northern sites, 3 May Southern sites) (Table 2.2). Leaf emergence provides a good index of crop development, though it didn’t always correlate well with the stem extension stages as expressed in the crop growth stage key. Hence when considering crop growth stages and making crop husbandry decisions it is important to look at the stem, but then also to dissect down to establish how many leaves are yet to emerge.

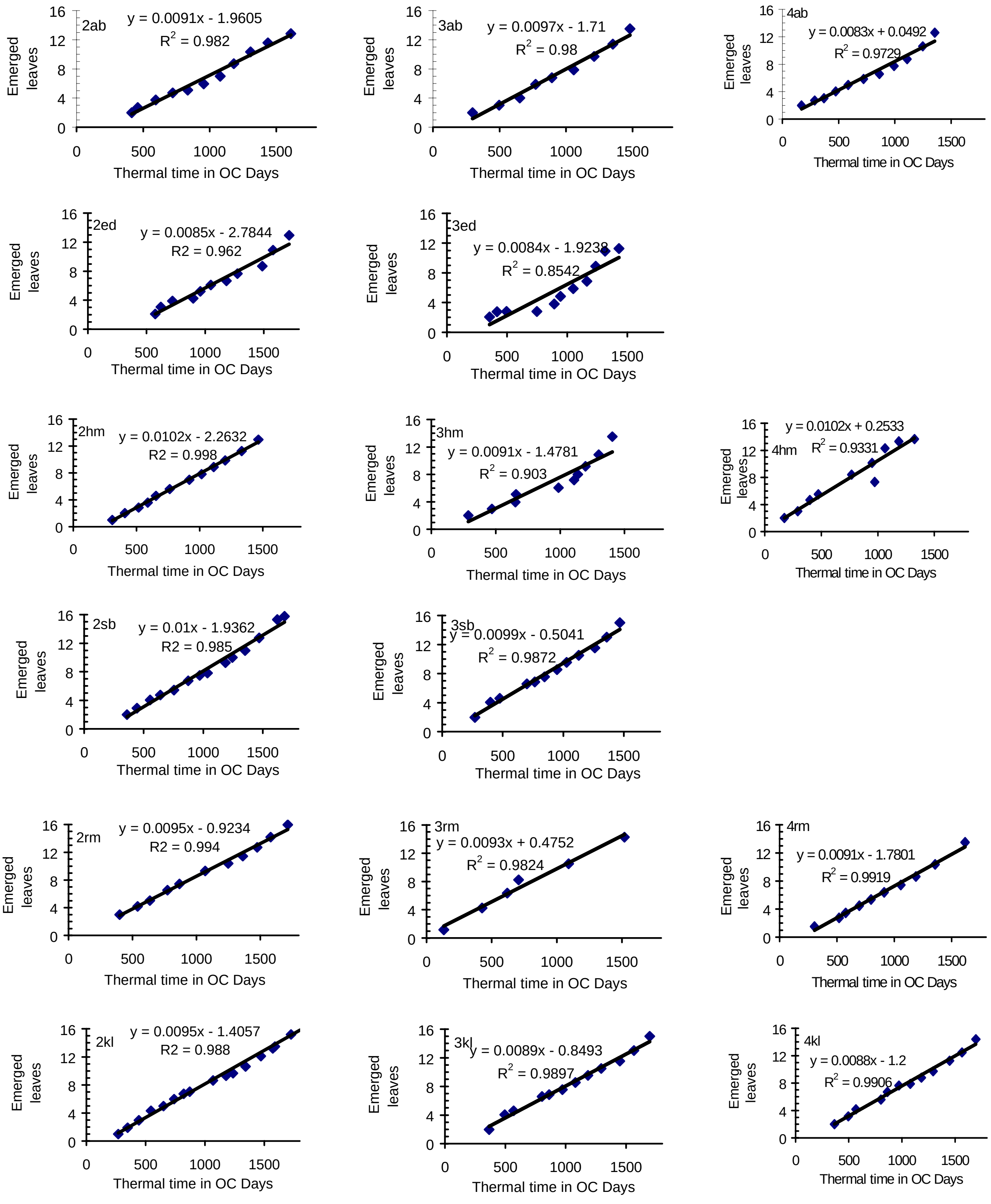


Figure 2.1. Leaf emergence expressed in thermal time (°C days, base temperature = 0), for Aberdeen 2002, 2003, 2004 (2ab,3ab,4ab), Edinburgh 2002, 2003 (2ed,3ed,), High Mowthorpe 2002, 2003, 2004 (2hm,3hm,4hm), Sutton Bonington 2002, 2003 (2sb,3sb), Rosemaund 2002, 2003, 2004 (2rm,3rm,4rm) and King’s Lynn 2002, 2003, 2004 (2kl,3kl,4kl).

Tillering

Tillering is an important developmental phase in the life-cycle of the barley crop and shoot numbers were recorded as part of the growth analysis made throughout the season using 0.72m^2 quadrats. In addition tagged plants (10 plants/plot) were used to study the tillering patterns of individual plants, and the relationship between tillering and leaf production. Autumn tillering was a feature of crops at all sites, with the highest rates of tiller production occurring before the end of December at around 400 shoots m^{-2} month^{-1}, extending into January for southern sites (Table 2.5). Tiller abortion generally started in March for southern sites, with final shoot numbers being 34% lower than the February maximum. For northern sites tillering tended to continue for longer, with the start of tiller abortion delayed until May. Maximum tiller numbers were frequently reached in April, and final tiller numbers showed that the percentage of tillers aborted was similar to southern sites.

Table 2.5. Total shoot numbers - median values for northern and southern sites over 3 harvest years (2002-2004).

Month	Northern sites Shoots (m^{-2})	Increase/decline from previous month	Southern sites Shoots (m^{-2})	Increase/decline from previous month
November	444	-	491	-
December	877	434	850	359
January	993	116	1021	171
February	1184	191	1111	90
March	1207	23	1006	-105
April	1270	63	978	-28
May	1148	-122	770	-208
June	819	-329	874	104
July	826	7	815	-59
August	852	26	737	-78

The first tiller was produced at the same time as third and fourth leaf was emerging. Plants produced on average six shoots/plant, with final shoot numbers of 4 shoots/plant (Table 2.6). Whilst maximum and final numbers on individual plants were comparable for northern and southern sites, both tillering and tiller death occurred earlier in the south.

Table 2.6: Shoot numbers/plant - average values for each site over 3 harvest years (2002-2004).

Site	Number of shoots/plant	final shoot number
Aberdeen	8.0	3.7
Edinburgh	6.5	4.5
High Mowthorpe	5.7	3.7
Northern average	6.7	3.9
King's Lynn	5.3	4.3
Rosemaund	6.3	4.0
Sutton Bonington	6.7	4.3
Southern average	6.1	4.2
Overall average	6.4	4.1

Maximum shoot number corresponded with stem extension (GS30) at northern sites, whilst at southern sites it occurred a month prior to this (median date 28 February), with tiller numbers already decreasing by the early stem extension (GS30 and GS31). The main period of tiller death occurred from this point until flowering when final tiller numbers were more or less established.

There were good correlations at full ear emergence between tiller number and total biomass, and tiller number and GAI (R^2=0.4346 and 0.4139 respectively) (Fig. 2.2). At this stage, crops were close to final fertile shoot numbers. However, the best relationship was between GS 59 tiller number and GAI at GS 71 (R^2= 0.554) indicating that there was still a small amount of tiller death occurring up until this time (GS 71). There was no correlation between tiller number and final yield, with the best relationship occurring at GS 59 (R^2 = 0.2554).

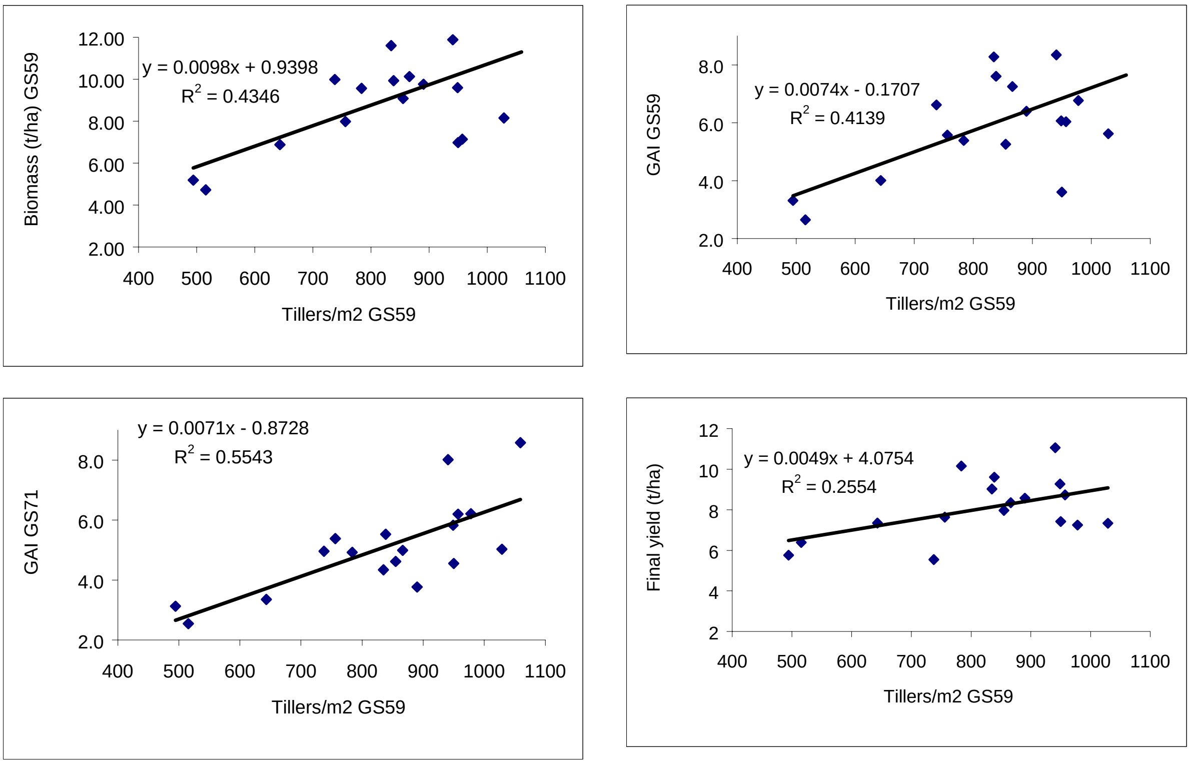


Fig. 2.2. Relationships between GS59 tiller numbers, and GS59 biomass, GS59 green area index, GS71 green area index and final yield.

Sites varied greatly in their degree of tillering, with King's Lynn having consistently lower shoot numbers than other sites. Differences between sites were most marked in the period from the start of stem extension (GS31) through to ear emergence and flowering (GS 59/61) due to differing rates of tiller abortion. (Fig. 2.3).

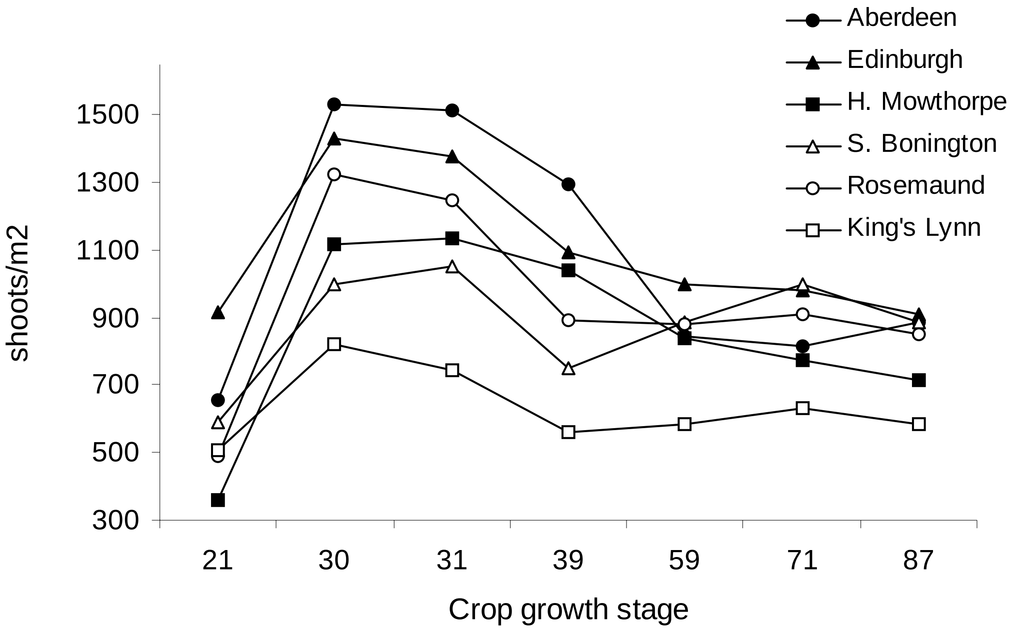


Fig. 2.3. Average shoot numbers (2002-2004) for all sites at benchmark growth stages

Final ear number and grain number m^{-2} at harvest.

Final ear number at harvest did not differ significantly amongst years, and was in the range 782-794 m^{-2} (Table 2.7). Averaging across years, the crops at Edinburgh (961) had more ears m^{-2} than those at King's Lynn (659; $P< 0.05$), with intermediate values for other sites. Site differences were generally consistent in the individual years, although in 2004 Edinburgh and King's Lynn produced less extreme ear populations, and Sutton Bonington produced more ears m^{-2} relative to other sites than in other years. Although ear numbers were similar in each year, grain number m^{-2} *ca* 500 m^{-2} lower in 2003 than in other years ($P<0.05$; Table 2.8). This was associated with fewer grains per ear in 2003. Averaging across seasons, the high and low ear population densities for Edinburgh and King's Lynn were reflected in high and low grains m^{-2} in the range 14,103-21,608 ($P< 0.001$). However, Edinburgh only produced the second highest number of grains m^{-2} overall, the highest values being achieved at Rosemaund. High ear fertility (i.e. spikelets/grains per ear) principally accounted for more grains at the Rosemaund site. Grain number differences amongst sites were generally expressed consistently in the individual years. Exceptions to this were High Mowthorpe in 2003 and Sutton Bonington in 2004, which produced relatively fewer and more grains respectively, compared with other sites, than in other years.

Table 2.7. Mean ear number per m^2. Mean values for site-years for 3 replicate plots per site-year, with SEDs and probabilities for year and site differences (NS=not significant).

Site	Harvest year 2002	2003	2004
Aberdeen	775	737	725
Edinburgh	948	1053	852
High Mowthorpe	853	603	669
King's Lynn	564	676	737
Rosemaund	807	814	768
Sutton Bonington	817	807	920

SED year = 31.9, df 36; site = 45.1, df 36; site x year = 78.1, df 36.

P year, NS; site, <0.05; year x site, <0.001

Table 2.8. Mean grain number per m^2. Mean values for site-years and SEDs and probs from ANOVA (completely randomised design) for 3-7 replicate plots per site-year.

Site	Harvest year 2002	2003	2004
Aberdeen	19221	18729	16601
Edinburgh	17366	20169	no data
High Mowthorpe	17828	13688	18447
King's Lynn	14113	14700	13497
Rosemaund	23467	21807	19729
Sutton Bonington	16620	16294	21713

SED year = 186.6 df 36; site = 263.9 df 36; site x year = 457.1 df 36

P year, <0.01; site, <0.001; year x site, <0.001

Crop growth and ear partitioning in the pre-anthesis period

Crop dry matter growth and ear partitioning

Above-ground biomass (AGDM) at the onset of stem extension (GS31) was greater in 2004 (2.8 t ha^{-1}) than in other years (2.2 t ha^{-1} in 2002 and 2.0 t ha^{-1} in 2003) (2. 9). Averaging across years, biomass was in the region of 2 t ha^{-1} at four of the sites, with higher values of about 2.8 t ha^{-1} at Rosemaund and Edinburgh.

At the end of ear emergence (GS59), there were clear seasonal differences in biomass with heavier crops in 2004 than in 2003, and intermediate values in 2002. Averaging across seasons, biomass was greatest at Rosemaund (11.2 t ha^{-1}) and least at King's Lynn (6.7 t ha^{-1}; $P< 0.001$), with Aberdeen and Edinburgh tending to show greater biomass than High Mowthorpe and Sutton Bonington within this range.

Ear biomass was about 0.3 t ha^{-1} greater in 2004 than in either 2002 or 2003. Site differences for ear biomass tended to be less consistent than those observed for above-ground biomass. The lowest values of about 0.6t ha^{-1} were observed at King's Lynn in 2002 and 2003 associated with lower plant populations and generally smaller crops. In 2004 at King's Lynn, however, ear biomass was comparable to the other English sites. In general, ear biomass was greatest at Edinburgh and Rosemaund, with a tendency for lower values at High Mowthorpe compared to other sites. The proportion of biomass allocated to the ear at GS59 (ear index) did not vary greatly across seasons (range 0.19 to 0.21), but differed greatly across sites, being much greater at Sutton Bonington (0.26), for example, than at either High Mowthorpe or Aberdeen (0.17).

Table 2.9. Above-ground DM at GS 31, GS 59 and increment between GS 31 and GS 59; and ear DM and ear index at GS 59. Mean values for site-years with SEDs and probabilities for year and site differences.

		Above-ground DM			Ear DM	Ear Index
		GS31 t ha^{-1}	GS59 t ha^{-1}	GS31–GS59 t ha^{-1}	t ha^{-1}	
2002	Aberdeen	2.61	9.76	7.16	1.15	0.160
	Edinburgh	2.66	10.07	7.10	1.40	0.197
	High Mowthorpe	1.70	8.15	6.45	1.20	0.186
	King’s Lynn	1.88	5.19	3.31	0.55	0.168
	Rosemaund	2.73	11.88	9.15	1.82	0.197
	Sutton Bonington	1.73	7.98	6.25	1.40	0.228
	Mean	2.22	8.84	6.57	1.25	0.189
2003	Aberdeen	1.66	9.57	7.91	1.18	0.149
	Edinburgh	1.95	7.73	5.78	*	*
	High Mowthorpe	1.91	6.88	4.97	1.03	0.207
	King’s Lynn	1.72	4.73	3.01	0.70	0.232
	Rosemaund	2.62	11.60	8.98	1.48	0.166
	Sutton Bonington	2.08	6.97	4.89	1.39	0.294
	Mean	1.99	7.91	6.38	1.25	0.216
2004	Aberdeen	1.77	9.08	7.31	1.34	0.185
	Edinburgh	3.98	12.88	8.90	2.38	0.269
	High Mowthorpe	2.61	9.93	7.33	0.94	0.128
	King’s Lynn	2.55	10.18	7.63	1.62	0.212
	Rosemaund	3.04	10.13	7.08	1.63	0.232
	Sutton Bonington	2.96	9.60	6.64	1.63	0.247
	Mean	2.82	10.30	7.73	1.59	0.212
	SED year df = 36	0.119	0.246	0.269	0.0478	0.0079
	Prob. year	< 0.001	< 0.001	< 0.001	< 0.001	< 0.01
	SED Site df =36	0.268	0.348	0.381	0.0669	0.0114
	Prob. site	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	SED year x site df = 36	0.291	0.603	0.659	0.1158	0.0193
	Prob. year x site	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

The relationship between crop growth and partitioning in the pre-anthesis period and grain number

There was a weakly significant positive linear relationship between above-ground biomass at GS59 and final ear number m^{-2} at harvest across the 18 site-years ($P = 0.10$; Fig 2.4a) This indicated improved tiller production and/or survival in site-years in which pre-anthesis biomass productivity was greatest. There was a positive linear association between biomass per shoot at GS59 and grains per ear ($P < 0.05$) indicating that crops with larger shoots were able to support more grains per shoot (Fig 2.4b). The crop at Edinburgh in 2004 suffered severe bird damage just before harvest and so no yield data are available. Thus the analysis of yield and grains m^{-2} is based on 17 site-years rather than 18.

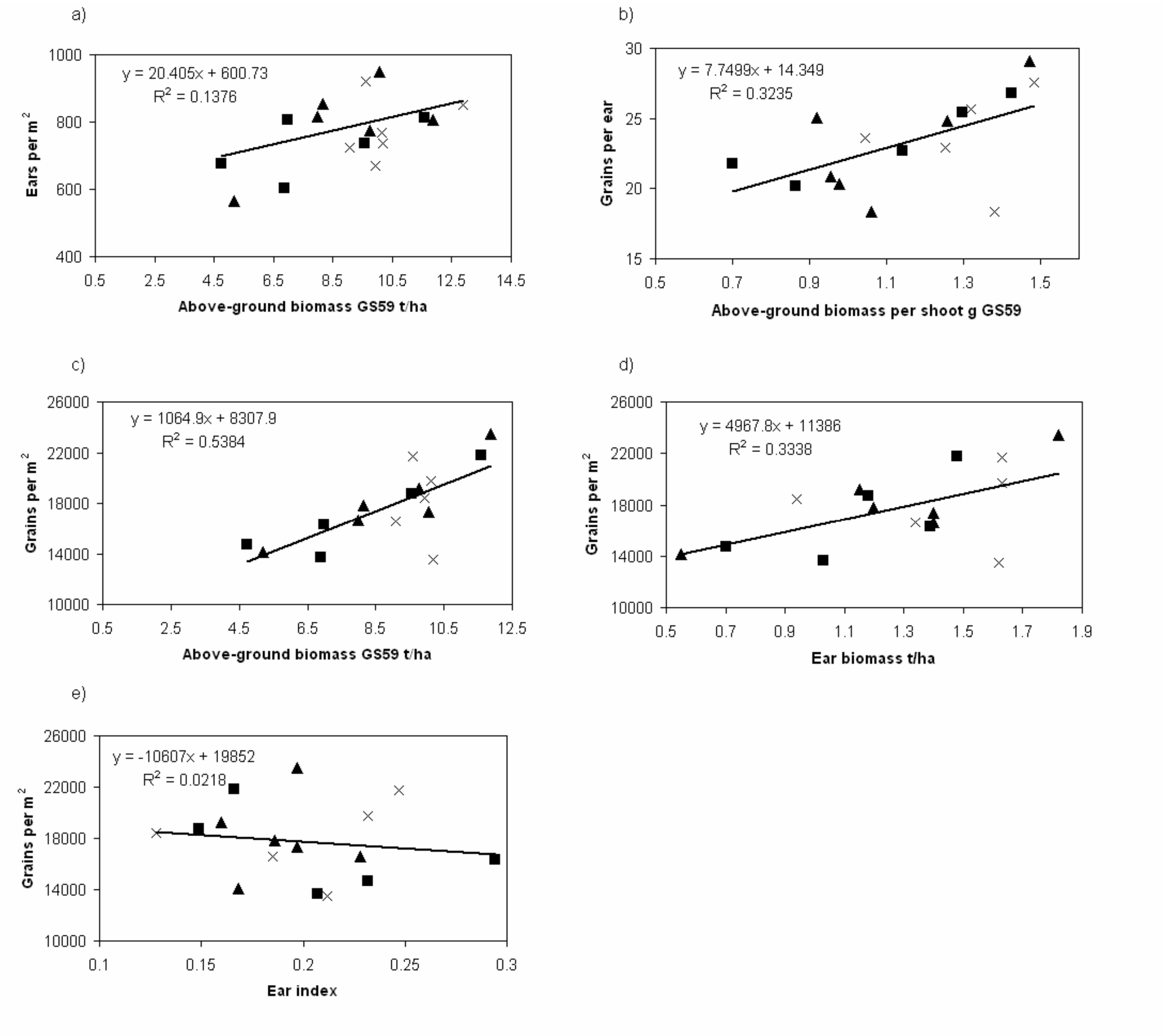


Fig. 2.4. Linear relationships between a) above-ground biomass (AGDM) m^{-2} at GS59 and final ear number m^{-2}, b) AGDM per shoot at GS59 and grains per ear, c) AGDM m^{-2} at GS59 and grains m^{-2}, d) ear biomass at GS59 and grains m^{-2}, and e) ratio of ear and AGDM at GS59 (ear index) and grains m^{-2}, for 17 site-years. Triangles are site values for 2002, squares for 2003 and crosses for 2004.

The net effect of the relationships described in Figs 2.4a and b is a positive linear relationship between pre-anthesis biomass accumulation and grains m^{-2} ($P< 0.001$) across the 17 site-years (Fig 2.4c). The crop at King's Lynn in 2004 represented an outlier from this overall relationship, in that large biomass was associated with low grain number, due to a low number of grains per ear. As expected there was a positive linear association between ear biomass at GS59 and grains m^{-2} (Fig 2.4d) although somewhat surprisingly ear biomass accounted for less of the total variation in grain number than above-ground biomass. This reflected a non-significant association between the fraction of accumulated above-ground biomass partitioned to the ear (ear index) and grains m^{-2} across the 17 site-years (Fig 2.4e). Therefore the most important factor in determining grains m^{-2} for the variety Pearl in these 17 site-years was the amount of above-ground biomass accumulated in the pre-anthesis period**.**

Physiological basis of differences in pre-anthesis biomass amongst the 18 site-years

Interception of photosynthetically active radiation (PAR) (400-700 nm) was measured at growth analysis sample times using a SunScan System (Delta-T Devices, Burwell, Cambridge, UK) in three plots per site-year as described in the materials and methods (Appendix 1). For each site-year, the extinction coefficient (K_{PAR}) was calculated, using a modified version of Beer's Law (Monsi and Saeki, 1953), from the slope of the regression of LN ((1/(1-F)) on GAI fitted through the origin for sample times during the stem extension period (GS31 to GS59), where F is the fraction of PAR intercepted, calculated as:

(Incident PAR above crop - Transmitted PAR at ground level) / (Incident PAR above the crop)

To calculate K_{PAR} for each site-year, all samplings were included in the period from GS31 to GS59, plus those which fell outside this period by up to 4 days. Accumulated intercepted PAR during the GS31 to GS59 period was calculated by applying K_{PAR} to incident PAR and GAI, assuming GAI changed linearly with calendar time between sequential samplings. Radiation-use efficiency (RUE) (g MJ^{-1}) was estimated from the slope of the linear regression of cumulative PAR interception on AGDM fitted through the origin from the sequential samplings occurring within the GS31 to GS59 period. Slopes to estimate K_{PAR} and RUE for each site-year were calculated using the mean values of the relevant variables from the three plots at each sampling time.

Across the 18 site-years K_{PAR} varied in the range 0.44 to 0.63 (Table 2.10). Parallel regression analysis indicated that there was no statistically significant main effect, of either year or site, on K_{PAR}. There was, however, a year by site interaction with K_{PAR} at Edinburgh in 2003 showing a higher slope than the overall slope fitted to all data ($P< 0.05$). For this reason, year-site-specific values of K_{PAR} were used in the calculation of intercepted PAR from GS31 to GS59. Because PAR interception from GS 31 to GS 59 was estimated using mean values for GAI and K_{PAR}, it was not possible to perform ANOVA on data for this variable. However, there was an apparent tendency for lower interception in 2003 (228 MJ m^{-2}) than in either 2002 (275 MJ m^{-2}) or 2004 (265 MJ m^{-2}). Site differences were also apparent with crops at Rosemaund (335 MJ m^{-2}) showing greater interception during the stem extension period than at King's Lynn at (217 MJ m^{-2}).

Table 2.10. Mean values for K_{PAR}, calculated as the slope of LN(1/(1- fraction PAR interception)/GAI, fitted through the origin (R^2 in parenthesis) and PAR interception, calculated as biomass increment from GS31 to GS 59 divided by RUE, between GS 31-GS 59.

	K_{PAR} GS 31 – GS 59 (R^2)			PAR Interception GS 31 toGS 59 (MJ m^{-2})		
	2002	2003	2004	2002	2003	2004
Aberdeen	0.47 (0.61)	0.47 (0.75)	0.49 (0.97)	253.0	256.8	244.5
Edinburgh	0.55 (0.61)	0.51 (0.95)	0.44 (0.62)	257.2	209.4	278.1
High Mowthorpe	0.44 (0.64)	0.48 (0.94)	0.50 (0.68)	241.6	229.0	257.2
King's Lynn	0.52 (0.85)	0.54 (0.81)	0.45 (0.57)	258.6	126.5	265.9
Rosemaund	0.47 (0.44)	0.45 (0.88)	0.52 (0.52)	401.3	332.6	270.2
Sutton Bonington	0.53 (0.86)	0.57 (0.95)	0.63 (0.75)	237.6	188.1	276.7

Estimates for radiation-use efficiency for the stem extension period for the individual site-years are shown in Table 2.11. Pooling data across sites, RUE varied from 2.34 - 2.89 g MJ^{-1} in the three seasons, shown as the slopes of the fitted lines in Fig 2.5a. However, parallel regression analysis indicated these differences were not statistically significant at the 5% level. Pooling data across years, RUE varied amongst the sites from 2.39g MJ^{-1} at King's Lynn to 3.00g MJ^{-1} at Aberdeen and Edinburgh (Fig 2.5b). Parallel regression analysis indicated that site differences were significant with King's Lynn showing a lower RUE than the slope of the line fitted to all data ($P< 0.05$), and also that the year by site interaction was statistically significant. For example, King's Lynn had a higher RUE relative to other sites in 2004 than in other years.

Table 2.11. Estimates for RUE (g MJ^{-1}) from GS31 to GS59, calculated as the linear slope of cumulated biomass on cumulated interception of photosynthetically active radiation over this period, and P values for the linear slopes in each site-year.

	RUE (g MJ^{-1})			Significance, P		
	2002	2003	2004	2002	2003	2004
Aberdeen	2.83	3.08	2.99	<0.001	<0.001	<0.001
Edinburgh	2.76	2.76	3.20	<0.001	<0.01	<0.001
High Mowthorpe	2.67	2.17	2.85	<0.001	<0.001	<0.001
King's Lynn	1.28	2.38	2.87	<0.001	<0.01	<0.001
Rosemaund	2.28	2.70	2.62	<0.001	<0.001	<0.001
Sutton Bonington	2.63	2.60	2.40	<0.001	<0.001	<0.01

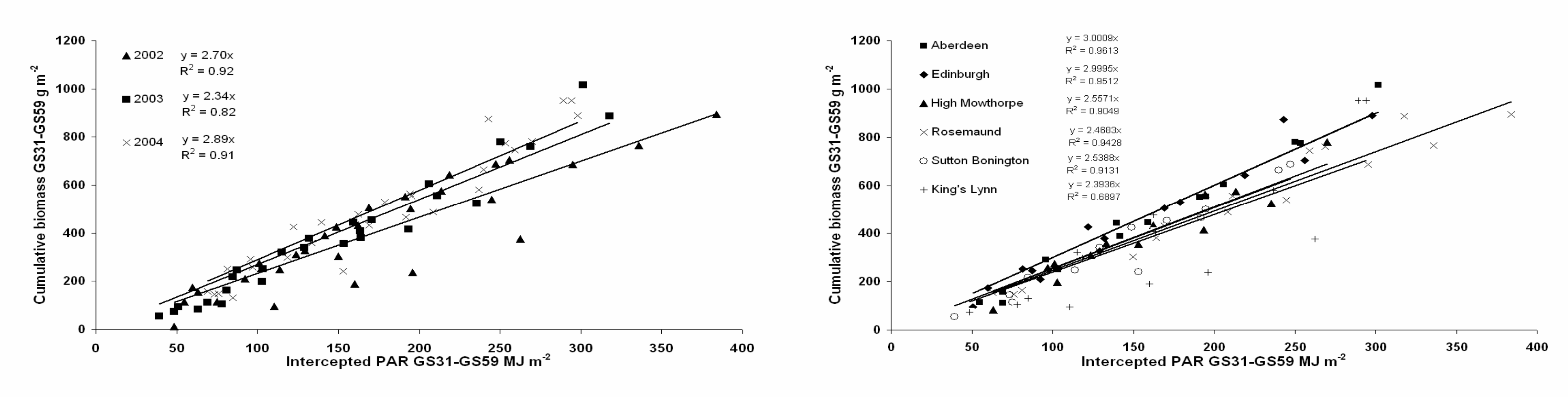


Fig. 2.5. Regression of cumulative intercepted photosynthetically active radiation on cumulative biomass for the GS31 to GS39 period for (a) 2002, 2003 and 2004 and (b) the six sites. The slopes of the lines estimate radiation use efficiency (RUE).

The linear relationships between accumulated PAR interception and above-ground biomass, and between RUE and above-ground biomass, during the stem extension period, are shown in Figs 2.6a and b. There were statistically significant relationships between both RUE and biomass ($P< 0.001$; $R^2 = 0.40$) and intercepted PAR and biomass ($P< 0.001$; $R^2 = 0.59$). This indicated that both RUE and PAR interception determined differences amongst site-years in biomass at GS59, although PAR interception was the more important of the two. Seasonal effects were mostly explained by differences in interception, whereas site effects were due to both the influence of interception and RUE.

Managing the canopy in order to maximize light interception between GS31 and GS59 is important to maximize grain number in the variety Pearl in UK growing conditions. Alongside this it is important to minimise any pre-anthesis stresses due, for example, to poor rooting affecting water and/or nutrient uptake, so depressing biomass productivity through effects on RUE. Such effects may have contributed to the low RUE at the King's Lynn site in 2002.

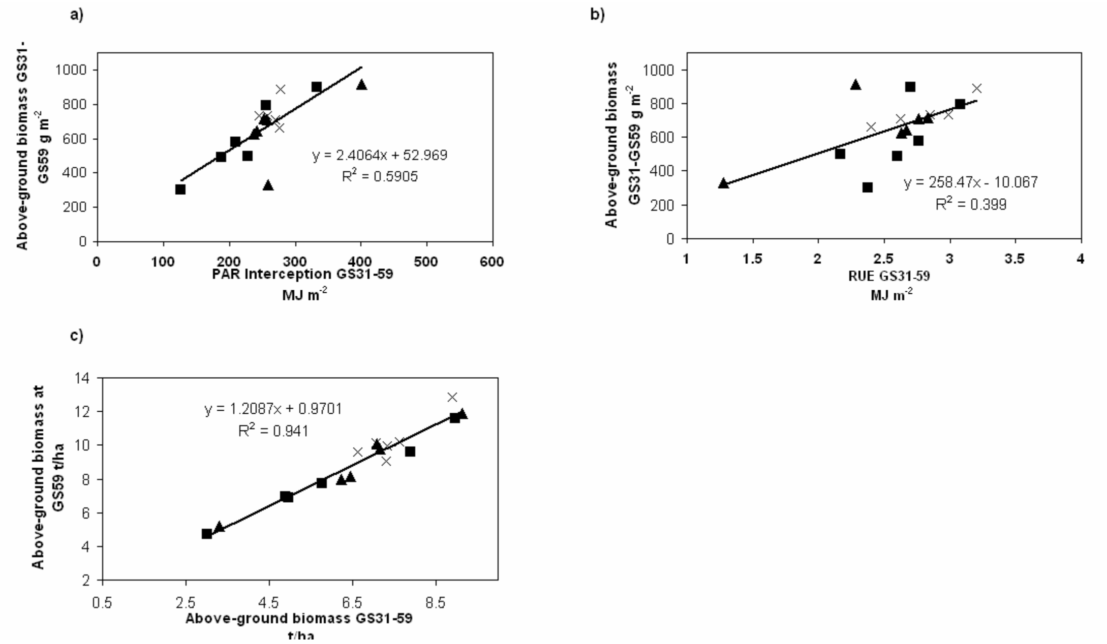


Fig. 2.6. Linear regression of a) PAR interception and b) RUE_{PAR} on biomass accumulated during the period from GS31 to GS59; and c) linear regression of above-ground biomass accumulated from GS31 to GS59 on above-ground biomass at GS59, for 18 site-years

Discussion

Project results showed that the contribution to grain yield of grain number m^{-2} was more important than that of individual grain weight across the 17 site-years. Grain number m^{-2} has two components, ears m^{-2} and grains^{-1}. Across the 17 site-years, these two components were broadly of equal importance in determining grain number (Fig. 2.7). Maximizing light interception in the stem-extension period will favour increasing both ears m^{-2} and grains^{-1} (Fig 2.4). In these experiments, greater biomass accumulation in the stem-extension period was mainly associated with greater PAR interception, although there was also a smaller contribution from RUE. Since there was a strong positive correlation between the duration of the GS31 to GS59 period and (i) GS31 to GS59 biomass accumulation and (ii) grains m^{-2} (Fig. 2.8), it can be concluded that the duration of this phenophase (Fig. 2.2) is critical in determining pre-anthesis growth. Therefore manipulating the duration of this phenophase must be a principal target for barley breeders in future years. Several studies in wheat point to the potential advantages of increasing the proportion of thermal time to anthesis accounted for by the stem elongation period to increase grain number m^{-2} (Sylvester-Bradley *et al.,* 2005; Slafer *et al..,* 2005). Delaying flowering significantly in the UK could increase grain losses associated with late harvesting, so advancing GS31 whilst maintaining GS59 is the most realistic target. An extended stem-elongation period should simultaneously favour greater ear biomass, stem WSC and crown root growth at anthesis. Since greater GS31 to GS59 biomass was also associated with greater pre-anthesis RUE in the present study, UK barley breeders might in future consider ways of selecting for this trait in their breeding programmes. In wheat, an analysis of a set of eight historic UK cultivars, recently found yield potential to be positively associated with RUE linked to increased flag leaf specific weight (thicker leaves). Greater flag-leaf specific dry weight may indicate increased photosynthetic tissues per unit leaf area and hence improved RUE. Selection for this trait may offer scope for genetic improvement in pre-anthesis RUE in barley. Estimating RUE in breeders' plots is infeasible, so further work seems justified to identify surrogates or 'smart-screens' for RUE, including genetic markers, and to develop appropriate protocols for their use in breeding programs in the UK environment**.**

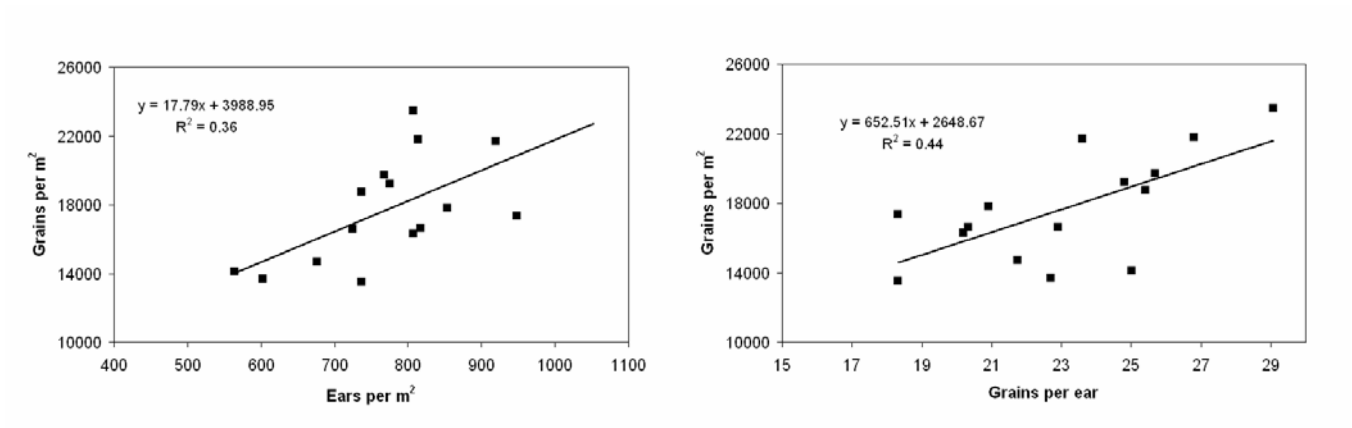


Fig. 2.7. Relationship between ears m^{-2} and grains ear^{-1}, and grain number m^{-2} across the 17 site-seasons

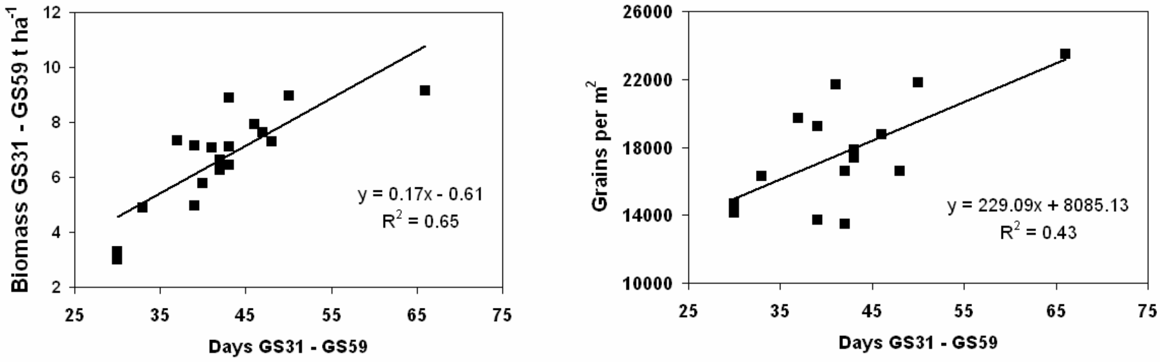


Fig. 2.8. Relationship between days from GS31 to GS59, and GS31 to GS59 biomass increment and grains m^{-2} across the 17 or 18 site-seasons

In these 17 site-years, there was no statistically significant relationship between regression of ears m^{-2} on grains ear^{-1}. In wheat there is often a negative relationship between these two yield components due to competition for assimilate between shoots affecting ear fertility. In two-row barley, ear fertility is likely to exhibit less plasticity than in wheat since there is only one floret per spikelet. In this data set, differences in grains ear^{-1} were not evident between seasons, but were between sites, with Rosemaund showing higher grains ear^{-1} compared to other sites, especially Edinburgh (Table 2.12). These site differences in ear fertility were associated with differences in individual ear weight (Fig. 2.9), e.g. crops at Rosemaund had most grains ear^{-1} and heaviest ears. However, the physiological basis of the heavier individual ears cannot be identified with certainty from the present data. It may be that developmental responses of vernalization and photoperiod differed between the sites and led to differences in spikelets per ear. These differences in spikelet number could then result in differences in ear weight at GS59. Alternatively, differences in assimilate supply per ear may have led to more surviving spikelets per ear, in cases where the total spikelet number per ear was the same across sites. Since the average number of spikelets on tagged main shoots in these experiment was 30, and the number of infertile spikelets was only 3, the scope for differences in spikelet (= floret) survival to affect ear fertility is apparently quite small, e.g. compared to wheat where there are up to 4 to 5 surviving florets per spikelet. Therefore the developmental processes determining spikelet number, e.g. spikelet primordia production rate (plastochron), may be underpinning the present site differences in ear fertility. Further studies seem justified to look at varietal variation in these developmental processes. Our recent work on novel 'large ear' types in wheat shows that there is genetic variation in spikelet number linked to 'earliness *per se*' effects, i.e. developmental effects acting independently of photoperiod and vernalisation responses, and it may be worth searching for genetic variation in intrinsic 'earliness *per se*' responses in barley germplasm, in order to improve ear fertility.

Table 2.12. Grains per ear at harvest in 17 site-seasons

Site	Harvest year		
	2002	2003	2004
Aberdeen	24.8	25.4	22.9
Edinburgh	18.3	19.2	*
HighMowthorpe	20.9	22.7	27.6
King's Lynn	25.0	21.7	18.3
Rosemaund	29.1	26.8	25.7
Sutton Bonington	20.3	20.2	23.6

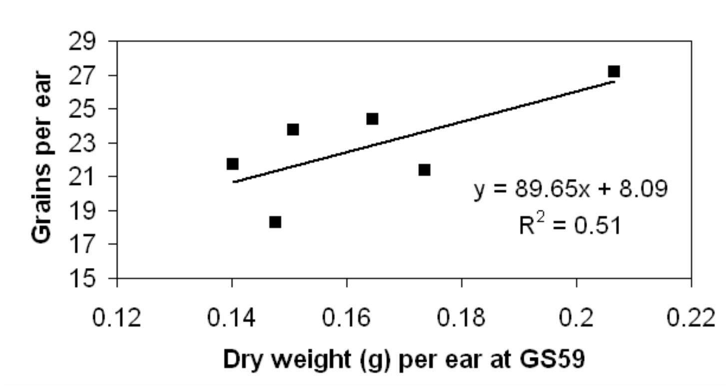


Fig. 2.9 Relationship between dry weight per ear and grains per ear at 6 sites.

APPENDIX 3: REALISATION OF GRAIN YIELD

Introduction

Fertilisation of florets and the subsequent development of grains constitute the final phase of yield formation in cereals. After the number of potential grains has been established, how well each of the grains fills determines the eventual yield. Carbohydrates for grain filling are supplied by concurrent photosynthetic activity and from temporary storage reserves (Gallagher *et al.,* 1975; Schnyder 1993). In barley, photosynthesis by the flag leaf and the ear are considered to supply most of the photosynthate to the developing grain (Biscoe *et al.,* 1975b; Smith *et al.,* 1999). Storage reserves, deposited in the elongating stem internodes before and shortly after ear emergence, contribute a variable proportion of the grain dry matter depending on conditions during the grain filling period. Estimates for barley range from 11% to 12% under well-watered conditions to 44% under dry conditions (Biddinger *et al.,* 1977; Austin *et al.,* 1980). The available evidence suggests that accumulation of storage reserves occurs when current photosynthetic activity exceeds the demand by developing sinks, and re-translocation from reserves occurs when sink demand exceeds photosynthetic activity (Bonnett and Incoll 1993; Schnyder 1993).

The control of grain filling has often been considered in terms of the supply of photosynthate (source limitation) or the capacity of the grain to accumulate available carbohydrate (sink limitation). Evidence for source limitation comes from experiments in which a change in individual grain weight is observed in response to a change in assimilate supply induced by shading, defoliation, thinning or ear manipulation treatments (Martinez-Carrasco and Thorne 1979; Habgood and Uddin 1983; Bonnett and Incoll 1993; Grashoff and d’Antuono 1997; Voltas *et al.,* 1998). Relationships such as the positive association between grain yield and post anthesis leaf area duration, reported for some crops, are also consistent with source limitation (Thorne, 1973).

Sink capacity is a function of the number of grains m^{-2} and their potential size. Grain yield in barley and wheat is often strongly related to the number of grains m^{-2} (Gallagher *et al.,* 1975; Gales 1983). When an increase in grain number is not accompanied by a decrease in mean grain weight, sink limitation of grain filling by potential grain size is suggested. It is not clear what the mechanisms determining potential grain size are, but both genetic and environmental factors appear to be involved. Genotypic differences in mean grain weight in barley and wheat have been related to variation in endosperm cell number established during early grain development (Brocklehurst 1977; Cochrane and Duffus 1983). However, earlier developmental events may also be important in contributing to potential grain size. Thus in a study of 12 spring barley genotypes, the growth rate and final weight of grains was found to be linearly related to the initial size of the carpel (Scott *et al.,* 1983). A curvilinear relationship between carpel size at anthesis and grain weight has been reported for wheat (Calderini *et al.,* 1999). Moreover both carpel size and final grain weight were reduced by short periods of high temperature between ear emergence and anthesis (Calderini *et al.,*1999).

One of the features of most ear manipulation experiments designed to enhance assimilate availability to the ear is that the increase in grain weight, if found, is rarely of the same magnitude as the increase in source:sink ratio imposed by the treatment (Voltas *et al.,* 1998). This may be the result of a shift in the crop from an initial state of relative source limitation before treatment to one of sink limitation afterwards. Alternatively, it may reflect a co-limitation or shared control of grain filling such that grain growth is partially controlled by both source and sink. Mechanistic concepts of shared control of plant growth between source and sinks have been developed over the last decade (Farrar 1996; Farrar and Jones 2000). Although these have not yet been widely applied to grain growth, it has long been recognised that both source and sink limitation may operate at different stages of grain development (Thorne 1973; Martinez-Carrasco and Thorne 1979). Integral components of shared control are the direct effects of carbohydrate supply on sink activity and their capacity to grow and the feedback control of photosynthetic activity by sink demand (Farrar 1996; Bingham and Stevenson 1993). The observations of a reduction in endosperm cell number in wheat when irradiance was reduced, albeit in controlled environments (Singh and Jenner 1984), suggests one possible mechanism linking source and sink during grain development.

As argued by Farrar (1996), the concept of source or sink limitation is a quantitative one and the important question is not whether grain filling is either source or sink limited, but the extent to which one or the other operates. Identifying the relative source-sink balance of a crop post anthesis, or the poise of any shared control of grain growth, has considerable practical significance. For example, crops that are strongly sink-limited may be more tolerant of post-anthesis foliar disease than those that are either source limited, or in which the source and sink are more closely matched. As such, early assessment of the likely source-sink poise of a crop may offer opportunities for modifying crop management.

We propose that the potential assimilate supply for grain filling in barley can be estimated as

$(PAR_{int} \times RUE) + WSC$

Where PAR_{int} is the amount of photosynthetically active radiation (PAR) intercepted post anthesis, RUE is the post anthesis radiation use efficiency and WSC is the water soluble carbohydrate reserves assimilated pre-anthesis. We also propose that in a crop where grain filling is predominantly sink-limited, an index of the relative source-sink balance is given by the difference between potential photosynthate supply and the actual grain yield.

In this chapter we conduct a detailed analysis of radiation interception, radiation use efficiency and grain growth of winter barley (*cv* Pearl) to test the following hypotheses.

The post anthesis source-sink balance of crops differs between sites and seasons.
Mean grain weight is determined by photosynthate supply during early grain development.
Simple measures of crop traits at ear emergence can be used to predict the relative source-sink balance during grain filling and the mean grain weight.

Materials and Methods

The full data set from the three years of reference crop trials was used, with the exception of data for Edinburgh in 2004. Here severe damage by birds during grain filling rendered the harvest data and measurements of post anthesis growth unreliable.

An additional set of treatments to modify the source-sink balance of the crop was imposed in 2003 and 2004 to test whether grain filling at each site was source limited. In 2003, 28 days after ear emergence (Zadocks GS59) 10 ears in each of three plots were selected at random and tagged. The spikelets along one side of the rachis were removed, leaving those on the other side intact. The number of grains on each ear was recorded before and after dissection. At the final destructive sampling prior to combine harvesting the plots, the ears were oven dried and the weight of three central grains, two distal grains (one from the base of the ear and one from the tip) and the whole ear was determined. Controls were intact ears. In 2004 the same treatment was imposed at 21 and 28 days after ear emergence.

Definitions

For the purpose of this chapter we define the source:sink ratio as the size of source structures (i.e. the GAI of the canopy) relative to the size of the sink (the number of grains m^{-2}). The source-sink balance, on the other hand, is defined as the difference between the potential amount of assimilate available for grain filling and the capacity of the grains to store it.

Calculations and Data Analysis

Grain filling

To determine the duration of grain filling, a logistic function was fitted to plots of the mean ear dry weight per shoot against either time or thermal time (^oC d) from flowering (Zadocks GS59). The logistic function was of the form:

$$EW = EW_i + [EW_m - EW_i]/1+\exp[(t_{50} - t)/\text{slope}]$$

Where EW is the ear dry weight, EW_m is the fitted maximum ear weight, EW_i the fitted initial weight, t_{50} is the time when ear weight is half way between the initial and the maximum, and t is the time from ear emergence in days or ^oC days.

For calculation of thermal time, a base temperature of 0 °C was used. The function fitted the data well, with r^2 exceeding 0.98 in 14 of the 17 site/year combinations; of the others the lowest r^2 was 0.93. The end of grain filling was estimated from the fitted curves and defined as the time at which the ear reached 98% of its final dry weight. The mean rate of grain growth was then calculated from the duration of grain filling and the mean grain weight (@100% dry matter). This, therefore, includes the lag period of slow growth early post anthesis, before the onset of rapid grain filling.

The end of the slow phase of grain growth and the start of the rapid rate of grain filling was determined from the fitted curves as follows. The equation for the curve was differentiated with respect to time to give the instantaneous rate of ear growth and the time identified when the percentage change in rate in the accelerating phase was minimised. An example curve highlighting the end of the slow phase of growth is given in Fig. 3.1.

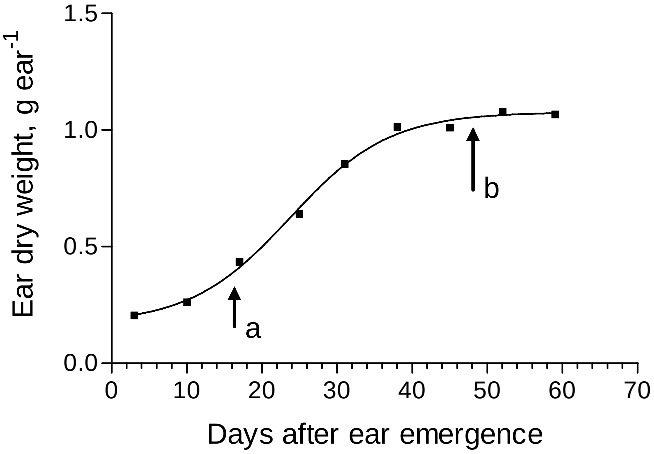


Fig. 3.1. Mean ear dry weight with time after ear emergence for crop at Aberdeen 2004. The end of the slow growth phase is shown at a) and the end of grain filling at b)

Post-anthesis radiation interception

A specific extinction coefficient (Kpar) for each site/season was calculated from measured values of fractional PAR transmission and GAI

$$Kpar = \ln (I/I_0)/GAI$$

where I_0 is the incident PAR and I is the PAR transmitted to the base of the canopy.

Kpar was estimated at each sample time, and the average value taken between GS49 and GS65 when the canopy was at its maximum GAI and before senescence had begun. The fraction of PAR intercepted by green tissue was then estimated for the entire post anthesis period from measurements of GAI and Kpar using the Beers law analogy:

Fraction PAR intercepted = 1-exp (-Kpar.GAI)

Cumulative PAR interception was calculated from meteorological records of daily incident radiation and the average fractional interception for the time interval between destructive amples. Post anthesis radiation use efficiency (RUE) was determined by plotting cumulative PAR interception against the cumulative increase in above ground biomass from the destructive sample closest to GS59.

Adjustment in Kpar during canopy senescence

The extinction coefficient for light transmission through a canopy (Kpar) depends on the leaf angle distribution, the solar angle and the nature of the incident radiation (direct versus diffuse). As the canopy senesces, the green area of leaf laminae declines before that of the stem (including leaf sheaths) and ear. Since the stem is essentially vertical and the leaf laminae have a range of angle distributions, the angle distribution of green surface will change during senescence. Measurements of leaf angle distribution were not made, but the effects of changes in ratio of stem plus ear green area to the total green area on Kpar were estimated. This allowed an assessment to be made of the likely sensitivity of light interception and radiation use efficiency to changes in Kpar during senescence.

The procedure to adjust Kpar was as follows. The measured Kpar of the crop at Aberdeen in 2003 at GS59 was 0.55. This was the value for a solar angle of 40° and a high fraction of direct to total radiation. The distribution of canopy leaf elements can be described by the Ellipsoidal Leaf Angle Distribution Parameter (ELADP) (Campbell 1986). The ELADP that corresponds to a Kpar of 0.55 under these conditions was calculated according to Campbell (1986) and equals approximately 0.5. The ELADP is also given by H/V; the ratio of the horizontally projected green area (H) to the vertically projected area (V). In our crops the vertically projected green area was considered to be the stem and ear green area plus a contribution from the laminae. The horizontal green area was the remaining leaf laminae. Stem, ear and lamina GAI was measured directly on the destructive growth analysis samples. The total lamina GAI at GS59 was approximately three. To estimate the horizontal and vertical components, a matrix of H to V GAI ratios giving a total GAI of three was constructed. For each ratio, the ELADP was calculated as:

Lamina horizontal GAI/ lamina vertical GAI + stem GAI + ear GAI

The ratio of H to V lamina GAI that gave an ELADP of 0.5 in the above equation thus provided an estimate of the horizontal to vertical components of lamina GAI present in the field.

It was assumed that the stem and ear remained vertical throughout the grain filling period and that the ratio of H to V components of the lamina GAI remained constant as lamina GAI declined. Thus the change in ELADP could be calculated from measurements of stem, ear and lamina GAI and a revised Kpar calculated for each sampling time. The ratio of the revised Kpar to Kpar measured in the field at GS59 was plotted against the ratio of stem plus ear GAI to total GAI. Fitting a logarithmic function to the plot enabled a Kpar correction factor to be derived for any value of (stem plus ear GAI)/total GAI. The correction factor was then used to adjust the Kpar values for crops in other years and at other sites.

Results

Weather conditions post-anthesis

Ear emergence occurred from mid to late May depending on the site, and grain filling was completed from late June to mid July. Crops at the more northerly sites (Aberdeen, Edinburgh and High Mowthorpe) were later to develop and tended to have slightly longer grain filling periods than those in the south. In 2002 mean daily temperatures were close to the long-term average for the site, with the exception of Aberdeen and King's Lynn where they were slightly higher (Table 3.1).

Table 3.1. Climatic conditions at each site during the period from ear emergence to the end of grain filling. The rainfall distribution factor is the fraction of the total rainfall that fell within the first/half of the post anthesis period.

Year	Site	Air temperature (^oC)			Total rainfall, mm	Rainfall distribution factor	Incident radiation MJ PAR
		Max	Min	Mean			
2002	Aberdeen	16.8	9.5	13.1	162	0.53	365
	Edinburgh	17.3	10.1	13.7	135	0.52	308
	High Mowthorpe	17.3	9.1	13.2	94	0.34	372
	King's Lynn	21.7	8.9	15.3	59	0.54	439
	Rosemaund	17.7	9.0	13.4	84	0.86	330
	Sutton Bonington	18.5	9.4	14.0	81	0.62	343
2003	Aberdeen	18.4	11.1	14.7	17	0.92	350
	Edinburgh	19.4	10.8	15.1	47	0.50	414
	High Mowthorpe	18.7	9.5	14.1	129	0.26	344
	King's Lynn	24.4	10.0	17.2	105	0.42	327
	Rosemaund	20.1	9.9	15.0	63	0.36	382
	Sutton Bonington	21.2	11.1	16.2	103	0.35	388
2004	Aberdeen	16.8	9.6	13.2	119	0.27	333
	High Mowthorpe	16.9	8.4	12.7	136	0.08	418
	King's Lynn	23.0	9.7	16.4	92	0.24	282
	Rosemaund	20.0	8.9	14.4	50	0.40	344
	Sutton Bonington	19.6	8.9	14.2	55	0.33	315

The amount of rain falling during this period was also similar to the long-term average, except at Aberdeen and Edinburgh where it was considerably greater. Although 2003 was warmer than average at all sites, at High Mowthorpe, Sutton Bonington and King's Lynn it was also wetter. In contrast, it was unusually dry at Aberdeen and Edinburgh over this period, with less than half the normal rainfall. Conditions in 2004 were, in general, comparable with those in 2002.

Mean grain weight

The mean grain weight (MGW), determined on samples from combine harvested plots, differed significantly between sites and years (Table 2). Here the MGW has been expressed on the basis of 85% dry matter for ease of comparison with data from commercial crops and variety trials. There appeared to be no pattern of MGW with site that was consistent between years. Thus, Rosemaund had the highest MGW in 2002, but the lowest in 2003. The main exceptions are that King's Lynn and Edinburgh tended to produce grain of low MGW in all years.

Mean grain weight was only weakly related to yield (P = 0.074) and accounted for less than 20% of the variation in yield between sites and years (Fig.3.2).

Table 3.2. Mean grain weight (at 85% dry matter). Values are predicted means from REML variance components analysis on samples from 4 to 7 replicate plots per site and year.

Site	Harvest year		
	2002	2003	2004
Aberdeen	44.62	54.25	47.97
Edinburgh	41.78	43.28	-
High Mowthorpe	41.52	53.63	52.12
King's Lynn	40.84	43.52	41.22
Rosemaund	47.15	41.51	42.56
Sutton Bonington	46.12	46.14	42.79

SED site x year = 1.191, LSD $P_{0.05}$ df 54 = 2.39

The final weight achieved by grains is a function of both their average rate of growth and the duration the grain filling period. The duration of grain filling was estimated from curves fitted to weekly measurements of ear growth. This provided a more reliable estimate than measurements made on dissected grains because a larger sample size was involved. It also averages more effectively across grains at different locations on the ear and on ears of contrasting size and tiller hierarchy. Estimated in this way, the duration of grain filling ranged from 35 to 51 days after flowering, corresponding to a range in thermal time of 547 to 727 ^{o}C days. Differences in the duration of grain filling accounted for little of the variation in MGW between sites and seasons whether expressed on a calendar or thermal time basis (Fig. 3.3). To more accurately reflect the process of dry matter deposition during grain filling, MGW has been expressed here on the basis of 100% DM. The rate of grain filling, on the other hand, was positively associated with MGW and when expressed as calendar time accounted for 36% of the variation in MGW between sites and years (Fig. 3.3c). Expressing the rate on the basis of thermal time accounted for a greater amount of the variation (58%).

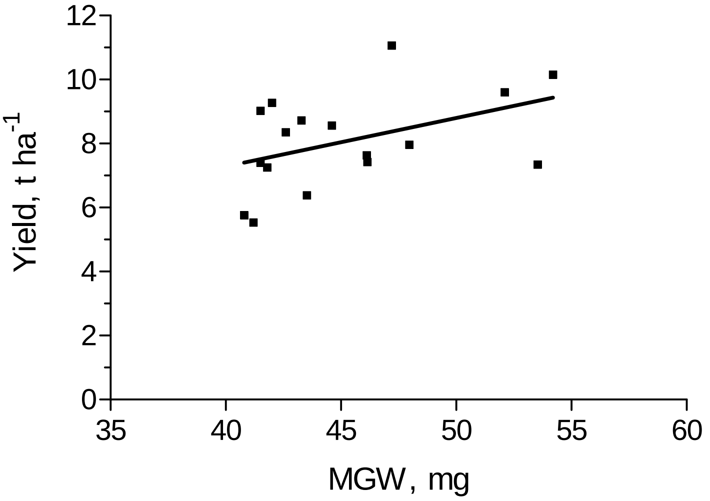


Fig. 3.2. Relationship between mean grain weight (@ 85% DM) and grain yield (@85% DM) for 17 site/years. Line fitted by least squares regression y = 0.151x + 1.25; P = 0.074; r^2 = 0.198.

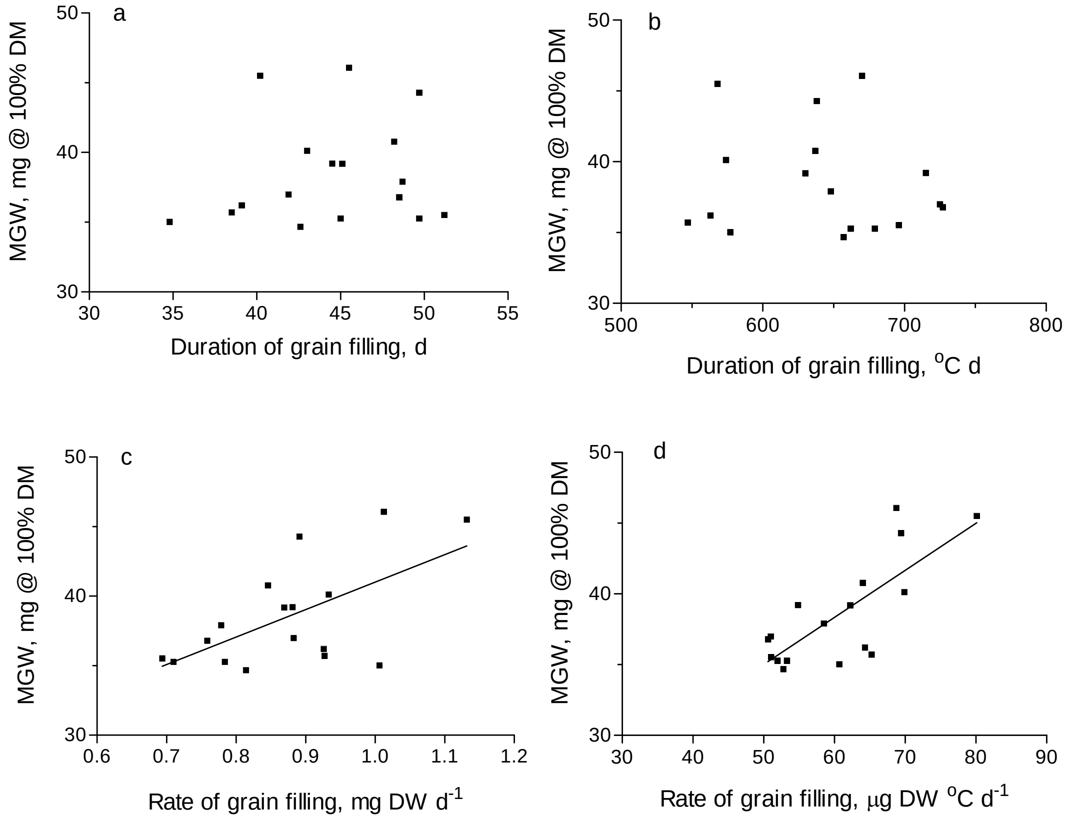


Fig. 3.3. Relationship between MGW and the duration (a, b) and average rate of grain filling (c, d) expressed on the basis of calendar (a & c) or thermal (b & d) time. Lines fitted by least squares regression c) $r^2 = 0.360$, $P = 0.011$; d) $r^2 = 0.581$, $P < 0.001$. For a) and b) $P > 0.05$.

Canopy lifespan post ear emergence

The size of the canopy differed widely between sites and between years, but showed a broadly similar temporal pattern of senescence. Fig. 3.4 shows data for 2002 only, but these are fairly typical of the other years. After a period of approximately 10 to 15 days from ear emergence where GAI changed relatively little, there was a near linear phase of canopy senescence to low values of GAI (<1). The rate during this linear phase was dependent on the initial size of the canopy. Edinburgh was the most unusual site in that canopy senescence proceeded relatively slowly at first, followed by a rapid loss of green area in the final week. A comparable pattern at Edinburgh was also found in 2003 (data not shown).

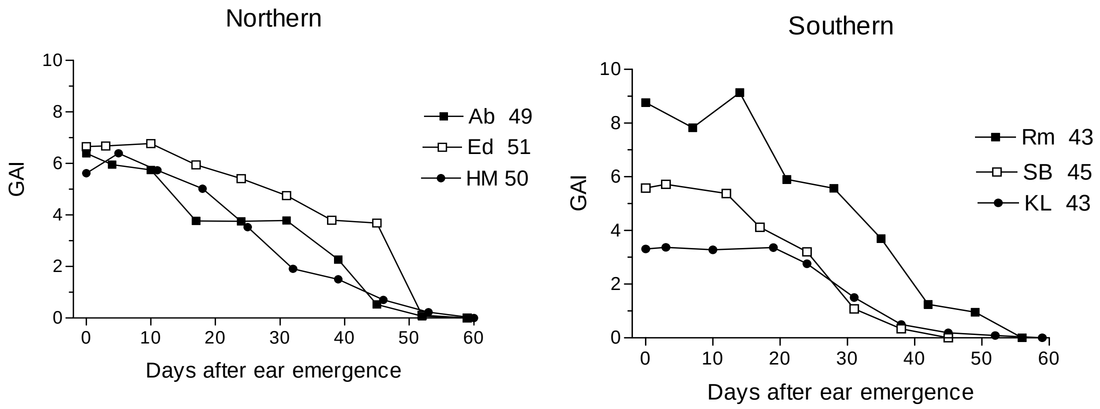


Fig. 3.4. GAI for crops after ear emergence in 2002. Each point is the mean of 3 replicate plots per site. Errors bars have been omitted for clarity; cvs for GAI > 3 were AB 15-30%; Ed <15%; HM <15%; Rm <15%; SB 15-30%; KL 10-20%. Numbers in the legend are the times of the end of grain filling (days after ear emergence).

Final canopy senescence broadly coincided with the end of grain filling. Values of GAI at the time of 98% maximum ear DW were interpolated from measurements of GAI by assuming that GAI changed linearly between sampling times. The GAI at the end of grain filling differed significantly between sites and years (Table 3.3), but the effects were generally small. With the exception of Edinburgh in 2003, the GAI remaining at the end of grain filling ranged from 0 to 0.9. At Edinburgh the GAI was exceptionally high (2.15), but this fell rapidly over the next four days.

Table 3.3 Canopy GAI remaining at the end of grain filling. Values are predicted means from REML variance components analysis on 3 replicate plots per site and year.

Site	Year		
	2002	2003	2004
Aberdeen	0.27	0.10	0.53
Edinburgh	0.62	2.15	-
High Mowthorpe	0.43	0.48	0.37
King’s Lynn	0.00	0.28	0.77
Rosemaund	0.28	0.54	0.32
Sutton Bonington	0.88	0.05	0.25

SED site*year = 0.13 LSD, 34 df, $P_{0.05}$ = 0.26

Radiation interception and RUE

Quantifying radiation interception and utilisation post-anthesis is problematic because the canopy begins to senesce during grain filling. In the present work PAR interception by green tissue was estimated from measured values of Kpar at maximum canopy size, and the GAI of the canopy determined at each sampling occasion. This approach assumes that Kpar does not change during the course of canopy senescence. The validity of this assumption is discussed later.

Fig. 3.5 shows the cumulative PAR interception post-anthesis plotted against the gain in total above-ground biomass for the six sites in 2002. The relationship differed markedly between sites and years; for some it was linear, whilst for others it was clearly non-linear. The slope of the relationship is the radiation use efficiency (RUE_{total}). The subscript denotes that the coefficient is based on total above ground dry matter production. Second order polynomials were fitted to data for each site/year combination. The estimated quadratic term, which is a measure of the degree of curvature of the fitted line, and its statistical significance (P value) are given in Table 3.4.

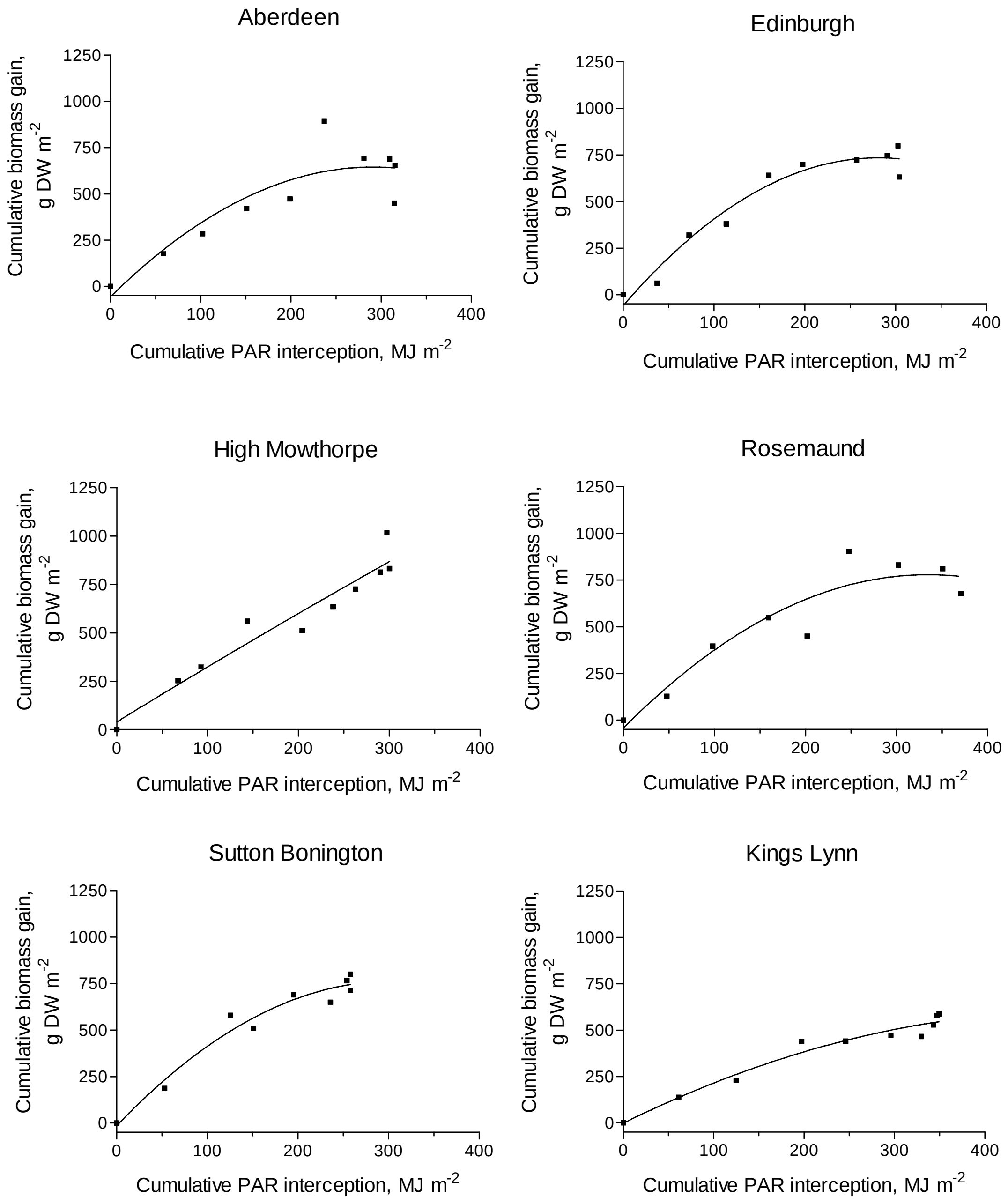


Fig. 3.5. Relationship between the cumulative PAR interception post anthesis and gain in above-ground biomass for sites in 2002. Lines are fitted 2nd order polynomials.

Table 3.4. Estimates of the quadratic term of 2nd order polynomials fitted to plots of cumulative PAR interception against above ground biomass, and their significance level.

	Quadratic term			Significance, P		
	2002	2003	2004	2002	2003	2004
Aberdeen	-0.00826	-0.00100	-0.00096	0.126	0.761	0.863
Edinburgh	-0.01006	-0.00513		0.006	<0.001	-
High Mowthorpe	-0.00041	-0.00338	-0.00536	0.912	0.302	0.100
King's Lynn	-0.00239	0.00404	-0.01792	0.090	0.302	0.011
Rosemaund	-0.00734	-0.00377	-0.00908	0.060	0.271	0.010
Sutton Bonington	-0.00839	-0.00280	-0.00392	0.042	0.478	0.444

Adjusting the Kpar value of the crop according to the stem plus ear GAI relative to the total GAI had only a small effect on the estimated cumulative PAR interception (Fig.3.6). PAR interception was reduced towards the end of the grain filling period, but this had little effect on the estimates of RUE, even when all the data points are included (i.e. for linear RUE_{total} plots such as High Mowthorpe). Parallel regression analysis of the data at High Mowthorpe showed no significant difference in slope between plots derived from adjusted compared to constant Kpar values ($P = 0.67$). Furthermore, at sites where plots of RUE_{total} were non-linear, there was little effect of the adjustment on the extent of non-linearity. Quadratic terms for data from Edinburgh were –0.01006 ($P = 0.006$) for constant Kpar and –0.01059 ($P = 0.008$) for adjusted Kpar.

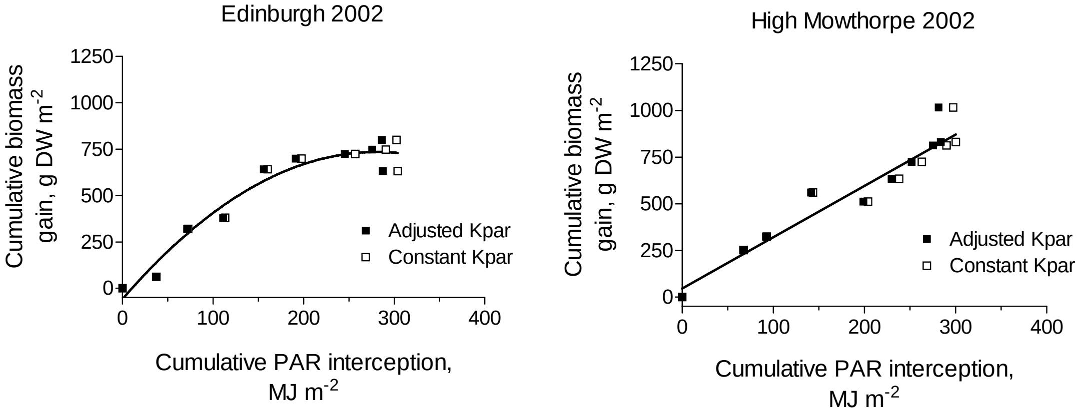


Fig. 3.6. Effects of using constant or variable (adjusted) Kpar values in the estimation of light interception during the grain filling period. Data are shown for two crops with contrasting patterns of RUEtotal. Lines are fitted second order (Edinburgh) or first order (High Mowthorpe) polynomials to data for constant Kpar values.

Fig. 3.7 shows the relationship between cumulative PAR interception post anthesis and the gain in ear dry weight for each site in 2002. As was the case with RUE_{total}, the nature of the relationship differed between sites; for some it was linear, whilst for others it was non-linear. The slope of the relationship provides a measure of the apparent efficiency of conversion of intercepted radiation into ear biomass (RUE_{ear}). In 2002 the RUE_{ear} at Aberdeen, Edinburgh and Rosemaund, was relatively constant throughout the period of light interception, whereas at the other sites it tended to increase towards the latter half of the post anthesis period (Fig. 3.7). Second order polynomials were fitted to data for each site/year combination. The estimated quadratic term, and its statistical significance (P value) are listed in Table 3.5.

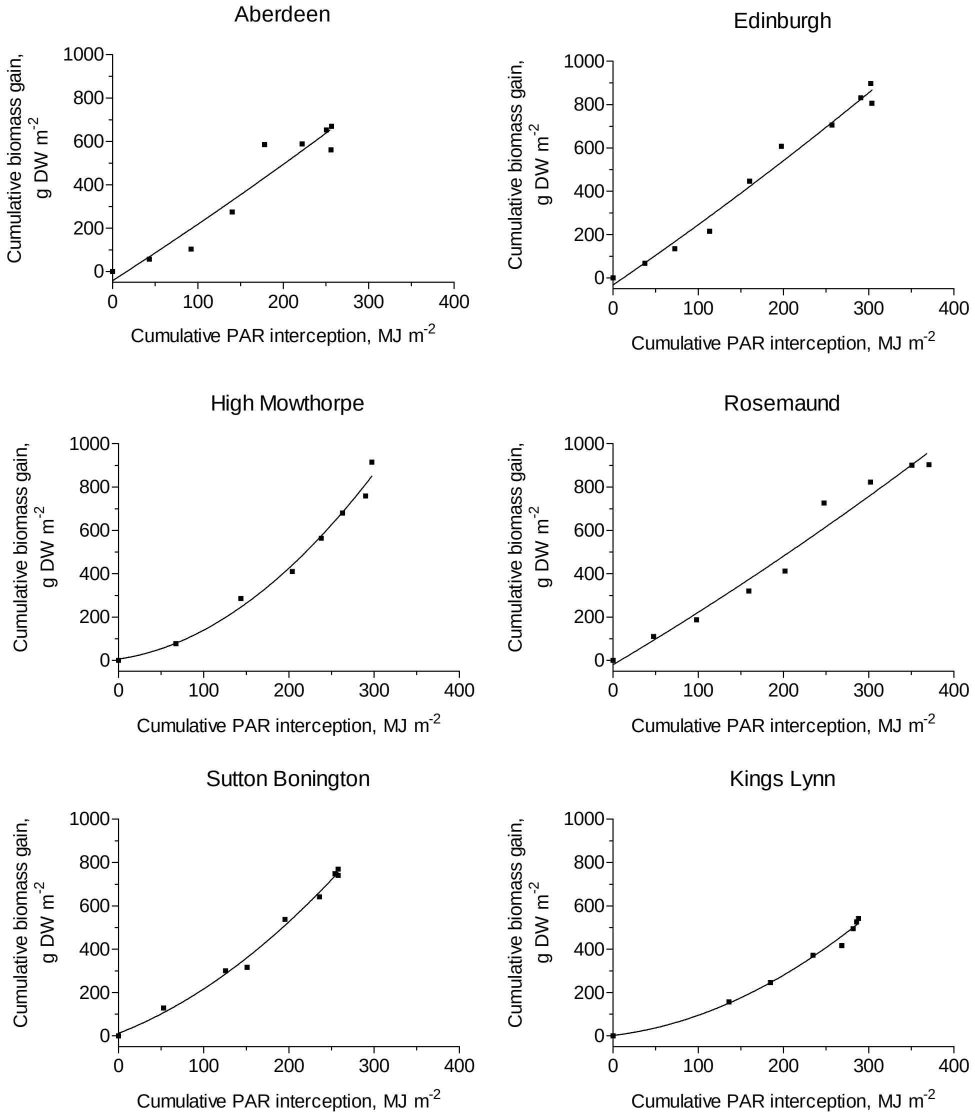


Fig. 3.7. Relationship between the cumulative PAR interception post anthesis and gain in ear dry weight for sites in 2002. Lines are fitted 2nd order polynomials.

Table 3.5. Estimates of the quadratic term of 2^{nd} order polynomials fitted to plots of cumulative PAR interception against the increase in ear dry weight, and their significance level.

	Quadratic term			Significance, P		
	2002	2003	2004	2002	2003	2004
Aberdeen	0.00079	0.01021	0.00570	0.873	0.011	0.078
Edinburgh	0.00088	-0.00056		0.651	0.569	-
High Mowthorpe	0.00762	0.00515	0.00316	0.011	0.040	0.151
King's Lynn	0.00461	0.01081	0.00199	0.006	0.001	0.596
Rosemaund	0.00084	0.00996	0.00936	0.664	0.053	<0.001
Sutton Bonington	0.00524	0.00286	0.00540	0.011	0.291	0.031

Crops that showed the greatest decline in RUE_{total} towards the end of the grain filling period tended to have the most stable RUE_{ear} over the same period. Thus the value of the quadratic term (degree of curvature) from plots of RUE_{total} was inversely related to that from plots of RUE_{ear} (Fig. 3.8).

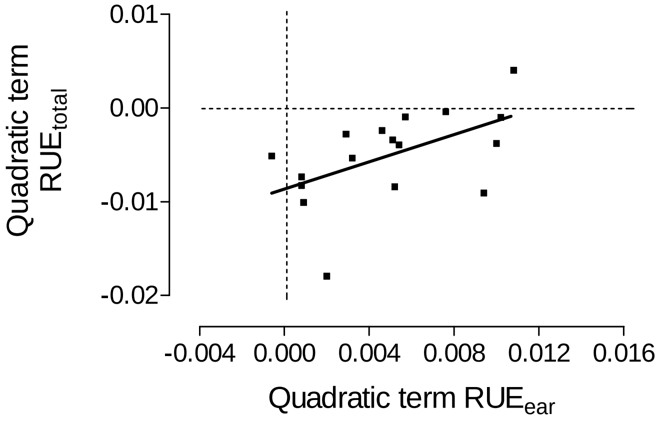


Fig. 3.8. Relationship between the value of the quadratic term for plots of RUE_{ear} (Table 3.5) and RUE_{total} (Table 3.4) for 17 site/years. Extent of curvature of RUE plots is shown by the departure of the quadratic term from zero (highlighted for reference by the broken lines); the direction of curvature is indicated by the + or – sign of the term. Solid line is fitted by least squares regression ($P = 0.026$, $r^2 = 0.289$).

RUE_{total} was determined from the slope of the relationship between cumulative intercepted PAR and total biomass gain. Where the significance of the quadratic term in Table 3.4 was >0.10, the relationship was considered to be sufficiently linear for a single value of slope to apply across the whole grain filling period, and RUE was estimated from a linear regression fitted to all points. Where the quadratic term had a significance level of ≤ 0.10, RUE was estimated from linear regression fitted to the 4 or 5 points making up the initial most linear part of the curve. This is taken to be the maximum RUE during the post-anthesis period. The only exception to the application of this criterion was for Aberdeen in 2002. In spite of a relatively large quadratic term (large degree of curvature) the probability level was only 0.126, because one outlying point had a large impact. Here, RUE_{total} was estimated from linear regression on the first five points, instead of all points, in recognition of the extent of curvature.

Parallel regression analysis indicated that RUE_{total} did not differ significantly ($P > 0.05$) between years, but did differ between sites and specific site/year combinations. Values ranged from approximately 2g DM/MJ PAR at High Mowthorpe in 2003, and King’s Lynn in 2002, to over 3.8 for Sutton Bonington in 2002 (Table 6). There was no clear relationship between the site and RUE_{total} that was consistent over the three years. Thus King’s Lynn had the lowest RUE_{total} in 2002, but the highest in 2004. Edinburgh had a high RUE (>3.7) in both 2002 and 2003, but there were no data for 2004 to establish whether this was a consistent feature of the site.

Table 3.6. Maximum RUE_{total} for the post anthesis period, g DW MJ^{-1} PAR

Site	Harvest year		
	2002	2003	2004
Aberdeen	2.558	2.578	2.39
Edinburgh	3.763	3.781	
High Mowthorpe	2.919	1.996	2.531
King’s Lynn	2.097	2.537	3.350
Rosemaund	3.518	2.389	2.905
Sutton Bonington	3.834	2.896	2.311

RUE_{total} tended to be greatest in those crops where, the relationship between cumulative PAR interception and biomass production showed the most non-linearity (Fig. 3.9).

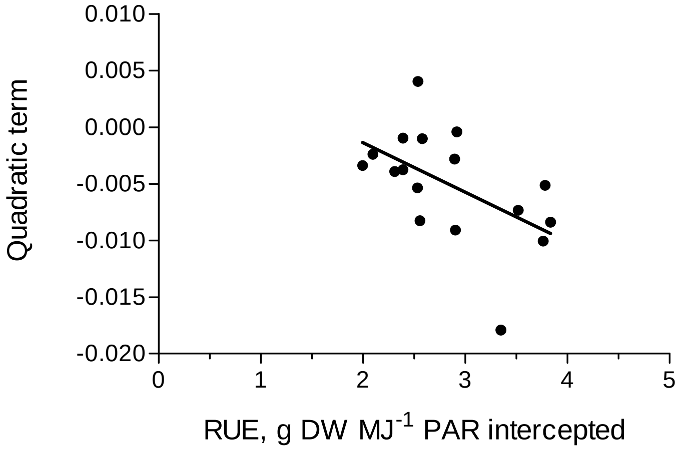


Fig. 3.9. Relationship between RUE post anthesis and the value of the quadratic term from Table 4, $r^2 = 0.286$, P = 0.028.

Factors influencing the pattern of post-anthesis RUE_{total}

There was no significant association between any of the climatic variables in Table 3.1 and the value of the quadratic term of RUE_{total} (Table 3.5). Pearson's correlation coefficients [r] for the associations were all less than 0.15 (data not shown). Nor was there any significant association between the duration of the grain filling period and the quadratic term (data not shown).

There was, on the other hand, a significant relationship between the size of the canopy at GS59, both in terms of above ground biomass and GAI, and the value of the quadratic term (Fig. 3.10). Thus larger canopies were associated with a greater curvature of RUE_{total} plots (greater deviation of the quadratic term from zero). There was also a significant linear relationship between specific leaf nitrogen (SLN) and the value of the quadratic term. SLN is the amount of N in leaf laminae per unit of lamina green area. Here a high degree of curvature in RUE_{total} plots was associated with low SLN. When N in the canopy as a whole was considered as an explanatory variable (specific canopy N, SCN) less of the variation in the quadratic term between sites and years was accounted for, and the relationship was not significant (P = 0.073). SCN is the amount of N in above ground parts per unit of canopy green area.

Although significant associations were found between the quadratic term and GAI, biomass and SLN, these canopy traits at best explained only 30% of the variation in the quadratic term between sites and years. A much greater proportion of the variation was accounted for (63 %) by the green area per unit grain number (Fig. 3.11). Thus crops with a large green area per grain showed a greater degree of curvature in plots of RUE_{total} than those with a small area.

In spite of the weak associations found between canopy size and SLN at GS59 with the pattern of post-anthesis RUE and the general trend towards higher values of maximum $\mathrm{RUE}_{\mathrm{total}}$ with non-linear RUE plots, no significant relationship was found between the max RUE and any measure of canopy size (GAI and biomass), canopy N (SLN, SCN) or sink size (grains m^{-2}) at GS59 (data not shown).

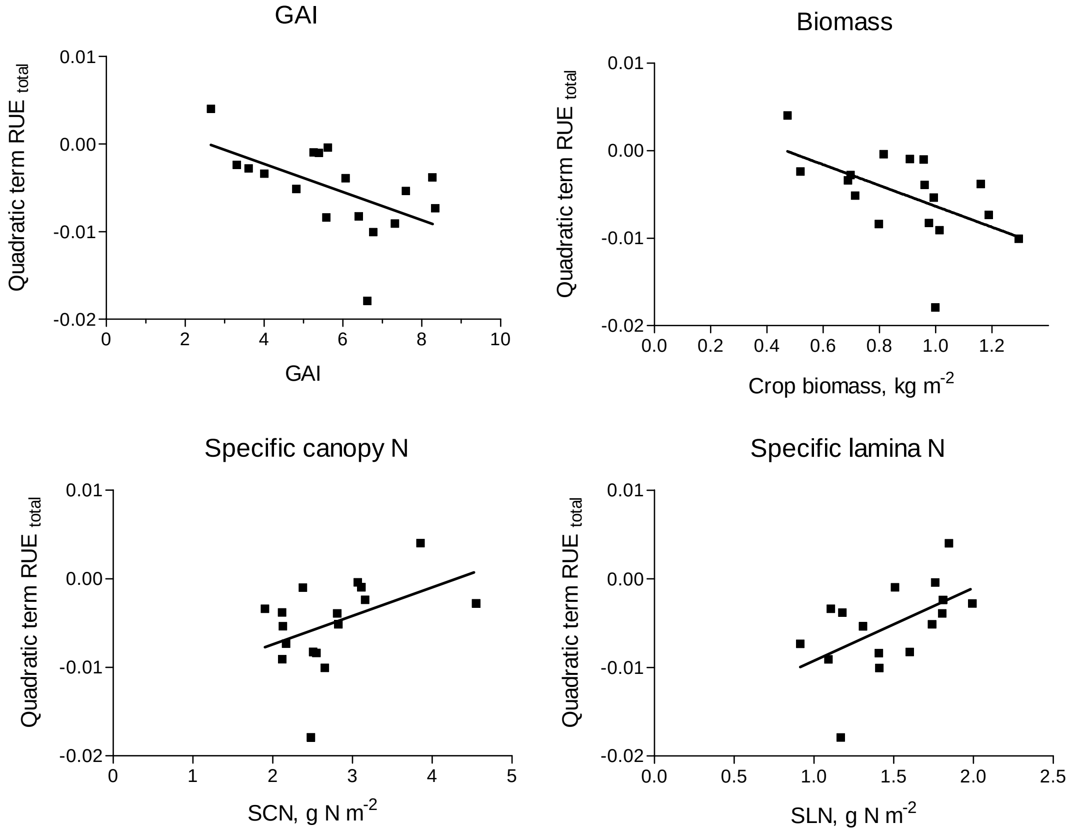


Fig. 3.10. Relationship between canopy traits at GS59 and the value of the quadratic term for $\mathrm{RUE}_{\mathrm{total}}$. Lines fitted by regression: GAI, P = 0.022, $r^2 = 0.303$; biomass, P = 0.023, $r^2 = 0.297$; SCN, P = 0.073, $r^2 = 0.199$; SLN, P = 0.030, $r^2 = 0.294$.

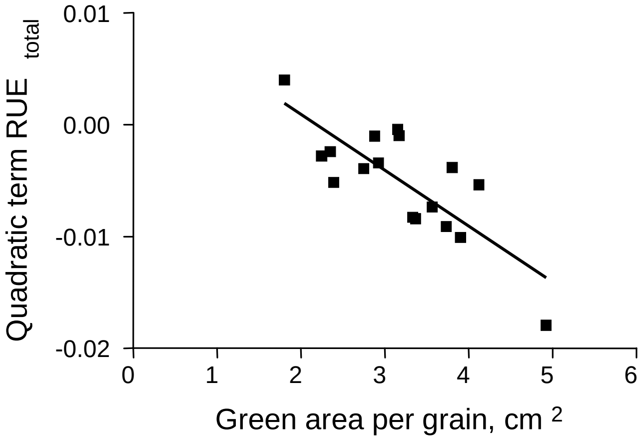


Fig. 3.11. Relationship between the green area per unit grain number at GS59 and the value of the quadratic term from plots of RUE_{total}. Line was fitted by least squares regression $P < 0.001$, $r^2 = 0.628$.

Stem water soluble carbohydrates (WSC)

There was a three-fold range (approximately 1-3 t/ha^{-1}) in the maximum soluble carbohydrate reserves deposited in the stem (Table 3.7). In general, reserves were greater in 2004 compared to 2003, but there was a significant site by year interaction. Although a significant site by year interaction was also found in the amount of reserves remaining at the end of grain filling, in general differences between sites and years were small. The difference between the maximum content and that remaining at the end of grain filling represents that utilised either for grain filling, transfer below ground, or respiration. Again variation between sites and years was large with values ranging from 0.7 to 2.87 t/ha^{-1}. This represents an apparent utilisation of 63% to 94% of the reserves (unutilised fraction 6% to 37%).

Table 3.7. Variation between sites and years in stem water soluble carbohydrate reserves. Values are means of three replicate plots per site and year.

Year	Site	Max WSC, t/ha^{-1}	WSC at end grain filling, t/ha^{-1}	WSC utilised, t/ha^{-1}	% unutilised
2002	Ab	2.21	0.29	1.92	13.54
	Ed	3.00	0.22	2.78	7.36
	HM	1.49	0.28	1.21	19.44
	KL	1.21	0.38	0.83	31.22
	Rm	2.32	0.43	1.89	18.57
	SB	2.85	0.17	2.67	6.21
2003	Ab	2.61	0.15	2.46	5.95
	Ed	1.78	0.43	1.35	23.27
	HM	1.91	0.49	1.42	26.08
	KL	1.21	0.31	0.90	25.83
	Rm	1.96	0.12	1.84	5.81
	SB	1.09	0.39	0.70	36.76
2004	Ab	2.27	0.48	1.79	21.32
	Ed				
	HM	3.05	0.91	2.14	30.01
	KL	2.47	0.37	2.10	15.17
	Rm	2.34	0.18	2.15	7.24
	SB	3.33	0.46	2.87	14.38
SED site x yr		0.250	0.090	0.255	4.168
LSD $P_{0.05}$ 34 df		0.508	0.183	0.518	8.469

Estimating the extent of source and sink limitation of grain filling

The potential supply of photoassimilates for grain filling has been estimated as follows.

$$(\text{max RUE}_{\text{total}} \times \text{PAR interception}) + \text{WSC at flowering}$$

The WSC at flowering is used rather than the maximum stem reserves (which occurs a week or two later) because net assimilation calculated for the entire post-anthesis period (as RUE x PAR interception or as DW gain) will include photosynthates used directly in grain development and filling plus any temporarily allocated to storage. The additional supply not accounted for in this is the material stored before flowering.

We propose that the difference between the potential photosynthate supply and the actual grain yield provides a measure of the extent to which supply may exceed demand by the grain. The grain yield has been reduced by a constant 3mg per grain to account for the likely weight of the husk present at flowering (Scott *et al.,* 1983). Where the difference between potential supply and actual yield is close to zero, it implies that either supply and demand were closely matched, or that supply was insufficient and the final grain yield was supply (source) limited.

Table 3.8. Difference between potential photosynthate supply and grain yield, t ha^{-1} at 100% DM for each harvest year 2002-2004.

Site	2002	2003	2004
Aberdeen	1.84	0.62	1.53
Edinburgh	6.59	8.67	
High Mowthorpe	3.03	0.64	3.21
King's Lynn	2.88	1.28	3.78
Rosemaund	2.93	0.75	1.48
Sutton Bonington	3.82	2.99	-0.04

The results suggest that for all sites in 2002, the potential supply of photosynthates was more than sufficient to meet the demand of the grain and that at some sites (e.g. Edinburgh) it was far in excess (Table 3.8). In general, source and sink appeared to be in closer balance in 2003, since with the exception of Edinburgh the difference between potential supply and yield was lower than in 2003. In 2004 most sites appeared to have sufficient supply to more than satisfy the demand of the grain. Only at Sutton Bonington was grain filling potentially source limited, or that the source appeared to match sink size. Note that in practice grain yield cannot exceed the assimilate availability for grain filling, and thus the negative value for Sutton Bonington reflects an underestimate of the actual available assimilate or experimental error in the determination of yield.

Ear manipulation experiments

Table 3.9. Effects of partial de-graining on the mean weight (mg @ 100% DM) of central and distal grains in 2003. Ears were partially de-grained 28 days after ear emergence. Values are means of 10 ears from each of 3 replicate plots per site. LSD values are for P = 0.05

	Central grains			Distal grains		
	Control	De-grained	%	Control	De-grained	%
Aberdeen	56.5	51.6 *	91	52.6	52.2	99
Edinburgh	48.7	50.3	103	47.3	48.7	103
High Mowthorpe	52.1	57.1 *	110	43.8	43.3	99
King's Lynn	49.6	46.8	94	46.1	39.9 *	87
Rosemaund	44.1	45.5	103	42.2	42.8	101
Sutton Bonington	51.9	56.5 *	109	46.5	58.7 *	126
Site	P < 0.001; LSD 3.15			P < 0.001; LSD 4.22		
De-graining	P = 0.38			P = 0.336		
Site x de-graining	P = 0.019; LSD 4.45			P = 0.006; LSD 5.97		
df 24						

Table 3.10. Effects of partial de-graining on the mean weight (mg @ 100% DM) of central and distal grains in 2004. Ears were partially de-grained at either 21 or 28 days after ear emergence. Values are means of 10 ears from each of 3 replicate plots per site. LSD values are for P = 0.05.

	Central grains			Distal grains		
	Control	28 d	21 d	Control	28 d	21 d
Aberdeen	45.2	50.2*	53.2*	38.1	45.4	47.6*
High Mowthorpe	52.0	53.4	53.2	48.0	36.7*	39.3*
King's Lynn	55.4	45.1*	49.6 *	36.9	39.7	41.6
Rosemaund	44.5	42.6	54.3*	42.1	40.6	41.9
Sutton Bonington	46.4	49.9	47.0	45.5	42.3	41.4
Site	P < 0.001; LSD 2.11			P = 0.28		
De-graining	P = 0.028; 1.63			P = 0.631		
Site*de-graining	P < 0.001; LSD 3.65			P = 0.025; LSD 7.31		
df 30						

The de-graining treatments produced mixed and inconsistent effects. In 2003 there was a significant increase in the final weight of individual central grains at Sutton Bonington and High Mowthorpe, but this was accompanied by an increase in weight of distal grains only at Sutton Bonington (Table 3.9). In contrast, de-graining resulted in a significant *reduction* in the weight of central grains at Aberdeen, and in the weight of distal grains at King's Lynn. In 2004 similar mixed effects were observed, with increases in weight recorded at Aberdeen and Rosemaund, and decreases at High Mowthorpe and King's Lynn (Table 3.10).

Factors determining MGW

There was no significant relationship between the MGW and canopy size (GAI), grain number m^{-2}, or the ratio of green area to grain number at ear emergence (Fig. 3.10). Thus simple indicators of potential radiation capture, sink size and the ratio of source:sink do not predict the MGW. A range of other measures of crop structure at ear emergence, pre anthesis assimilation, early post anthesis assimilation and pre and post anthesis weather conditions were also examined for their relationship with MGW (Table 3.11). The pre-anthesis period was taken from GS39 (flag leaf emergence) to GS59 (ear emergence).

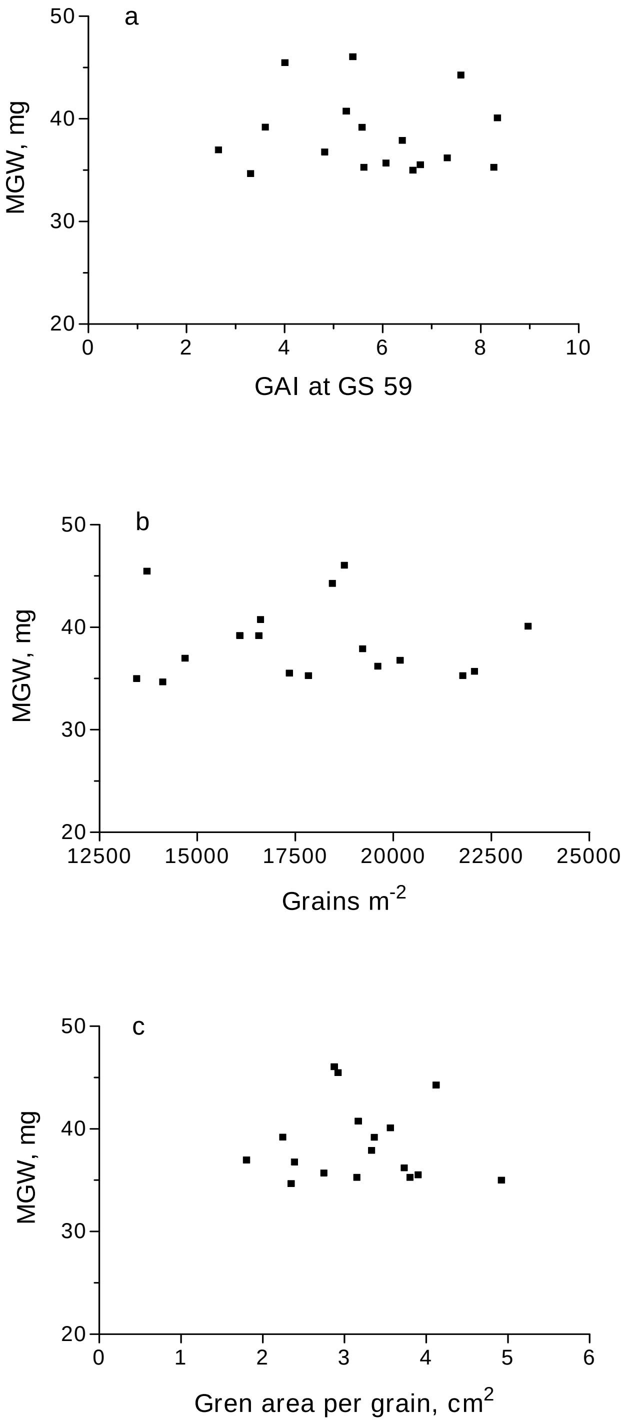


Fig. 3.10. Relationship between MGW (at 100% DM) and the canopy size at GS59 [a], the number of grains m^{-2} [b] and the green area grain^{-1} at GS59 [c]. Data are for 17 site/years.

Table 3.11. Results of linear regression analysis of MGW (at 100% dry matter) against a range of explanatory variables for 16 sites/years. Variables denoted by a subscript 1 relate to the pre-anthesis period (GS39 to GS59), those by 2 to the early post-anthesis period (GS59 to GS71), and 3 to the entire grain filling period (GS59 to end of grain filling). Total biomass refers to above-ground biomass i.e. excluding roots.

Symbol	Description of explanatory variable	P	r^2
PAR_1	PAR interception, kJ per eventual grain no.	0.410	0.049
RUE_1	RUE, MJ m^{-2}	0.555	0.025
A_1	Total DW gain per eventual grain no., mg	0.635	0.017
D_1	Duration GS39 to GS59, days	0.492	0.035
T_{max1}	Mean daily max air temp, °C	0.086	0.196
T_{min1}	Mean daily min air temp, °C	0.627	0.017
T_{mean1}	Mean daily air temp, °C	0.051*	0.245
R_1	Mean daily rainfall, mm d^{-1}	0.670	0.013
Sht	Final no. ear bearing shoots per plant	0.253	0.092
DW_{sht}	DW per shoot at GS59, g	0.755	0.007
GA_{sht}	Green area per shoot at GS59, cm^{-2}	0.818	0.004
DW_{gr}	Total biomass at GS59 per grain no., mg	0.748	0.008
DW_{ear}	Ear DW at GS59 per grain no., mg	0.851	0.002
WSC	Water soluble carbohydrates GS59, t/ha^{-1}	0.613	0.019
WSC_{gr}	WSC GS59 per grain no., mg	0.521	0.030
PAR_2	PAR interception, kJ per grain no.	0.023*	0.317
RUE_2	RUE, MJ m^{-2}	0.331	0.063
A_2	Total above-ground DW gain per grain no., mg	0.634	0.017
ΔDW_{ear2}	Increase in ear DW per unit grain no., mg	0.309	0.073
D_2	Duration GS59-71, days	0.590	0.021
T_{max2}	Mean daily max air temp, °C	0.625	0.018
T_{min2}	Mean daily min air temp, °C	0.653	0.005
T_{mean2}	Mean daily air temp, °C	1.000	0.000
R_2	Mean daily rainfall, mm d^{-1}	0.432	0.045
T_{max3}	Mean daily max air temp GS59-87, °C	0.184	0.122
T_{min3}	Mean daily min air temp GS59-87, °C	0.759	0.067
T_{mean3}	Mean daily air temp GS59-87, °C	0.298	0.077
R_{tot3}	Total rainfall GS59-87, mm	0.770	0.006

The early post-anthesis period was taken from ear emergence to the start of the rapid phase of grain filling (as determined from curve fitting to measurements of ear weight per shoot). This broadly equates to the period GS59 to GS71. For one variable during this period (PAR intercepted per unit grain number), a single data point (King's Lynn 2002) had an exceptionally large leverage. Removal of this outlier resulted in a significant linear relationship with MGW ($P = 0.023$), but without affecting the acceptance or rejection of the null hypothesis for any other relationship. On these grounds this site has been removed from all the analyses presented in Tables 3.11 and 3.12.

Of the other variables tested, the only one that explained a significant amount of variation in MGW was the pre-anthesis mean air temperature.

In order to determine whether a combination of variables could explain more of the variation in MGW than a single variable, a step-down multiple regression procedure was used. Two basic starting models were constructed. One was based on measurements of crop size at GS59 plus pre and post anthesis weather variables. The other was based on measurements of pre and early post anthesis assimilation (or its components PAR interception and RUE) expressed per unit grain number, ear weight at GS59 also expressed per unit grain number, the shoot number per plant, and pre and post anthesis weather variables. Measurements of crop size at GS59 in combination with weather variables could not explain a significant amount of the variation in MGW. In contrast, the model incorporating measurements of assimilation plus weather variables did explain a large amount of the variation (r^2 0.72, $P = 0.013$). Four variables were found to have a significant effect on MGW. Three were negatively related; the number of ear bearing shoots per plant, the mean temperature between GS39 and GS59 and the mean daily rainfall between GS59 and GS71. The other two were positively related; radiation interception per grain between GS59 and GS71 and the maximum RUE post-anthesis (Table 12).

Further analysis has shown that there is a very strong relationship between the amount of radiation intercepted per grain between GS59 and GS71 and the incident radiation over the same period (Fig. 3.11 $r^2 = 0.961$). This implies that differences in canopy size accounted for very little of the variation in radiation interception over this period. In turn, differences in daily incident radiation and the duration of GS59 to GS71 each accounted for about half the variation in total incident radiation per grain over this period (data not shown).

Table 3.12. Multiple regression of crop and weather variables on MGW for 16 site/years. Starting model included the following explanatory variables Sht +T_{mean1} + PAR_1 + RUE_1 + R_1 + DW_{ear} + WSC_{gr} + PAR_2 + RUE_2 + T_{mean2} +R_2. See Table 11 for definition of variables.

Variate	Estimate	SE	P
Constant	51.4	10.0	<0.001
Sht	-6.35	2.59	0.034
T_{mean1}	-2.613	0.895	0.015
PAR_2	2.783	0.709	0.003
RUE_2	7.30	2.47	0.014
R_2	-2.81	1.05	0.024
Regression P = 0.013, r^2 0.72, residual df 10			

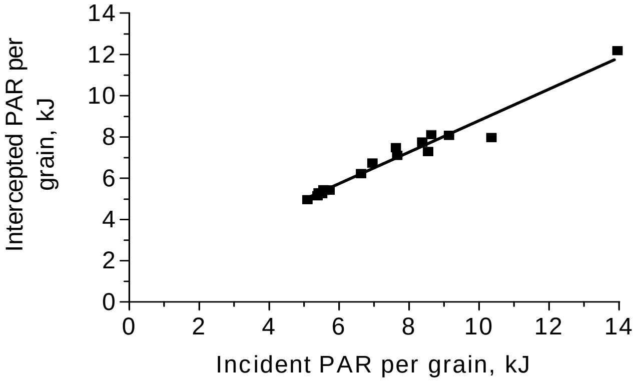


Fig. 3.11. Relationship between incident radiation and intercepted radiation over the period GS59 – 71, expressed per unit grain number. Line fitted by linear regression, y = 0.76 x + 1.15, r^2 = 0.961, P<0.001

Discussion

Post anthesis radiation capture and RUE

Most studies of RUE have confined themselves to the pre-anthesis, or early post-anthesis period before significant canopy senescence occurs (Goyne *et al.,* 1993; Gregory *et al.,* 1992). This is largely because of difficulties encountered in measuring radiation interception by the crop during the period of canopy senescence. Direct measurements of radiation interception by the whole canopy provide little useful information on the amount of radiation that can be effectively utilised, because they include radiation intercepted by dead and dying leaf tissue. In the current work we have avoided the problem by estimating the amount of interception from measurements of GAI and measured values of Kpar before canopy senescence. It has been assumed that Kpar does not change as the canopy senesces. This seems to be a reasonable simplifying assumption because when Kpar was adjusted for potential changes in the orientation of green tissue, it had only a small effect on the estimates of PAR interception and RUE (Fig. 3.6). The adjustment itself was based on the assumption that the ear remains vertical throughout grain filling, which is clearly not the case because the peduncle bends as the ear increases in weight. As such, the adjusted Kpar represents the extreme with regard to the potential vertical orientation of green tissue. Thus the true Kpar is likely to lie somewhere between that measured at full canopy size (near GS59) and the adjusted value. Since radiation interception and RUE were relatively insensitive to the adjustments in Kpar, a constant Kpar was used in all subsequent analyses of the canopy.

Plots of PAR interception against net dry matter gain showed distinct differences between sites and between years (Fig. 3.5 and Table 3.4). For some sites the relationship was significantly non-linear ($P<0.05$ for the quadratic term in a fitted second order polynomial). For others there was a trend towards non-linearity ($0.10>P>0.05$), whilst for a further group the relationship was linear ($P>0.10$). Non-linearity implies that green tissue continued to intercept radiation towards the end of grain filling, but that the crop accumulated less dry matter per unit of intercepted radiation than it did earlier. In other words, the RUE appeared to decline towards the end of grain filling. RUE is a coefficient that expresses the net outcome of a range of physiological processes, and thus several factors could be responsible for the apparent decline. Shedding and incomplete recovery of leaf tissue would result in an underestimate of the true biomass relative to radiation capture. An increase in respiration relative to photosynthetic activity as the canopy senesces could lead to a reduction in RUE. A reduction in photosynthesis itself might occur via an inherent decline in photosynthetic efficiency with leaf age, or possibly through some form of feedback control on photosynthetic activity or the capacity of photosynthetic machinery by a limited sink demand. Whatever the mechanism, it is evident that its expression differs between sites and years.

The degree of curvature in plots of RUE_{total} was inversely related to that in plots of RUE_{ear} (Fig. 3.8). This implies that the decline in RUE_{total} is influencing the size of the dry matter (photoassimilate) pool accessed by the ear for grain filling. Since necrotic leaf lamina tissue contains little in the way of accessible soluble carbohydrate, shedding and incomplete recovery of leaf tissue would affect RUE_{total} without significantly influencing RUE_{ear} and is therefore an unlikely explanation for the non-linearity of RUE_{total} observed in these experiments.

Re-analysis of data for spring barley has revealed similar non-linearity in plots of RUE_{total} ($P = 0.028$) (Biscoe *et al.,* 1975a). From measurements of canopy gas exchange, Biscoe *et al.,* (1975a) demonstrated how the decline in RUE after ear emergence was associated with a decrease in gross photosynthetic activity and an increase in canopy respiration. Late season stresses such as water stress and high temperatures can increase respiration and reduce photosynthesis and RUE (Hay and Walker, 1989; Goyne *et al.,* 1993). However, in the present study no significant correlation was found between temperature and rainfall and the degree of non-linearity of the RUE_{total} plots.

The biomass and GAI of the canopy at ear emergence was positively related to the degree of non-linearity, which is consistent with the view that differences in crop respiration associated with variation in standing crop biomass contribute to the variation in RUE_{total} between sites and years. However, the relationship was weak and only accounted for a relatively small amount of the total variation in the extent of RUE_{total} non-linearity (Fig. 3.10).

At the level of the individual leaf, rates of net photosynthesis decline with leaf age as a result of reductions in both the rate of photosynthetic activity per unit of green area and the area of green tissue, but the relationship can be complex. Data for field crops of barley suggest that during the early stages of leaf senescence the rate of photosynthesis may decrease more rapidly than green area, but during the later stages green area may be lost more rapidly (Biscoe *et al.,* 1975b). Since, in the present study, interception of radiation is estimated on the basis of GAI, it is only the reduction in photosynthetic activity per unit of GAI (rather than the loss of GAI itself) that can potentially contribute to the decline in RUE observed here. When time or thermal time between the date of flag leaf emergence and the end of grain filling was used as an indicator of canopy age, no significant relationship was found with the extent of non-linearity in RUE. This implies that the variation in non-linearity between sites and years is not the result of differences in leaf age. Indeed, reductions in photosynthetic capacity are not an inevitable consequence of ageing until late in the lifespan of a leaf. For example, in the flag leaf of rice high rates of light saturated photosynthesis were sustained until grain filling was nearly complete, even though reductions in Rubisco content and chlorophyll a/b ratio occurred much earlier (Murchie *et al.,* 2002). A high initial leaf Rubisco content allowed N to be mobilised and translocated to the grain without impairing photosynthetic activity (Murchie *et al.,* 2002).

There was appreciable variation in specific leaf N at ear emergence amongst our barley crops and a significant negative relationship with the extent of non-linearity in RUE_{total}. This is consistent with possible mobilisation of N for the grain in crops with low SLN reducing photosynthetic capacity and hence RUE_{total}. However, as with biomass and GAI, SLN accounted for only a relatively small amount of the total variation in RUE non-linearity ($r^2 = 0.29$). In contrast, the source:sink ratio of the crop at ear emergence (expressed as the green area of the crop per unit grain number) explained a much greater proportion of the variation ($r^2 = 0.63$). Crops with a large source:sink ratio had a greater degree of curvature in plots of RUE_{total}, than those with a smaller ratio. Moreover, when SLN was introduced as an explanatory variable in a multiple regression model along with the source:sink ratio, no additional variation in the RUE_{total} quadratic term was accounted for (P for SLN = 0.99). On the basis of these results we conclude that the major factor causing the decline in RUE_{total} towards the end of grain filling at some sites and in some years was a large source:sink ratio. SLN itself was strongly related to the source:sink ratio ($P = 0.001$, $r^2 = 0.53$), such that crops with high SLN had a small green area per grain (data not shown). Thus SLN appears to be indirectly related to the pattern of RUE through its association with the source:sink ratio.

Our data provide no information on the possible mechanism linking source:sink ratio with RUE. Feedback inhibition of photosynthesis by reduced sink demand, associated with an increase in leaf non-structural carbohydrate concentrations, has been reported for younger plants (Azcón-Bieto 1983, Hay and Walker 1989). As the canopy begins to senesce, the situation becomes more complex as the source:sink ratio can influence the supply-demand relationship for N as well as carbohydrate (Martinez-Carrasco *et al.,* 1993; Borrell *et al.,* 2001). Premature leaf senescence can be promoted by high as well low source:sink ratios during grain filling of some crops (Tollenaar and Daynard 1982; Rajcan and Tollenaar, 1999), although effects of modifying the ratio on senescence are not always found (Dreccer *et al.,* 1997). Early senescence (as indicated by visible loss of chlorophyll) cannot explain the decline in RUE_{total} observed at some sites in the present study because radiation interception was estimated on the basis of green area. If there was a premature senescence–related reduction in the integrity of the photosynthetic apparatus that preceded the loss of chlorophyll, a decline in RUE might be observed, as dry matter production would be restricted before radiation interception.

Potential assimilate supply for grain filling

Horie *et al.,* (1997) estimated the potential assimilate supply for grain filling in rice from the pre-anthesis storage reserves plus the total post anthesis net assimilation. The latter is given by the gain in total above ground dry weight from anthesis to the end of grain filling. An assumption of the above technique is that total dry matter gain is a reflection of the potential assimilation post anthesis, but by ignoring possible feedback inhibition of RUE by a limited sink capacity, it may underestimate the true potential. Since the evidence presented above suggests that there may be some form of sink limitation of RUE towards the end of grain filling in some crops, a better estimate of the potential assimilate supply in barley is given by the product of the maximum RUE and intercepted radiation plus storage reserves at ear emergence. When estimated in this way, potential assimilate supply exceeded grain yield in all site/years except Sutton Bonington in 2004, where it was approximately equal to the yield. These results suggest that grain filling was nearly always sink limited. However, the apparent source-sink balance differed between site/years. Thus in 2003, the potential supply appeared to more closely match the yield than in 2002 (with the exception of Edinburgh), which corresponds with less marked sink limitation in 2003 as shown by fewer sites with significantly ($P< 0.10$) non-linear RUE_{total}. It is interesting to note, however, that large differences between potential supply and yield were not just associated with non-linear RUE_{total}. A large difference was found at High Mowthorpe in 2002, even though the plot of RUE_{total} was linear.

Ear manipulation treatments were imposed to provide an independent assessment of possible source limitation of grain filling. They were imposed after the start of rapid grain filling in order to minimise the effects of a change in photosynthate supply per grain on endosperm development and potential grain size. However, the results were inconclusive. At some sites reducing the number of grains increased the weight of the remaining ones, at but at other sites there was no change or even a decrease. Ear manipulation treatments have been used extensively to modify the source:sink ratio of crops (Martines-Carrasco and Thorne, 1979; Ma *et al.,* 1990; Miralles and Slafer, 1995; Dreccer *et al.,* 1997; Voltas *et al.,* 1997), but their interpretation is not straightforward (Jenner, 1980). Supporting measurements of the amount of soluble carbohydrates in the remaining ear are seldom made, but some have shown a decrease in the grain endosperm after ear reduction even though grain weight increased, suggesting that some factor other than sugar supply was responsible (Jenner, 1980). Further, removing ears from the mainstem after anthesis can promote growth and carbon import by tillers (Bonnett and Incoll 1993), indicating that shoots are not independent of each other even after flowering. Thus when treatments are imposed on single stems, alternative sinks may utilise the additional assimilate assumed to be made available to the grain. In view of fact that grain weight was reduced as well as increased by ear manipulation in our experiments, there are serious doubts about the reliability of these treatments or the sampling strategy adopted.

Realisation of mean grain weight

Mean grain weight is often considered the most stable of the barley yield components (Gallagher *et al.,* 1975), but significant genotypic and environmental variation can occur, especially in environments where post anthesis drought and high temperatures are common (Voltas *et al.,* 1997, 1998). Appreciable variation in MGW was also found between crops grown under comparable husbandry regimes in the present study. Although it was only weakly related to yield, it is important to understand the cause(s) of this variation since MGW is an important component of grain quality.

The variation in MGW between site/years resulted from differences in the mean rate and not the duration of grain filling (Fig. 3.3). Differences in rate could not be explained by differences in temperature between sites during the grain filling period, because they remained when the rate was expressed on a thermal time basis. Nor was the final grain weight determined by potential assimilate supply when considered over the entire grain filling period. The above evidence suggests that potential supply was ample for grain filling in almost all site/years. Thus grain filling appeared to be limited by some property of the grain itself (sink limitation). This conclusion is supported by the lack of association between MGW and canopy size, the number of grains m^{-2}, and the green area per unit grain number (Fig. 3.10).

Control of potential grain size is poorly understood. Final weight is, in part, genetically determined and related to carpel weight at anthesis (Scott *et al.,* 1983; Calderini *et al.,* 1999). It has also been associated with the number of endosperm cells (Brocklehurst 1977; Cochrane and Duffus 1983), which in turn may be related to photoassimilate availability during early grain development (Singh and Jenner 1984). Thus both pre and post anthesis conditions may influence potential grain size. Multiple regression analysis identified five factors as having a significant effect on MGW. There was a positive association between MGW and both PAR interception and RUE during the period preceding rapid grain filling, which is consistent with the view that endosperm development is sensitive to assimilate availability and may limit the eventual grain size. MGW was also negatively associated with the mean temperature during the period GS39 to GS59. During this period the ovary is developing and thus temperature may influence the size of the carpel achieved by anthesis. Association of MGW with cool temperatures during this period may relate to a greater growth potential resulting from slower carpel development. No association of MGW with ear weight per grain number at GS59 was found, but the latter is a crude measure derived from estimates of ear weight and grain number per m^2. It lacks the precision of measurements made on individual grains (Scott *et al.,* 1983) and thus probably has insufficient resolution to detect differences in initial grain (carpel) weight. Interestingly, the effect of cool temps could not be substituted for by measures of pre-anthesis assimilation, suggesting that the pre-anthesis developmental event that influenced potential grain size was not affected by assimilate availability during this period.

The negative association of MGW with the number of shoots per plant probably relates to the later development and lower grain growth potential of higher order tillers. MGW tends to be greater on mainstems and declines with increasing tiller hierarchy (Lee *et al.,* 1989; Naylor *et al.,* 1997). The hierarchy of grain size with position within and between ears is often maintained when treatments are imposed to modify assimilate supply during early grain development (Bremner and Rawson 1978; Voltas *et al.,* 1998). The negative association of MGW with mean daily rainfall during the early post-anthesis period is more difficulty to explain mechanistically. It does not appear to arise through a simple correlation of dry weather with greater incident PAR (data not shown). The variation in temperature after ear emergence had no effect on MGW, in contrast to Mediterranean environments, where high temperatures can result in a reduction in MGW mostly through a reduction in the duration of grain filling (Voltas *et al.,* 1998).

Conclusions and implications

The results of this study suggest that the MGW of winter barley (*cv* Pearl) grown in the UK under standard agronomic conditions is determined, in part, by photoassimilate supply per grain number during the period of early grain development. However, additional pre- and post-anthesis factors are also involved in determining MGW, and thus our original hypothesis concerning the role of assimilate supply (see Introduction) is only partially supported. When the whole of the grain filling period is considered, the potential supply of assimilate appeared to exceed the demand of the grain, and the extent of this source-sink imbalance differed widely between specific site and year combinations. We conclude, therefore, that in most crops grain filling appeared to be sink limited, but the extent of the sink limitation varied. Moreover, the capacity of the sink itself (i.e. potential grain size) was partly determined by the source. This is consistent with the concept of shared control of barley grain growth by source and sink as proposed for other species. In rice, the final grain weight appeared to be related to the amount of non-structural carbohydrates during the period of endosperm development, but later, assimilate availability exceeded demand and a re-accumulation of soluble reserves was observed in the culm and leaf sheaths (Tsukaguchi *et al.,* 1996). No net re accumulation of reserves was observed in the current work, but we did find evidence of a possible sink-related feedback inhibition of RUE suggesting that in crops where alternative sinks are not available, or where their capacity is exceeded, regulation of RUE occurs.

Can the MGW be predicted and managed? The answer lies in whether it is possible to predict and manage potential grain size. Net dry matter assimilation during early grain development was a function of the amount of radiation intercepted and the RUE. Differences between crops in the amount of radiation intercepted over that period were almost entirely the result of differences in incident radiation, rather than canopy size. In turn the total amount of radiation received was dependent largely on the duration of the slow phase of grain growth. At present little is known about what controls the duration of this phase of grain growth. Thus it would be difficult to predict the variation in MGW between sites. Nevertheless, we would anticipate that at a given site, agronomic treatments that alter PAR interception per grain or the duration of the slow phase would also modify MGW. This mechanism could explain observations of greater MGW at low plant populations in barley if decreasing densities reduce grain numbers m^{-2} more than PAR interception, or increase the length of the period between GS59 and the start of rapid grain growth. There is some scope to influence MGW through crop management by ensuring a high proportion of mainstems in the ear population (e.g. Naylor *et al.,* 1997), but its impact is likely to be limited.

In our crops grain filling always appeared to be sink limited, although the extent to which potential assimilate supply exceeded yield differed. This suggests that the yield of some crops may be more vulnerable to any post-anthesis leaf loss (and hence assimilatory capacity) than others. This hypothesis is being investigated as part of an ongoing Defra LINK project (LK 0961) Targeting disease management in barley.

APPENDIX 4: NITROGEN UPTAKE – CHARACTERISTICS OF THE CURRENT UK WINTER BARLEY CROP

Introduction

Nitrogen (N) uptake affects all aspects of growth in barley, and influences both grain yield and quality. It is measured as the product of crop dry weight and the N concentration. Nitrogen assimilation and its rate of uptake in barley is affected by soil N concentrations, light, pH, temperature, the concentration of other ions (Glass *et al.,* 1990) and genotype (Bloom and Finazzo, 1986).

Previously studies on winter malting barley and spring barley have shown total N uptake per plant to increase until about anthesis, then decline slightly, then increase during grain filling (Corke *et al.,* 1989; Carreck and Christian, 1991).

From sowing through to harvest, the barley crop passes through a series of developmental phases. Each phase can be influenced by N and, in wheat, each phase is known to have a particular significance for yield formation (Sylvester-Bradley *et al.,* 1998). In the same way, each phase in barley is believed to impact on different aspects of yield formation.

In wheat recent approaches have considered crop requirement for N in each phase, based on the requirements for tillering and tiller survival, the formation and maintenance of the green canopy, and the N required post anthesis for canopy duration and grain protein formation (Sylvester-Bradley *et al.,* 1990). Based on leaf N concentrations, it has been estimated that, on average, 30 kg ha^{-1} of crop N uptake is required for each unit of green area index (GAI, the ratio of leaf area to ground area), and for optimum light interception the crop requires approximately 6 units of GAI.

Yield

For barley, canopy management is less well understood than for wheat. In some parts of the UK, autumn N is still favoured by growers of barley. If not required by the crop, this negatively affects the economic performance and environmental impact of the crop.

To develop a clearer understanding of canopy management in barley and a broader understanding of the requirements of winter barley crops, it is necessary to determine the crop N uptake required to form each unit of GAI, and the percentage of N recovery that can be expected from applied fertiliser.

Quality

Grain N in barley, a key parameter for the end user in crops grown for malting, is known to be provided by N uptake and assimilation post-anthesis and retranslocation of previously accumulated vegetative N (Bulman and Smith, 1994). Precisely when and how this occurs may impact on yield by having a direct effect on post anthesis green area duration. It may also assist in predicting the benefits (or otherwise) to yield and quality, of crop protection strategies for prolonging canopy survival.

Previous studies have shown that increases in N supply have been associated with increasing grain protein concentrations. In the past, end user requirements for low grain N content have prevented growers from applying sufficient N to meet crop requirements for maximum yield. Recent improvements in yield through breeding, and an increase in the permitted grain N concentrations for malting barley, have allowed growers to use higher N applications to achieve higher yields. As a result of these changes, total crop N requirements for winter malting barley and feed barley may now be similar.

To investigate the patterns and variation in N uptake and utilisation in barley, N applications in this research were made to optimise yield, rather than to target specific grain N parameters. It was considered that a more detailed knowledge of N requirements for yield in each developmental phase would prove useful in developing the most appropriate N strategies to optimise both yield and grain N concentrations.

This Appendix aims to describe the efficiency of N uptake by barley on 18 site/seasons across the UK, and provide benchmarks for the pattern of N uptake through key growth stages. This information can then be used to improve understanding of N requirements to manage canopy size, biomass, yield and quality.

Materials and Methods

Standard crops of winter barley were grown at six sites across the UK in each of three seasons (2001/02, 2002/03 and 2003/04). Crops were grown to a standard protocol designed to broadly reflect current standard farm practice. Crops were sown between 15 September and 9 October, with a target plant population of 250 to 300 plants m^{-2}. Robust crop protection strategies were designed to fully control all pests, weeds and diseases. The six sites were chosen to represent the major barley growing areas in the UK.

Soil mineral N analysis

In February of each season, two soil cores were taken for each replicate at 0cm to 30cm, 30cm to 60cm and 60cm to 90cm horizons for soil mineral nitrogen (SMN) analysis (as detailed in Appendix 1).

SMN test data were combined with the total crop N offtake information to determine the soil nitrogen supply. This showed wide variation between sites and seasons (Table 4.1).

Table 4.1. SMN, plant N in February, soil nitrogen supply and N applied for each of the 6 sites and seasons (kg ha^{-1}). Asterisk denotes missing data.

Site	YEAR	SMN 0-90cm	Plant N in Feb.	Soil N supply	N applied
Aberdeen	2002	42.8	14.0	56.8	180
	2003	133.0	13.5	146.5	168
	2004	*	28.6	*	120
Edinburgh	2002	55.0	14.3	69.3	180
	2003	256.0	13.4	269.4	*
	2004	*	58.4	*	*
High Mowthorpe	2002	41.6	11.5	53.1	200
	2003	196.2	15.5	211.6	17
	2004	151.6	29.1	180.7	135
King's Lynn	2002	35.3	12.6	47.9	154
	2003	50.2	8.7	58.9	181
	2004	37.6	11.9	49.5	127
Rosemaund	2002	69.8	75.4	145.2	89
	2003	121.0	30.4	151.4	110
	2004	107.0	34.0	141.0	77
Sutton Bonington	2002	64.5	18.7	83.2	150
	2003	48.8	9.2	58.0	172
	2004	94.4	39.6	134.0	157

Nitrogen and sulphur fertilisers

Nitrogen was applied as ammonium sulphate (21% N, 60% SO_3) at the start of rapid spring growth but before GS 30, and as ammonium nitrate at GS31/32, as for a typical feed barley crop. SMN analysis in February and soil nitrogen supply (SNS) index were used to determine the amount of N to be applied using 'Fertiliser Recommendations RB209' (Anon 2000, 7th edition)

Growth analysis and N sampling

Growth analysis measurements were carried out at monthly intervals, from approximately four weeks after emergence until early in March; at fortnightly intervals, from mid-March to late-April; and at weekly intervals, from early in May to physiological maturity. Nitrogen analyses of leaves, stems and ears (as appropriate), were done on alternate sampling times (Appendix 1).

Combine harvesting

At final harvest, plots were combine harvested and grain yield expressed at 85% dry matter. A grain sample was taken for screenings and specific weight, thousand grain weight, moisture content analysis and grain N%.

Meteorological records

Meteorological data including daily rainfall; daily maximum, minimum and mean air temperatures; total incident solar radiation (from a Kipp solarimeter), soil temperature at 10cm depth, and minimum grass temperature, were recorded at each site.

Results

Weather

Temperature and rainfall differences were evident between sites and seasons. The three northern sites, (Aberdeen, Edinburgh and High Mowthorpe), were on average 1.1ºC cooler over the whole growing season (September to June) than the southern sites (Sutton Bonington, Rosemaund and King's Lynn). Of the northern sites, Edinburgh was 0.6ºC warmer than both High Mowthorpe and Aberdeen. Of the southern sites, Sutton Bonington was the coolest, averaging 0.3ºC less than Rosemaund, which in turn averaged 0.3ºC less than King's Lynn (Tables 4.2 and 4.3).

In Autumn 2001 all sites had above average rainfall in October: Rosemaund and Edinburgh received double, and King's Lynn triple their 30 year means. Despite all sites having a colder than average December, mean temperatures in October, January, February and March were consistently above average at all sites. April was between 0.1- 1.0ºC colder than average at all sites and also drier. With the exception of the two Scottish sites, June was hotter and drier than average, with sites receiving between 53% and 73% of their average rainfall. Temperatures in June were highest in the east averaging 16ºC, at King's Lynn, 1.9ºC above the seasonal average (Tables 4.2 and 4.3).

A dry September in 2002, especially in southern sites, was followed by a warm, wet autumn with all sites having both rainfall and temperatures above the seasonal average in November and December. With the exception of the two Scottish sites, rainfall values in February, March, and April were 61%, 40%, and 68% of the seasonal averages respectively. Rainfall in May 2003 was close to the seasonal average and all sites, with the exception of Aberdeen, had above average June rainfall (Tables 4.2 and 4.3).

A warm dry September in 2003 was followed by a cool October. However, in a similar pattern to that seen in the previous season, temperatures post December were consistently above the seasonal average at all sites. Most sites had average levels of winter rainfall with the exception of King's Lynn, which had close to double (191%) average rainfall between October and February. In addition, all sites had above average rainfall in April (Tables 4.2 and 4.3).

Table 4.2. Meteorological data for Aberdeen, Edinburgh and High Mowthorpe in 2001, 2002, and 2003

.	Average monthly temperature (^{o}C)				Monthly rainfall (mm)			
	2001/02	2002/03	2003/04	1961-1990	2001/02	2002/03	2003/04	1961-1990
Aberdeen								
Sep	11.6	-	12.7	11.4	84.0	-	26.4	71
Oct	11.5	8.0	8.3	8.9	116.8	214.7	50.6	80
Nov	6.1	7.6	6.9	5.1	48.0	185.9	45.7	74
Dec	3.2	5.4	4.0	3.6	73.9	113.6	92.8	71
Jan	4.3	4.2	4.1	2.8	52.0	94.2	68.4	80
Feb	4.4	3.6	4.2	2.9	65.2	17.1	38.4	51
Mar	5.8	6.4	5.6	4.4	33.8	16.6	42.8	57
Apr	7.6	8.1	8.6	6.1	26.8	64.0	102.8	54
May	10.6	10.8	10.8	8.7	54.0	75.8	77.4	62
Jun	13.1	14.4	13.7	11.7	107.2	16.2	85.8	56
Edinburgh								
	2001/02	2002/03	2003/04	1961-1990	2001/02	2002/03	2003/04	1961-1990
Sep	-	-	13.6	12.6	-	-	48.2	66
Oct	12.5	7.9	8.1	9.8	127.0	58.8	49.0	63
Nov	7.4	7.1	8.0	5.8	74.6	111.6	28.6	56
Dec	3.3	4.6	4.4	4.3	61.8	52.9	62.2	52
Jan	5.3	3.8	4.7	3.7	82.0	71.8	93.4	54
Feb	5.5	3.5	4.7	3.7	100.6	26.4	44.6	40
Mar	7.1	7.0	6.2	5.5	67.3	19.0	31.0	47
Apr	8.6	9.2	9.0	7.3	28.0	48.6	64.8	39
May	11.4	11.6	11.5	10.2	57.6	51.0	36.7	49
Jun	13.1	14.3	13.9	13.2	69.0	36.4	102.8	50
High Mowthorpe								
	2001/02	2002/03	2003/04	1961-1990	2001/02	2002/03	2003/04	1961-1990
Sep	12.2	12.2	13.4	12.6	109.5	38.5	38.7	62
Oct	12.0	12.0	7.6	9.5	72.0	97.5	44.5	64
Nov	6.1	6.7	6.8	5.2	61.0	131.2	65.5	72
Dec	2.7	4.2	3.8	3.2	42.6	99.1	61.2	72
Jan	4.1	3.4	3.5	2.4	50.5	89.2	207.5	68
Feb	5.2	2.5	4.1	2.4	87.3	24.2	52.0	50
Mar	5.9	6.2	4.9	4.2	29.9	12.7	35.6	60
Apr	7.8	7.6	8.3	6.3	33.7	41.9	127.0	52
May	10.5	10.7	10.5	9.4	66.2	75.5	27.8	58
Jun	13.1	14.2	13.7	12.5	41.2	112.0	77.4	56

Table 4.3. Meteorological data for King’s Lynn, Rosemaund and Sutton Bonington, in 2001, 2002, and 2003.

	Average monthly temperature (^{o}C)				Monthly rainfall (mm)			
	2001/02	2002/03	2003/04	1961-1990	2001/02	2002/03	2003/04	1961-1990
King’s Lynn								
	2001/02	2002/03	2003/04	1961-1990	2001/02	2002/03	2003/04	1961-1990
Sep	-	14.9	14.5	14.0	-	26.2	19.4	47.8
Oct	13.3	10.4	8.7	10.8	163.5	109.2	78.2	46.1
Nov	7.4	8.1	7.6	6.4	86.8	116.0	86.4	58.7
Dec	2.9	5.6	4.1	4.4	43.2	111.6	75.2	50.4
Jan	5.2	4.3	4.4	3.5	68.2	79.8	168.6	50.7
Feb	6.7	4.7	4.9	3.5	66.4	34.4	60.0	35.2
Mar	7.6	8.0	6.1	5.7	33.0	24.2	47.0	46.5
Apr	9.5	10.9	9.6	7.8	41.6	26.8	75.5	41.8
May	12.6	14.4	12.4	11.2	40.5	62.0	39.8	49.7
Jun	16.0	18.1	16.7	14.2	38.1	113.8	89.0	52.7
Rosemaund								
	2001/02	2002/03	2003/04	1961-1990	2001/02	2002/03	2003/04	1961-1990
Sep	13.5	14.9	14.5	13.3	24.4	26.2	7.4	58
Oct	13.1	10.4	9.0	9.9	126.2	109.2	50.6	67
Nov	7.3	8.1	8.2	6.6	42.2	133.2	63.8	58
Dec	3.2	5.7	5.1	4.5	50.2	70.8	65.2	70
Jan	5.3	4.7	5.3	4.0	58.2	43.8	88.6	65
Feb	7.1	4.0	5.3	4.1	100.1	29.4	30.0	52
Mar	7.7	7.4	6.6	6.2	27.7	24.4	33.4	47
Apr	8.9	9.6	9.4	7.9	37.6	43.0	96.8	48
May	11.6	11.9	12.4	11.1	89.8	31.4	46.2	48
Jun	13.9	15.5	15.5	13.9	27.0	58.0	48.4	51
Sutton Bonington								
Sep	13.1	14.1	14.1	13.4	63.0	37.2	26.1	57
Oct	13.1	9.4	8.6	10.3	67.8	114.4	38.0	59
Nov	7.1	8.3	7.8	6.0	33.2	88.4	45.8	63
Dec	3.0	5.3	4.1	4.1	25.2	93.6	67.4	68
Jan	5.4	4.4	5.4	3.3	51.0	48.8	67.4	62
Feb	6.7	3.7	5.4	3.3	64.4	22.4	33.8	53
Mar	7.2	7.0	6.1	5.3	29.2	19.4	29.8	57
Apr	8.8	9.4	9.4	7.6	38.6	19.8	84.8	53
May	11.8	12.2	11.9	11.0	56.4	78.2	41.6	56
Jun	14.4	15.8	15.2	14.1	32.8	69.8	53.8	60

Pattern of N uptake

An underlying pattern of N uptake was present, despite considerable variation between sites and seasons. Through the late autumn and winter, N uptake was generally slow. Rates of uptake increased in March/April as warmer conditions stimulated canopy expansion through more rapid leaf emergence and tillering. On average, between GS31 and GS39 in late April, N uptake was at its most rapid. Between GS39 and GS59 N uptake slowed, and N uptake was generally low after GS59 (Fig. 4.1).

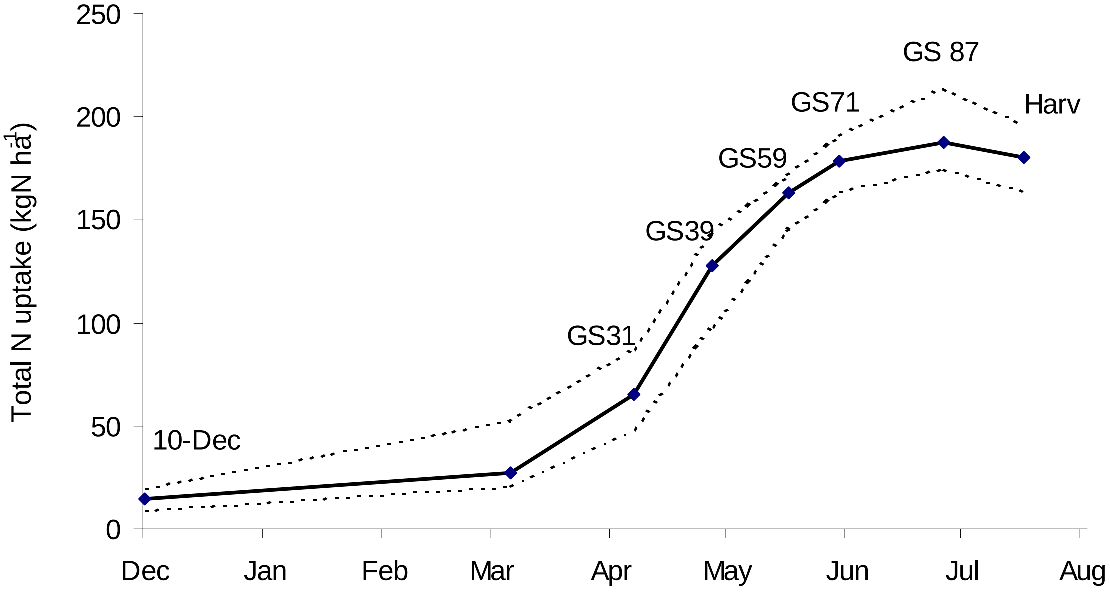


Fig. 4.1: Average pattern of N uptake, across all sites and seasons, dotted lines represent the interquartile range.

Green area index and N uptake

There was a close relationship at all sites between green area index and N uptake. Overall, the median amount of N uptake for each unit of green area was 27.6 kgN ha^{-1}, with a range between 20.1 and 40.3 kgN ha^{-1} (Table 4.4).

Table 4.4: Nitrogen uptake for each unit of green area index (kgN ha^{-1} GAI^{-1}), for all sites and seasons.

Sites	2002	2003	2004	2002-2004
Aberdeen	25.0	27.5	32.1	28.2
Edinburgh	25.5	27.5	26.5	26.5
H. Mowthorpe	29.9	22.9	23.7	25.5
King's Lynn	32.4	42.4	23.1	32.6
Rosemaund	20.1	20.7	22.6	21.2
S. Bonington	25.8	40.3	28.7	31.6
Mean	26.5	30.2	26.1	27.6

The relationship between N uptake and GAI varied as the season progressed, due to different N requirements of the canopy components (leaves, stems and ears) for N per unit of GAI. In addition within each component the amount of N uptake varied with time. N uptake at all stages of crop growth depends on temperature, water availability and rate of crop growth.

Crop N uptake over winter

Between sowing (late September/early October) and mid February, N uptake by most of the reference crops was between 10kg and 40 kgN ha^{-1}. However at Rosemaund in 2002 and at Edinburgh in 2004, a combination of early sowing and favourable autumn conditions allowed strong late autumn growth, with crops taking up 75 and 58 kgN ha^{-1} respectively. At Rosemaund in 2002 this represented a 531% higher February N uptake compared to the average of the other sites that year, and was associated with larger canopy size and biomass (508% and 620% higher respectively). At Edinburgh in 2004, crop N offtake of 58 kgN ha^{-1} was 204% higher than the average N offtake by other sites in February. This higher N uptake was also matched by an equivalently larger canopy size (206%) and biomass (184%). At both these sites these higher N uptakes were also associated with higher fertile shoot numbers, although the proportional increases compared to the average of the other sites were less (145% for Rosemaund and 185% for Edinburgh).

A clear linear relationship ($R^2 = 0.97$) between N uptake from October to February and green area index in February was evident, indicating that on average, at this time, 25.1 kgN ha^{-1} is required to form each unit of green area index (Fig. 4.2).

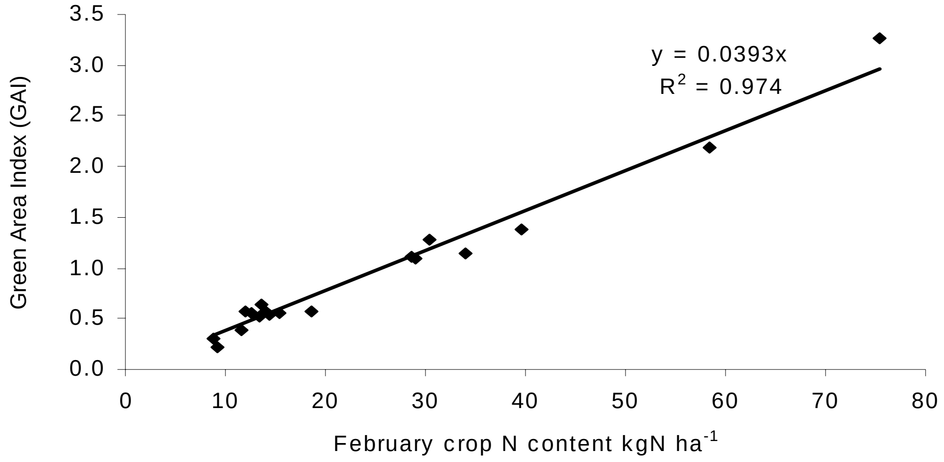


Fig. 4.2: Relationship between canopy size (GAI) in February and crop N content in February for all sites and seasons.

N content per unit of green area was significantly and inversely related to GAI (P=0.045) (Fig. 4.3). February N uptake per unit of GAI ranged from 20.1 kgN ha^{-1} at Rosemaund in 2002 where warm conditions favoured good autumn and winter growth, to 42.4 kgN ha^{-1} at King's Lynn in 2003, a site adversely affected by high winter rainfall.

By early February 2002, the Rosemaund crop had the largest canopy size of all site/seasons, with a GAI of 3.2. Here the rapid winter increases in green area were only partially matched by increased N uptake. By contrast, the crop at King's Lynn in February 2003 had one of the smallest canopy sizes, at a GAI of 0.3.

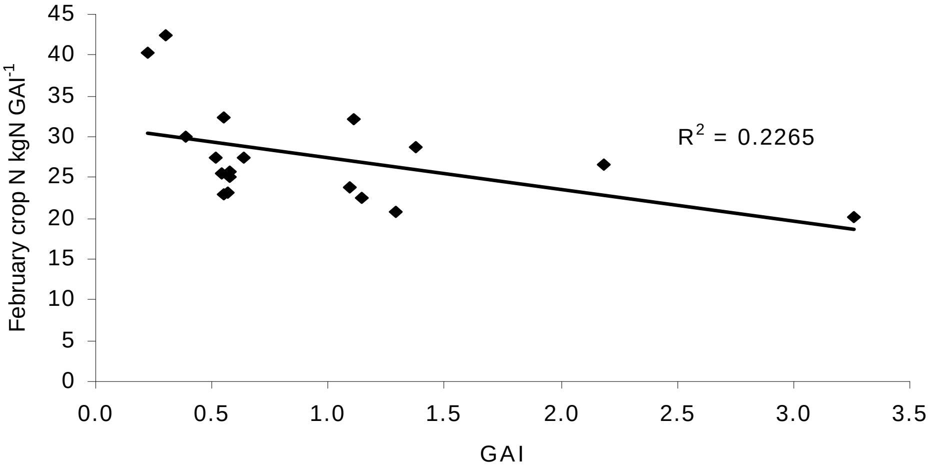


Fig. 4.3: Regression of canopy size (GAI) in February with crop N content per unit of GAI, for all sites and seasons.

There was also a significant positive correlation between N uptake and tillering (P<0.001) with differences in N uptake accounting for 66% of the variation in February shoot number. However where only 10 to 20 kgN ha^{-1} was taken up the crops were still able to produce over 800 shoots m^{-2} (Fig. 4.4).

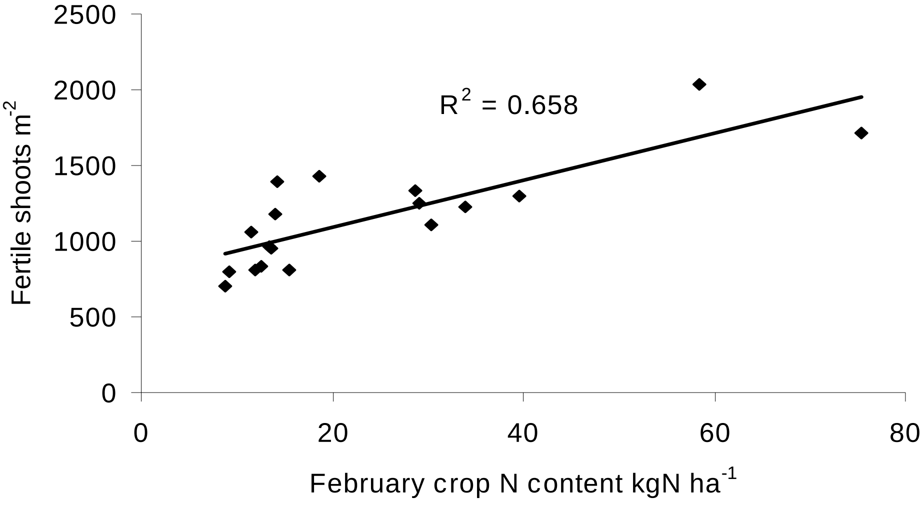


Fig. 4.4: Relationship between crop N content and shoot numbers in February.

Despite all of the sites having sufficient N uptake at this time to support an adequate shoot number, early N uptake was significantly correlated with yield: high crop N content in February, was associated with higher yields (P=0.002) (Fig. 4.5).

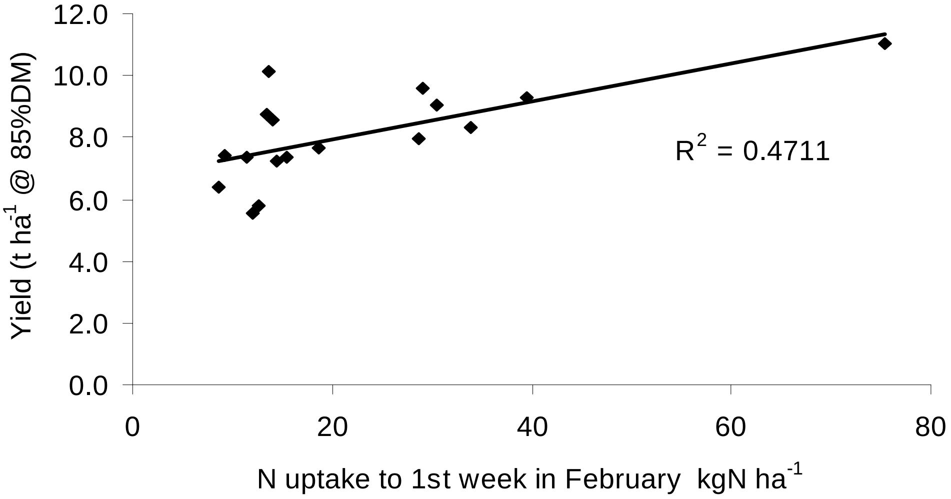


Fig. 4.5: Relationship between N uptake to the first week of February, and yield (t ha^{-1} @85% Dry Matter) at all sites and seasons.

Early February to GS31

Between early February and GS31 (mid April), both total crop N content (kgN ha^{-1}) and the rate of N uptake increased at nearly all sites. In this period the average rate of N uptake was 0.63 kgN ha^{-1} day^{-1}, with crops reaching 65 kgN ha^{-1} or 39% of total N uptake by GS31. It might have been expected that crops such as King's Lynn and Sutton Bonington in 2003, which showed slow winter growth, would compensate with strong early spring uptake, whereas high N uptake crops such as Rosemaund 2002 and Edinburgh 2004 might slow down as availability of N and demand from the plant reduced. Actually, responses appeared to be independent of earlier growth and N uptake. For example two crops characterised by high pre-February N uptake, Rosemaund in 2002, and Edinburgh in 2004, showed very different patterns of N uptake in this period. The crop at Rosemaund took up no additional N during this period, whilst the crop at Edinburgh continued to take up N at a rate close to the seasonal average.

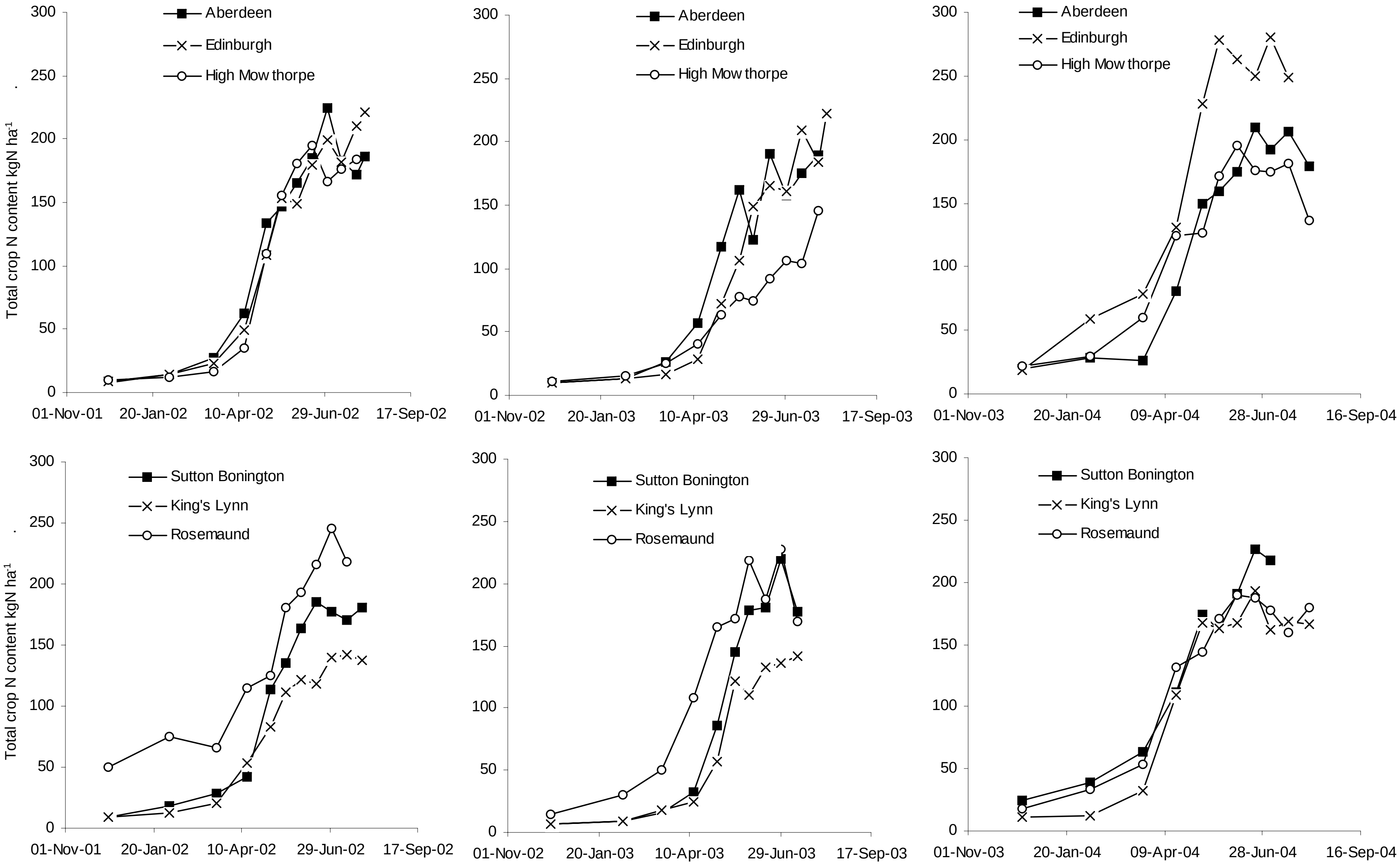
Other crops had low levels of N uptake overwinter, and equally low rates of N uptake between mid February and GS31: for example, the crop at King's Lynn in 2003 took up just 0.07 kgN ha^{-1} day^{-1} in this period. This followed a period of high winter rainfall, which may have restricted soil available N in spring, combined with low rainfall in February and March restricting uptake of spring-applied fertiliser N.

Low early N uptake was not necessarily indicative of low uptake between February and GS31. The crops at High Mowthorpe in 2004 and at Aberdeen in 2002, took up 84.1 and 72.3 kgN ha^{-1} respectively in this period, despite these crops having just 29.1 and 14.0 kgN ha^{-1} respectively in early February (Fig. 4.6).

Differences in N uptake were evident between seasons. Generally rates of N uptake were higher in this period in 2004 (1.03 kgN ha^{-1} day^{-1}) compared with the previous two seasons (0.55 and 0.3 kgN ha^{-1} day^{-1} for 2003 and 2002 respectively). Lower N uptake values in 2003 and, especially in 2002, coincided with spring drought conditions, which probably affected the availability fertiliser N.

At this time of rapid N uptake and canopy expansion, an increasing proportion of canopy N was partitioned away from the leaves in favour of the stems. Of the 65 kgN ha^{-1} taken up by GS31, on average 40 kgN ha^{-1} was in the leaves and 25 kgN ha^{-1} was in the stems plus leaf sheaths (hereafter referred to as stems). However, the leaves still accounted for 87% of the green area at this time, so had a much lower concentration of N per unit of green area (18.1 kgN ha^{-1} GAI^{-1}) compared to the stems (62.1 kgN ha^{-1} GAI^{-1}).

Fig. 4.6: Total N uptake for each site in 2002, 2003 and 2004 seasons.



Growth Stages 31 to 39

Between GS31 and GS39 (early May), N uptake was much more rapid at all sites, the rate of crop uptake increasing to an average of 3.14 kgN ha^{-1} day^{-1}, to achieve a total N uptake of 128 kgN ha^{-1} by GS39 (67% of the final crop N offtake).

Green area index was still closely linked to total crop N uptake with crop N uptake accounting for 75% of the variation in GAI (Fig. 4.7).

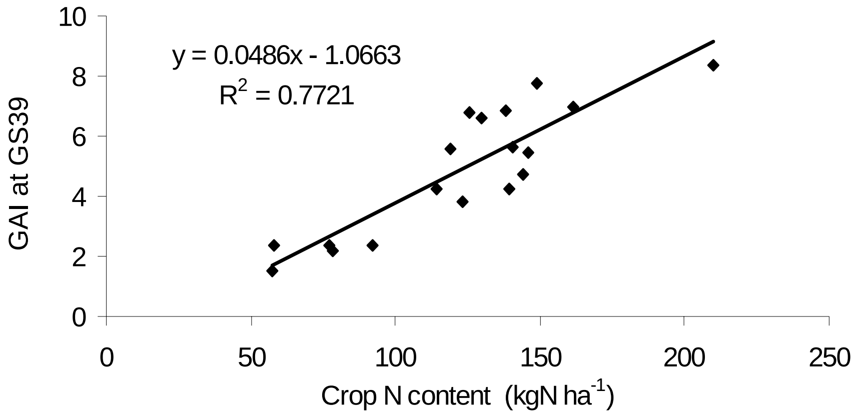


Fig. 4.7. Relationship between canopy size (GAI) and crop N content across all sites and seasons.

Low spring rainfall may also account for a proportion of the variation observed between sites and seasons. Such conditions were apparent at High Mowthorpe, Sutton Bonington and King's Lynn in 2003 and King's Lynn in 2002. For these crops, N offtake at GS39 as a % of the total N offtake was just 30.8%, 44.2%, 34.5%, and 35.6% respectively. In addition green area index was more restricted than uptake at these sites. As in February there was a clear inverse relationship between GAI and kgN GAI^{-1} at GS39, suggesting that the restrictions in N uptake were a symptom rather than cause of poorer growth under these conditions (Fig. 4.8).

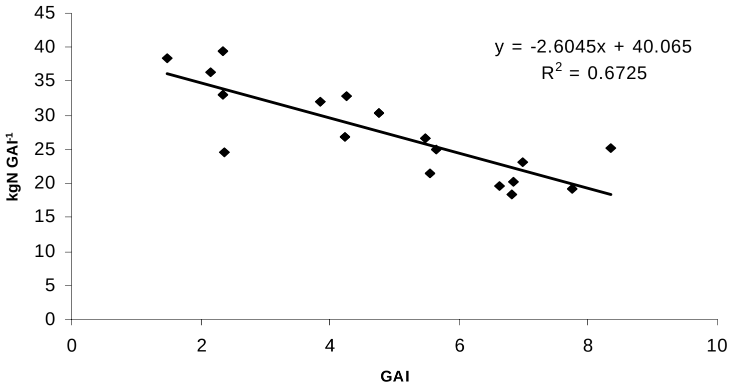


Fig. 4.8: Relationship between canopy size (GAI) and N uptake per unit of GAI at GS39 for all sites and seasons.

As crops approached GS39, N taken up by the plant was increasingly partitioned towards the stem rather than of the leaves. By GS39, crops had taken up an average of 122 kgN ha^{-1}, with more in the stems (55.1 %) than in the leaves (44.9%) (Fig. 4.9). Despite this, the leaves accounted for an average of 76.9% of the total green area, reflecting the lower quantity of N per unit of green area in the leaves. At this point the leaves contained just 15.4 kgN ha^{-1} of green area (GA), compared to 39.2 kgN ha^{-1} GA in the stems.

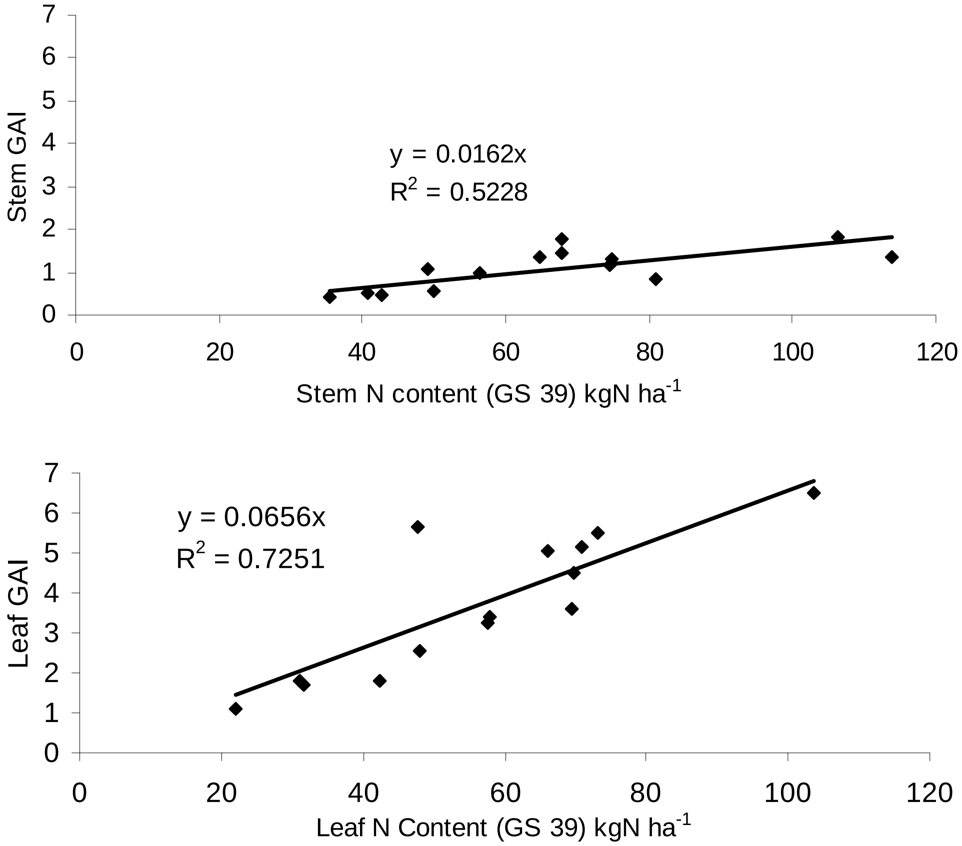


Fig. 4.9: Relationship between GAI and N uptake by the leaves and stems at GS39.

Growth stages 39 to 59

Crop N uptake generally slowed between GS39 and GS59, averaging 1.75 kgN ha^{-1} day^{-1} across sites, and reaching, on average, a total of 163 kgN ha^{-1} (90.1% of total N uptake) by GS59.

Overall, there was still a close relationship between total N uptake and GAI, (Fig. 4.10) with N uptake accounting for 62.6% of the variation in GAI. The reciprocal of the gradient indicates that each unit of green area had 26.3 kgN ha^{-1}.

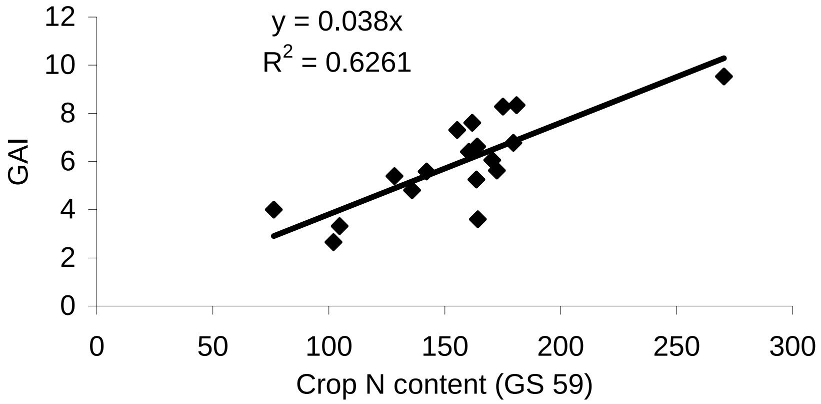


Fig. 4.10: Relationship between canopy size (GAI) and crop N content (kgN ha^{-1}) at GS59 across all sites and seasons.

By GS59, further N partitioning had occurred between leaves stems and ears. The newly emerged ear contained the least, with between 12.4 and 54.9 kgN ha^{-1} (average 29.7 kgN ha^{-1}). Leaves contained between 19.5 and 82.2 kgN ha^{-1} at this time (average 46.2 kgN ha^{-1}) and the stems generally contained the most with between 44.3 and 133.4 kgN ha^{-1} (average 83.6 kgN ha^{-1}) (Fig. 4.11)

Despite an overall increase in green area between GS39 and 59, this was mainly due to increases in stem green area and the emergence of the ear. Leaf area, on average, decreased by 12.3% from GS39 to GS59, and leaf N content reduced more rapidly by 18.2%, such that each unit of green leaf area contained just 14.2 kgN ha^{-1} by GS59.

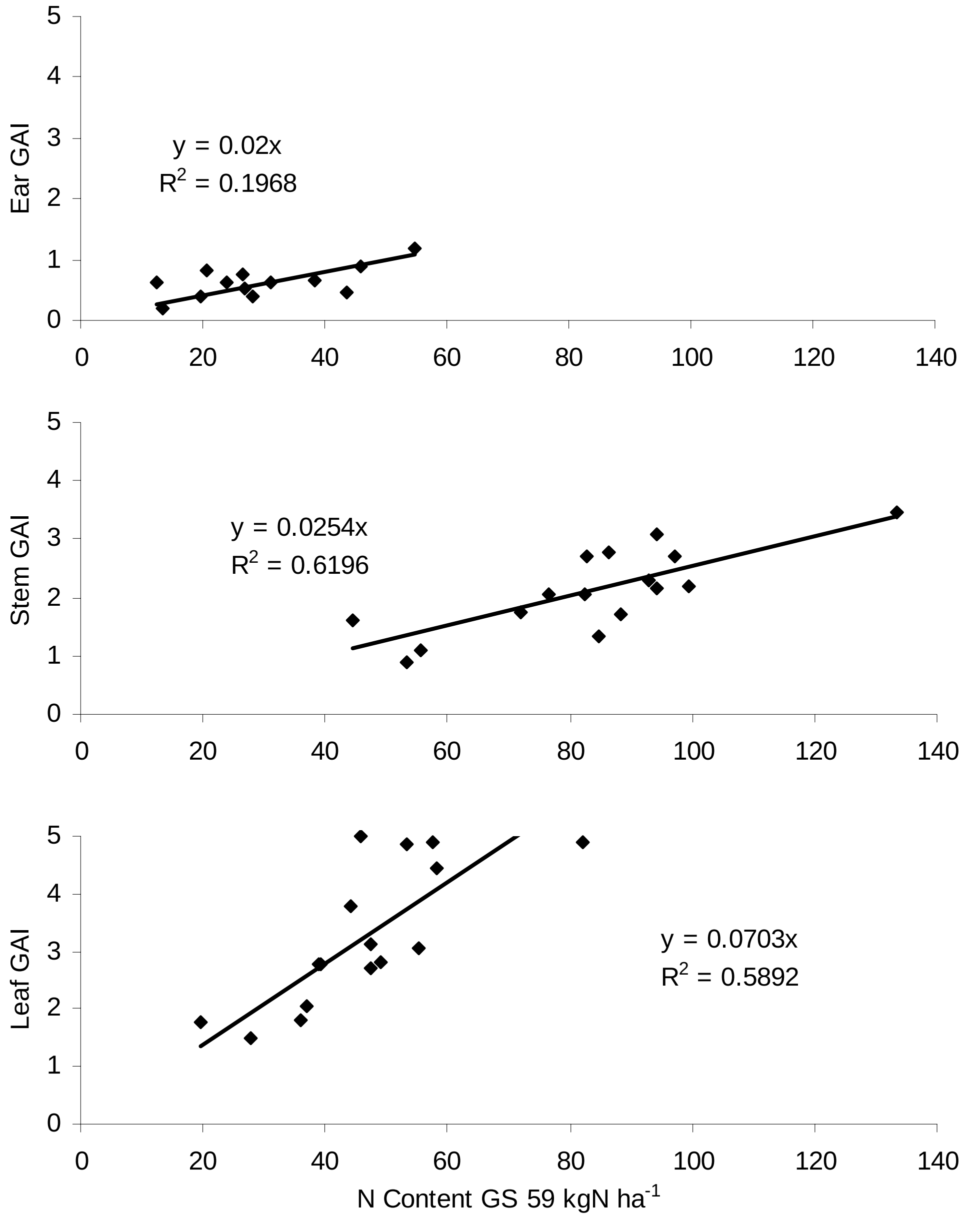


Fig. 4.11: Relationship between GAI and N uptake by the leaves, stems and ears at GS59.

By GS59 with stem elongation almost complete, stem GAI was very close to its peak, at a GAI of between 0.9 and 3.1. Variation in GAI still accounted for 62% of the variation in stem N. Ear N did appear, at this early stage, to be associated with GAI, with GAI accounting for 19% of the variation in ear N. As the ear does not increase in size, but does act as a store for grain N, we would expect any relationship between ear N and GAI to be weak, and to dissociate as grain filling progresses.

Post Growth Stage 59 N uptake and redistribution

Post GS59, associations between GAI and N uptake were less clear as the canopy started to senesce. Grain N accumulation occurred through re-location of N in the stem and leaves, as well as through continued uptake from the soil (Table 4.5).

Table 4.5: Post GS59 N uptake from the soil.

Site	2002	2003	2004	2002-04
Aberdeen	22.7	25.1	26.0	24.6
Edinburgh	35.0	73.1	*	54.1
High Mowthorpe	13.4	47.1	*	30.3
King's Lynn	30.7	21.1	8.5	20.1
Rosemaund	82.2	2.0	22.0	35.4
Sutton Bonington	37.1	27.7	56.4	40.4
Mean	36.85	32.68	22.58	31.2

* missing data

Late N uptake from the soil was highest at Rosemaund 2002, Edinburgh 2003, and Sutton Bonington 2004, and was associated with dry conditions in March, that restricted N availability. In barley grown for malting, the timing of fertiliser applications is considered important due to the perception that delayed N uptake will result in an undesirable increase in the grain N%. However, in this experiment this delayed N uptake did not appear to be associated with an increase in grain N% (Fig. 4.12).

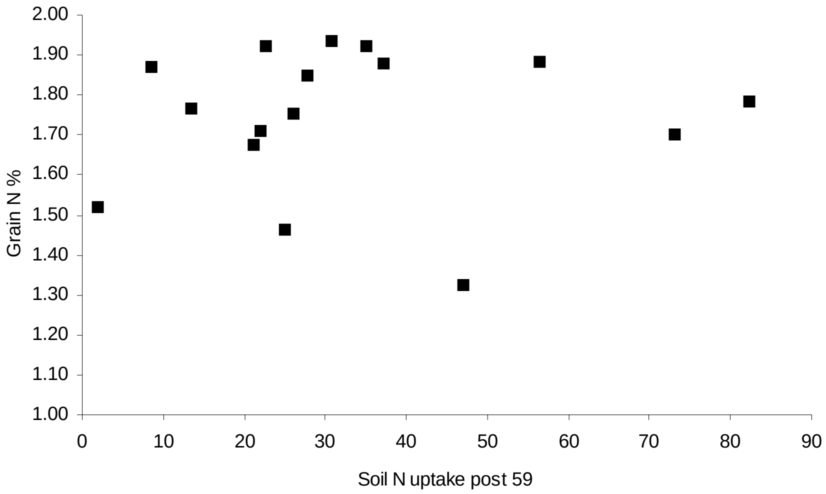


Fig. 4.12: Post GS59 soil N uptake (kgN ha^{-1}) and grain N% at/harvest.

In all seasons, after GS59 the amount of N in leaves declined steadily from a range of 19.5 to 58.3 kgN ha^{-1} at GS59, to a range of 5.5 to 17.5 kgN ha^{-1} at harvest. Stems likewise showed a similar pattern of decline, although starting from a higher point, initially containing around double the amount of N compared to the leaves at GS59, (range 44.3 to 133 kgN ha^{-1}). Ear N uptake initially increased rapidly at all sites after GS59, before slowing down, or stopping as harvest approached (Fig.s 4.13, 4.14 and 4.15).

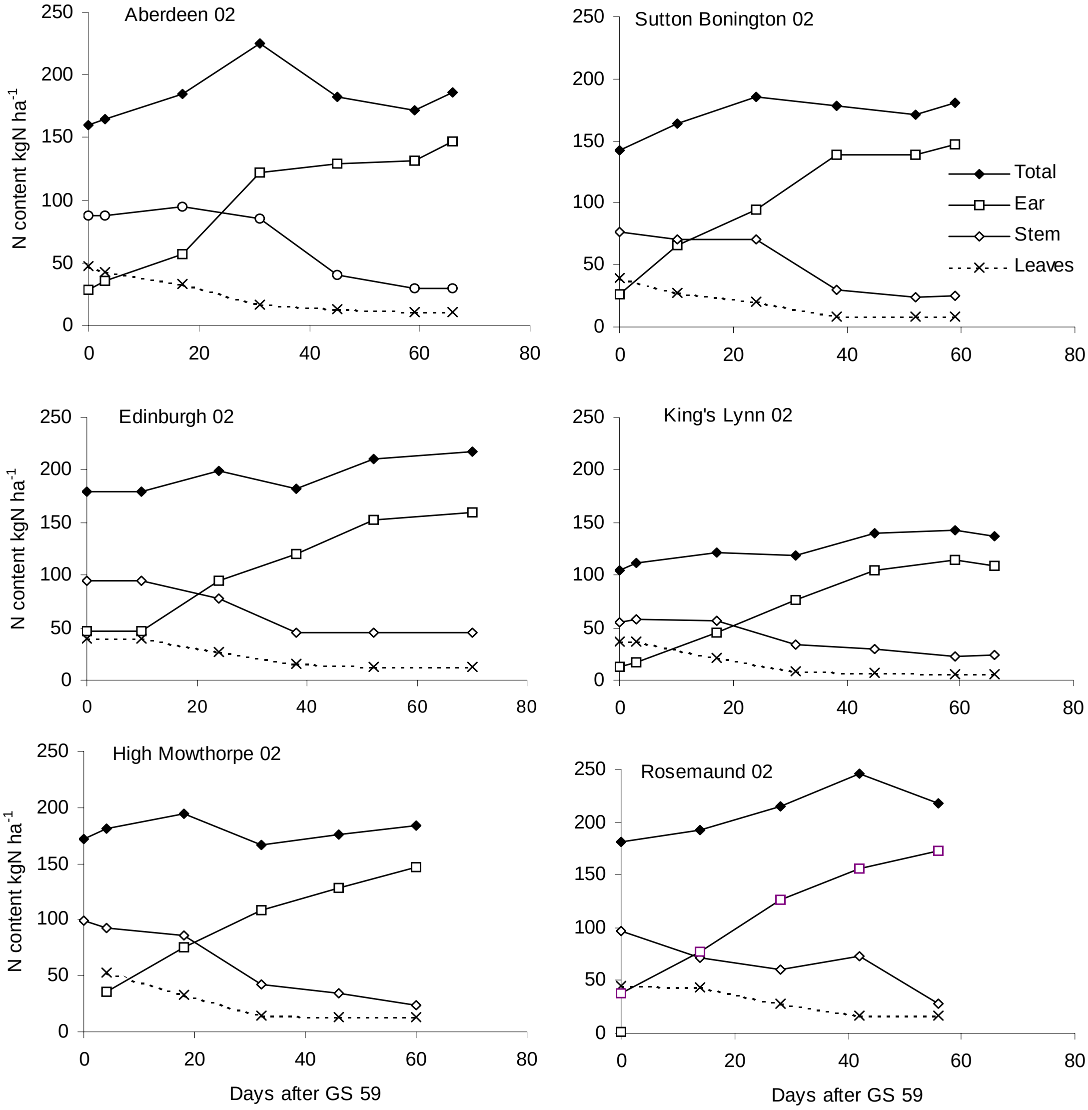


Fig. 4.13. Total crop N content (kgN ha^{-1}) and partitioning of N between leaf, stem and ear, from GS59 to harvest in 2002.

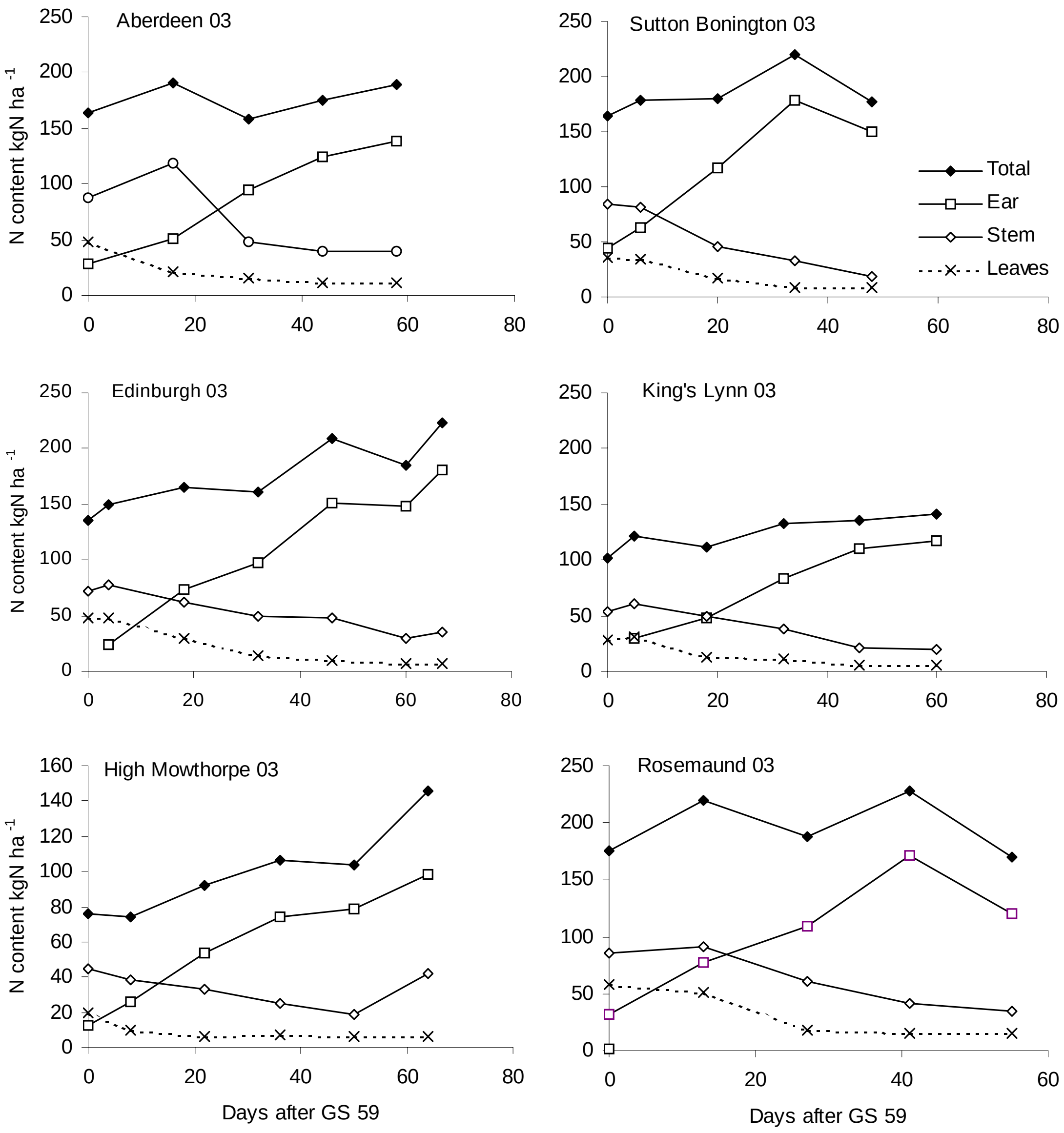


Fig. 4.14: Total N content (kgN ha^{-1}) and partitioning of N between leaf, stem and ear from GS59 to harvest in 2003.

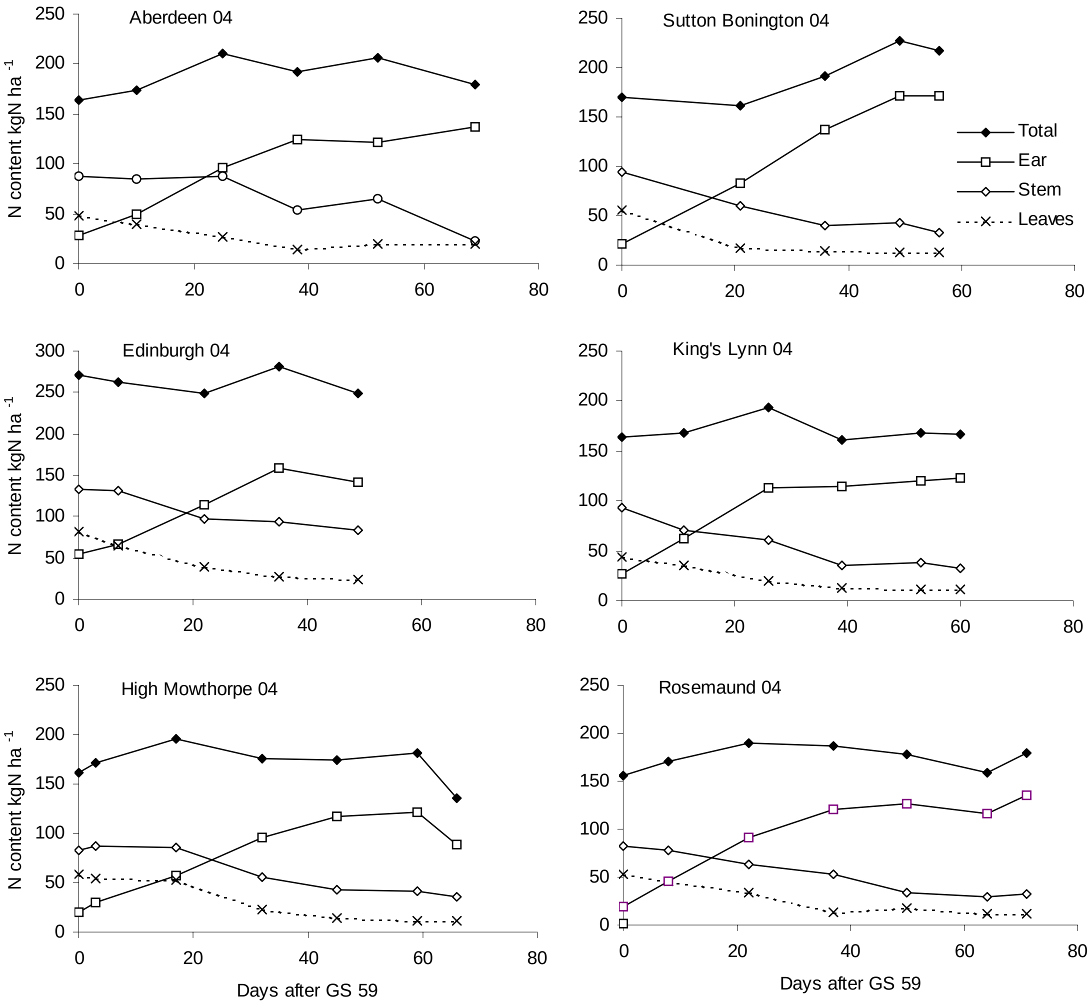


Fig. 4.15: Total crop N content (kgN ha^{-1}) and partitioning of N between leaf, stem and ear from GS59 to harvest in 2004.

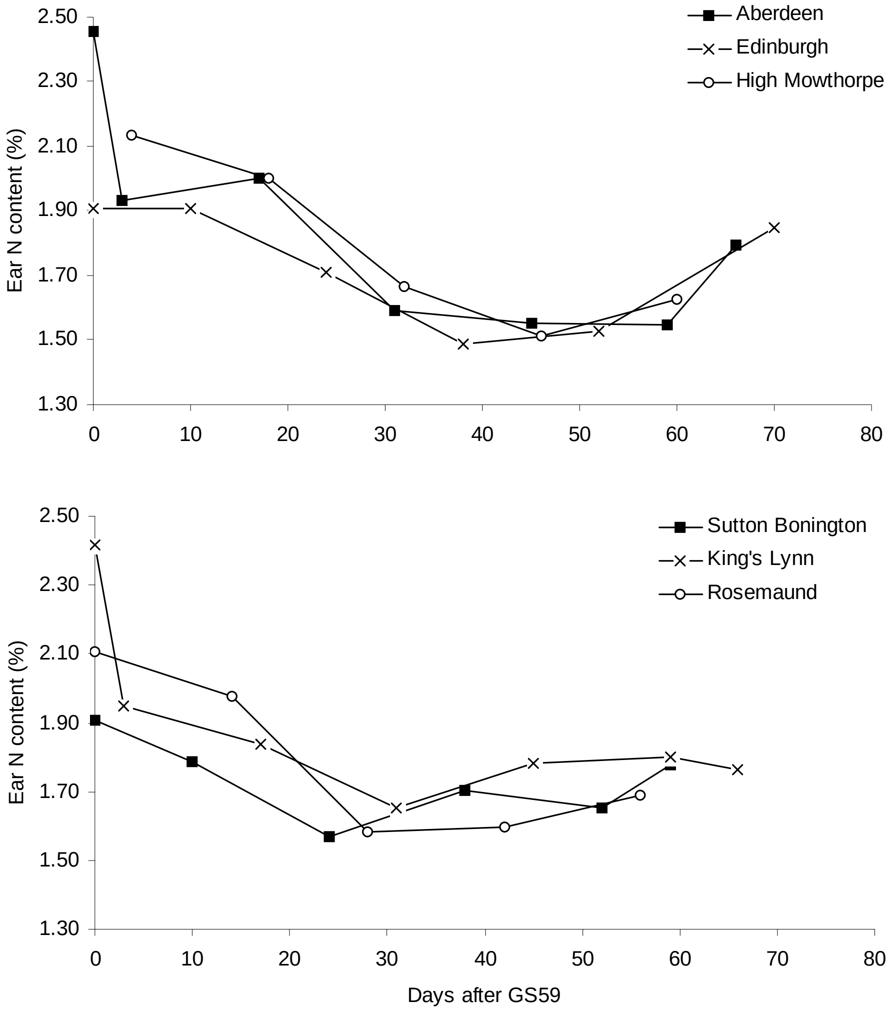


Fig. 4.16. Change in ear % N content from GS59 to Harvest in 2002.

In 2002, following GS59, increases in both the total ear N (kg ha^{-1}) and ear dry weight (t ha^{-1}), were initially almost in parallel at all sites. Differences were evident, however, towards the end of grain filling, around 50 days after GS59, when the rate of ear dry weight gain slowed and in some cases stopped (Fig. 4.16). At the same time further increases in ear N concentration (%) were clearly evident at High Mowthorpe, Rosemaund, Sutton Bonington and Aberdeen (Fig. 4.17). Between 72% and 91% of this post GS59 increase in ear N % was accounted for by redistribution of plant N rather than further uptake from the soil (data not shown).

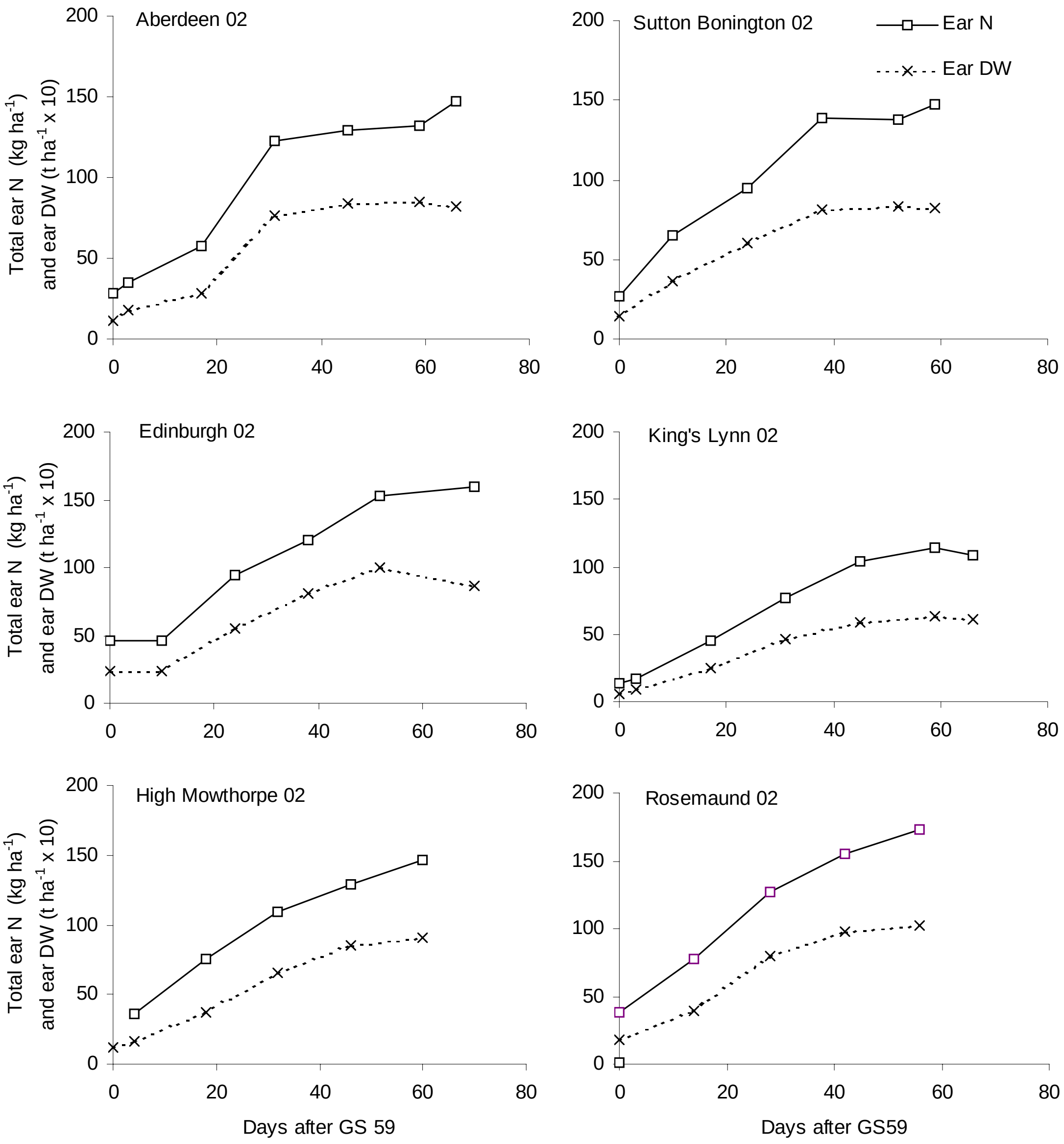


Fig. 4.17. Total ear N (kg ha^{-1}) and dry weight (DW) increases, post GS59 in 2002.

In 2003, all crops showed a decline in ear N concentration (%) from GS59, with the exception of the crop at High Mowthorpe, which showed a similar decline from 10 days after GS59. Ear N concentration (%) declined further and faster in 2003 than in the previous season, reaching average lows of 1.24% N after 30 to 40 days at northern sites, and 1.54% N after 25 to 35 days at southern sites. These lows were reached at around the point of inflection in ear dry weight gain (Fig. 4.19). This more rapid reduction in ear N concentration (%) appears to be related to a more rapid rate of dry weight gain in 2003. Following this period of decline, at northern sites there was a tendency for ear N concentration (%) to increase towards harvest, although this was less pronounced than in the 2002 season, probably because ear dry weight continued to increase for a longer period in the post anthesis period. At southern sites the rapid decline in ear N concentration (%) was soon followed by an similarly rapid decline in the rate of both ear dry weight gain and total ear N (kg ha^{-1}), and resulted in little or no change in late season ear N concentration % (Fig. 4.18).

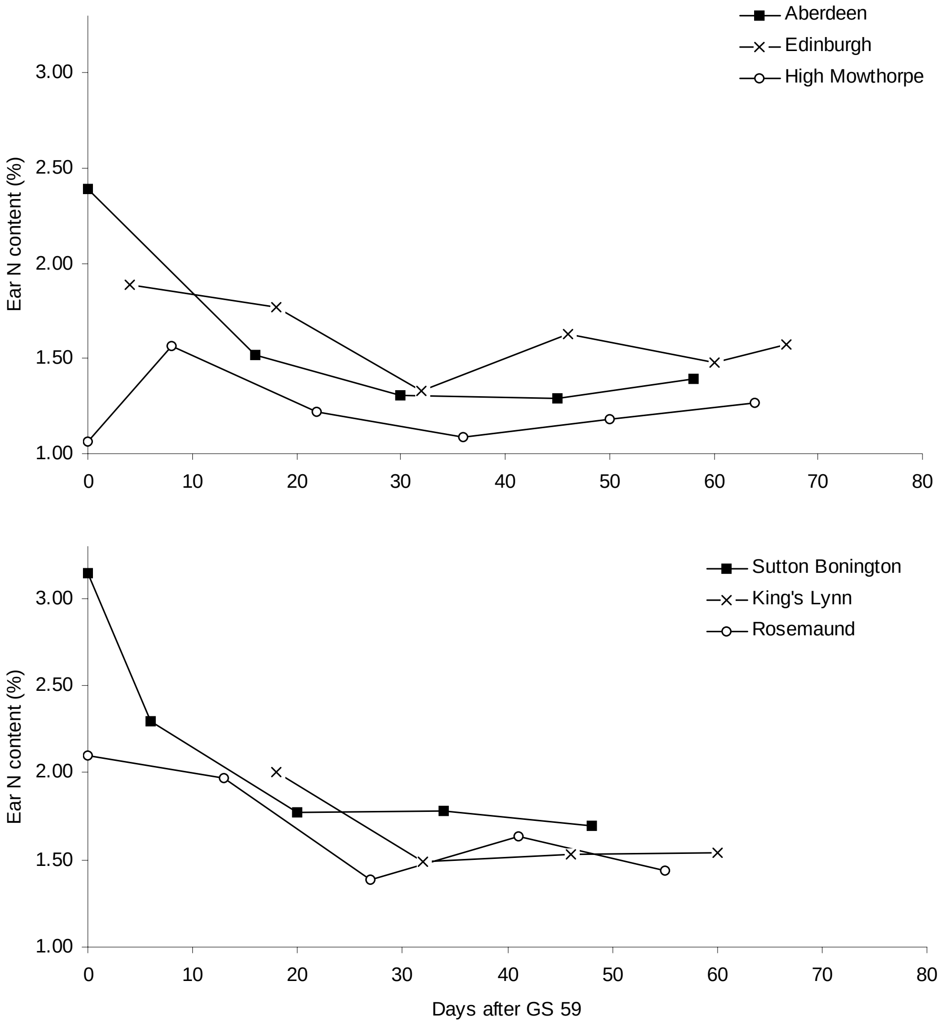


Fig. 4.18: Change in ear N content (%) from growth stage 59 to harvest in 2003.

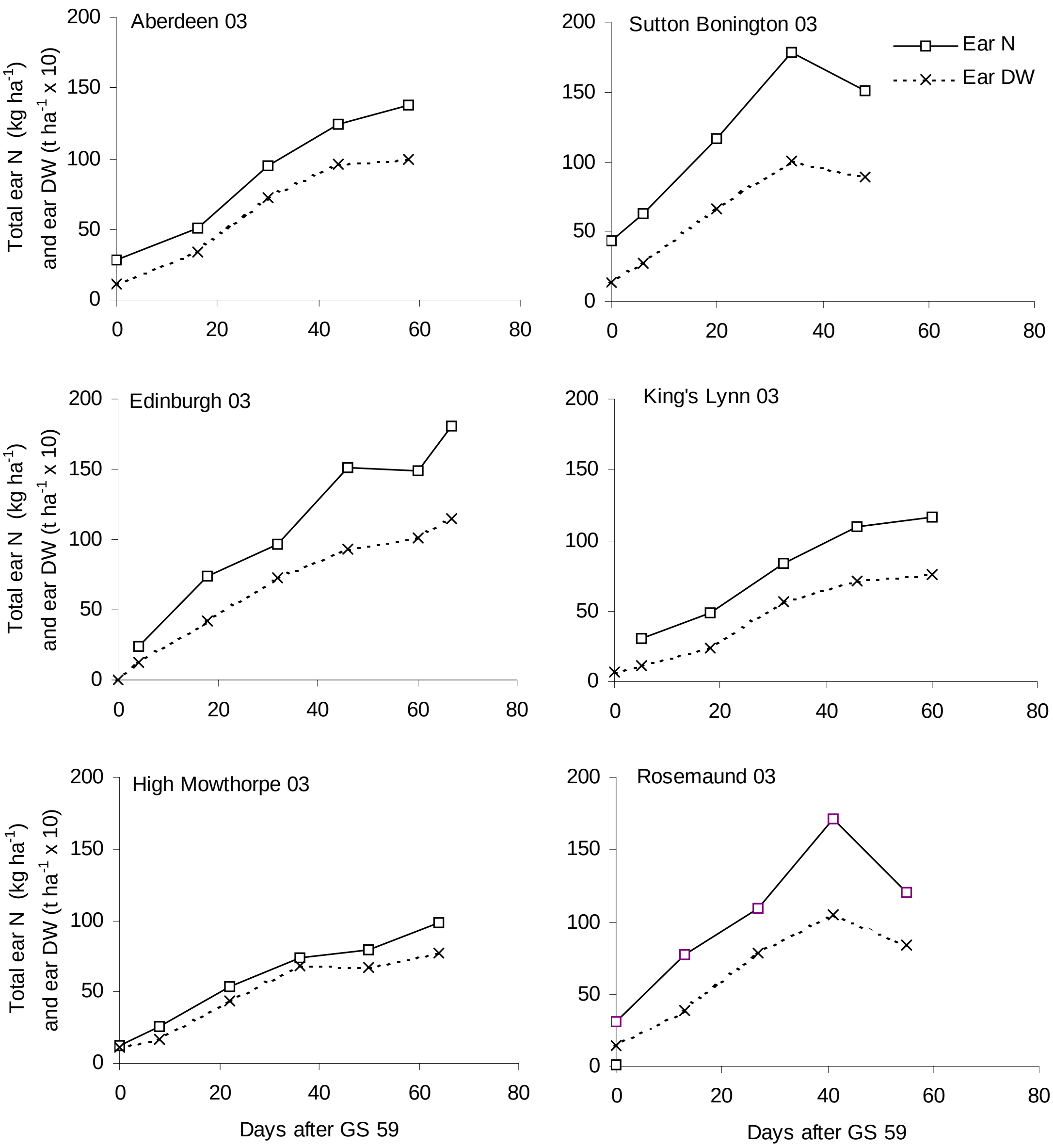


Fig. 4.19: Total ear N (kg ha^{-1}) and ear dry weight (t/ha^{-1} x10) post GS59 in 2003.

In 2004 crops at High Mowthorpe and Aberdeen showed a similar pattern of ear N concentration (%) change to that in 2002, with a steady decline in ear N concentration (%) in the first 30 days after ear emergence (GS59). As in northern sites in 2002, there was a tendency for increases in late season ear N %, at all sites in 2004 (Fig. 4.20). Although patterns were more variable in 2004, this was related to the rate of grain N uptake decreasing more slowly than the rate of ear dry weight gain (Fig. 4.21).

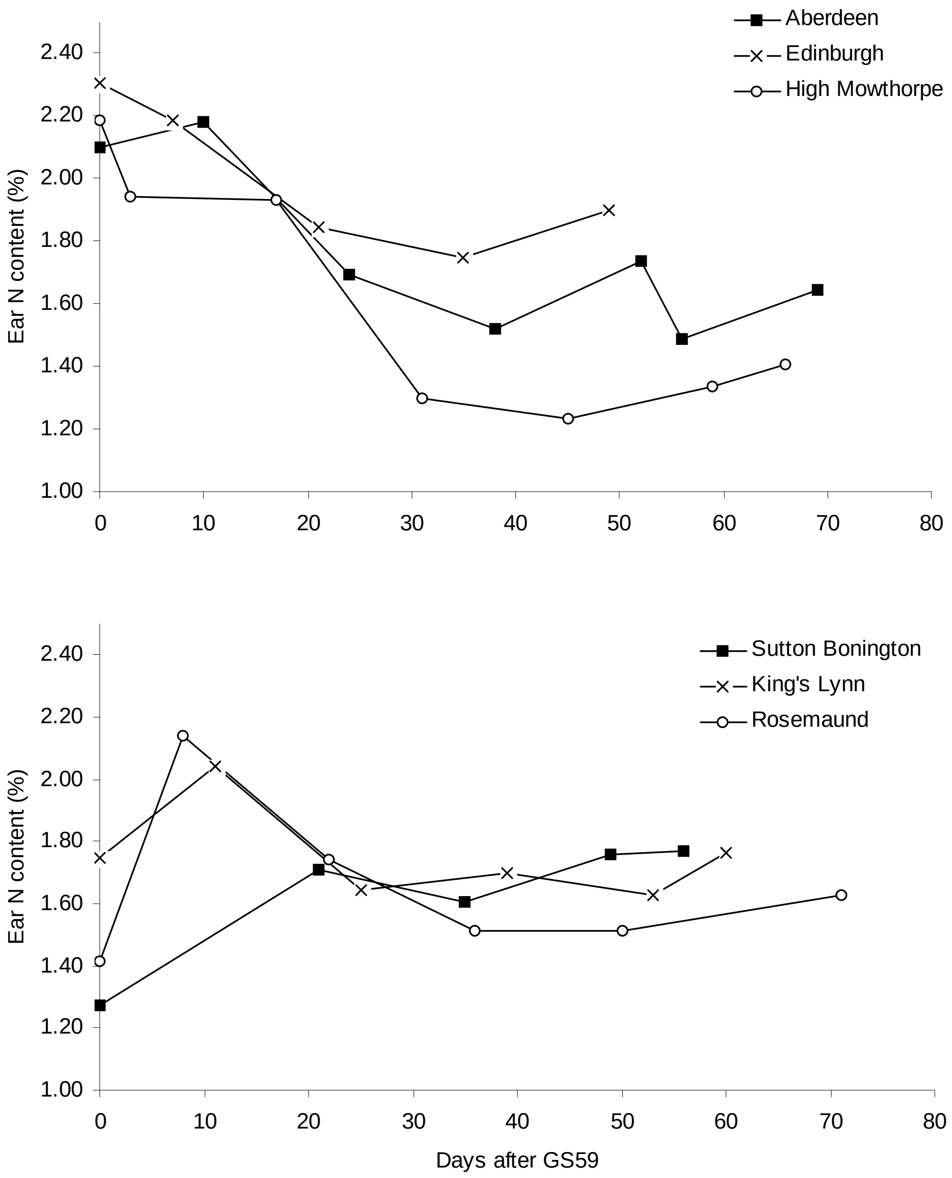


Fig. 4.20: Change in ear N concentration (%) post GS59 to harvest in 2004.

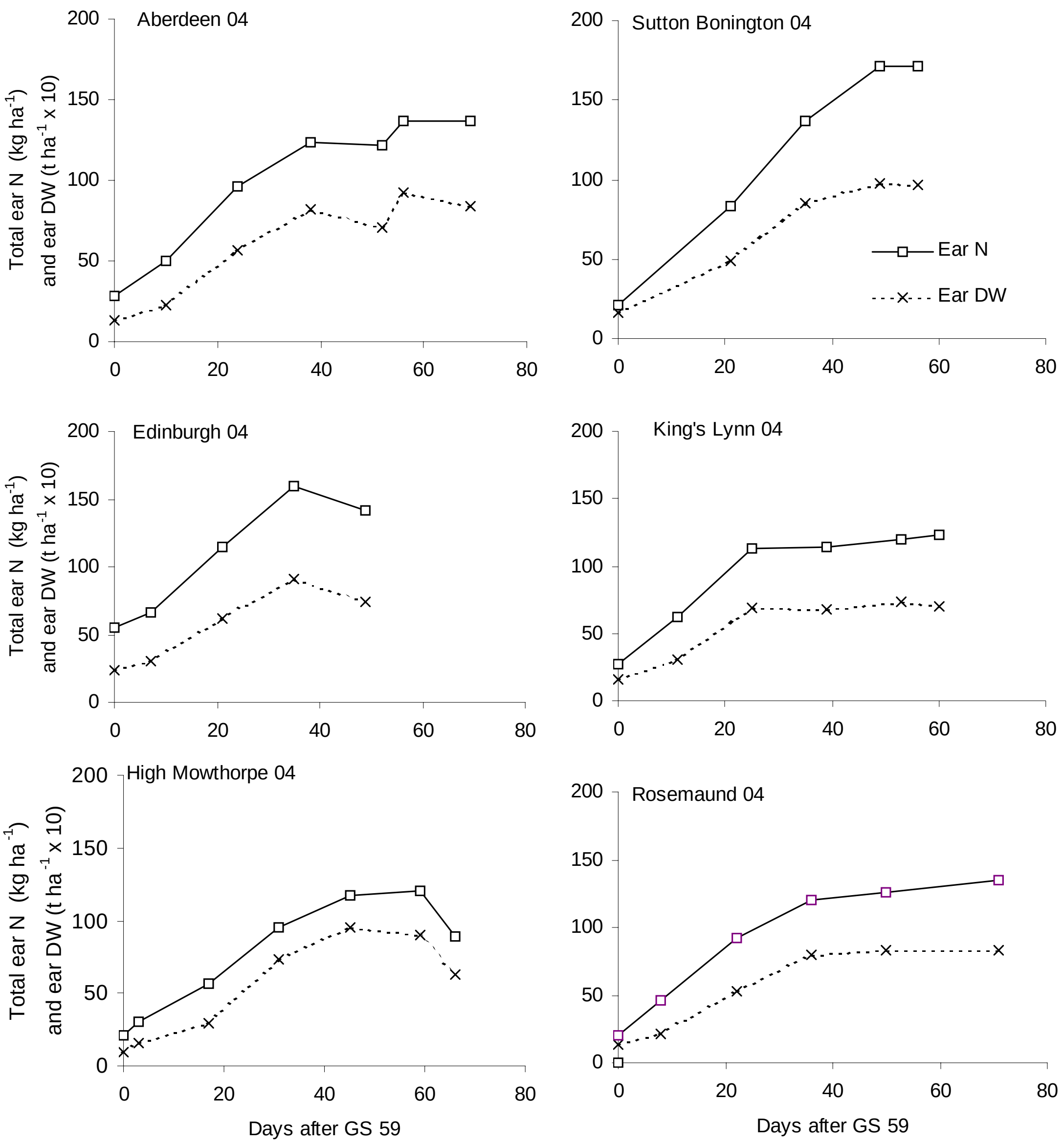


Fig.4.21. Ear N and dry weight (DW), post GS59 in 2004.

Yield and total N uptake

Total N uptake at harvest across the 18 site/seasons ranged from 135.9 kgN ha^{-1} to 222.8 kgN ha^{-1}. This did not appear to be in any way associated with the yield differences observed (Fig. 4.22).

It would be expected that where low levels of N uptake occurred, canopy size and yield would be affected. It appears that in this study, as all crops were grown to a standard protocol for feed barley, N uptakes were not sufficiently low have a direct adverse effect on yield.

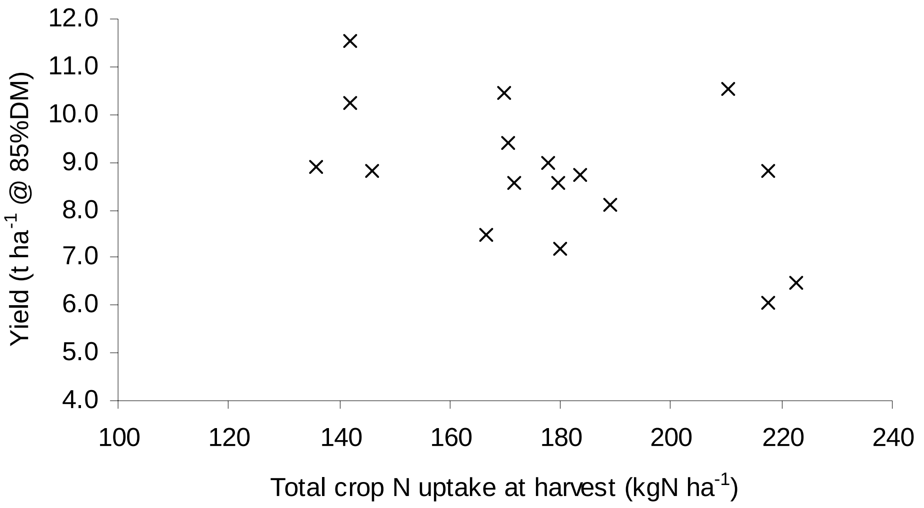


Fig. 4.22. Yield (t ha^{-1} @85%dm) and total N uptake by the crop (kgN ha^{-1}).

Effects of drought on grain N%

Of the six sites, two, Sutton Bonington and King's Lynn, were prone to summer drought. At these two sites there appeared to be a relationship between May / June rainfall and grain N (Fig. 4.23).

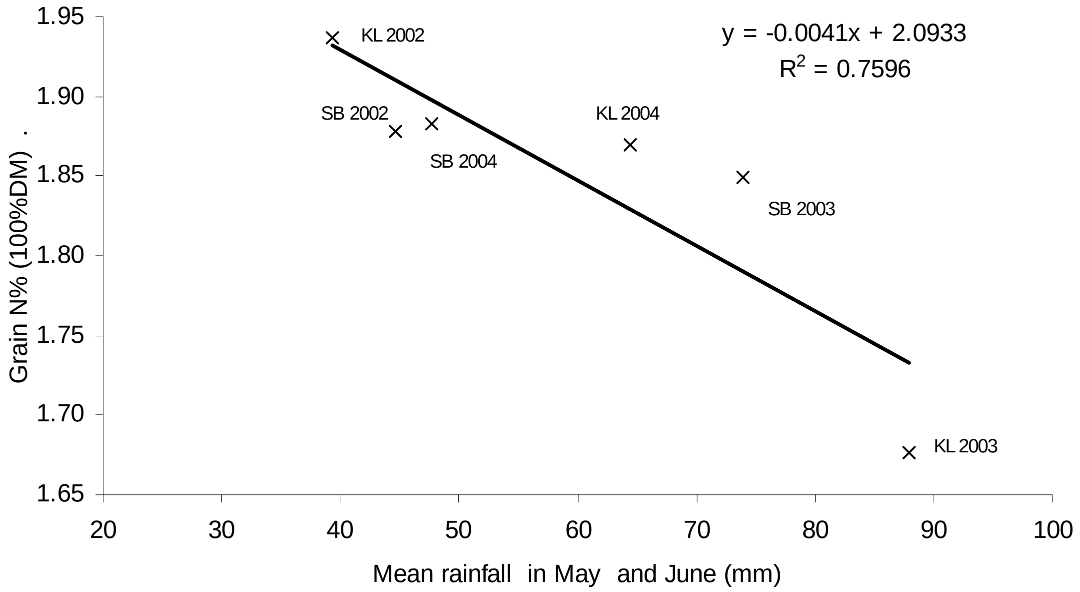


Fig. 4.23. Relationship between May/June rainfall and grain N (%) at King's Lynn and Sutton Bonington in 2002, 2003, and 2004.

At King's Lynn in 2002 and Sutton Bonington in 2002 and 2004, a low average May/June rainfall was associated with high grain N % at harvest, whereas water availability during this period was less restricted at Sutton Bonington and King's Lynn in 2003, and grain N % was generally lower at harvest.

Effects of yield and yield components on grain N%

Grain N was not related to yield across the six sites (Fig.4.24), but certain yield components were related to grain N% (Fig. 4.25).

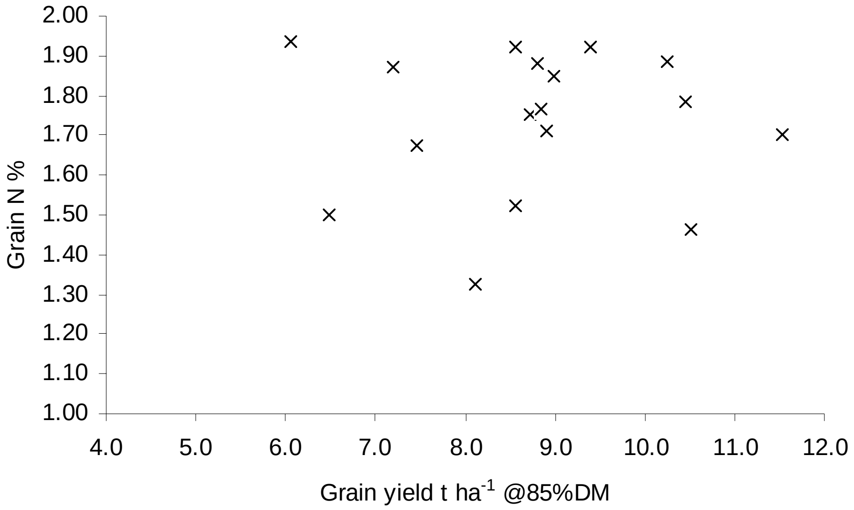


Fig. 4.24 Yield (t/ha^{-1} @85%DM) and grain N (%) across all sites and seasons.

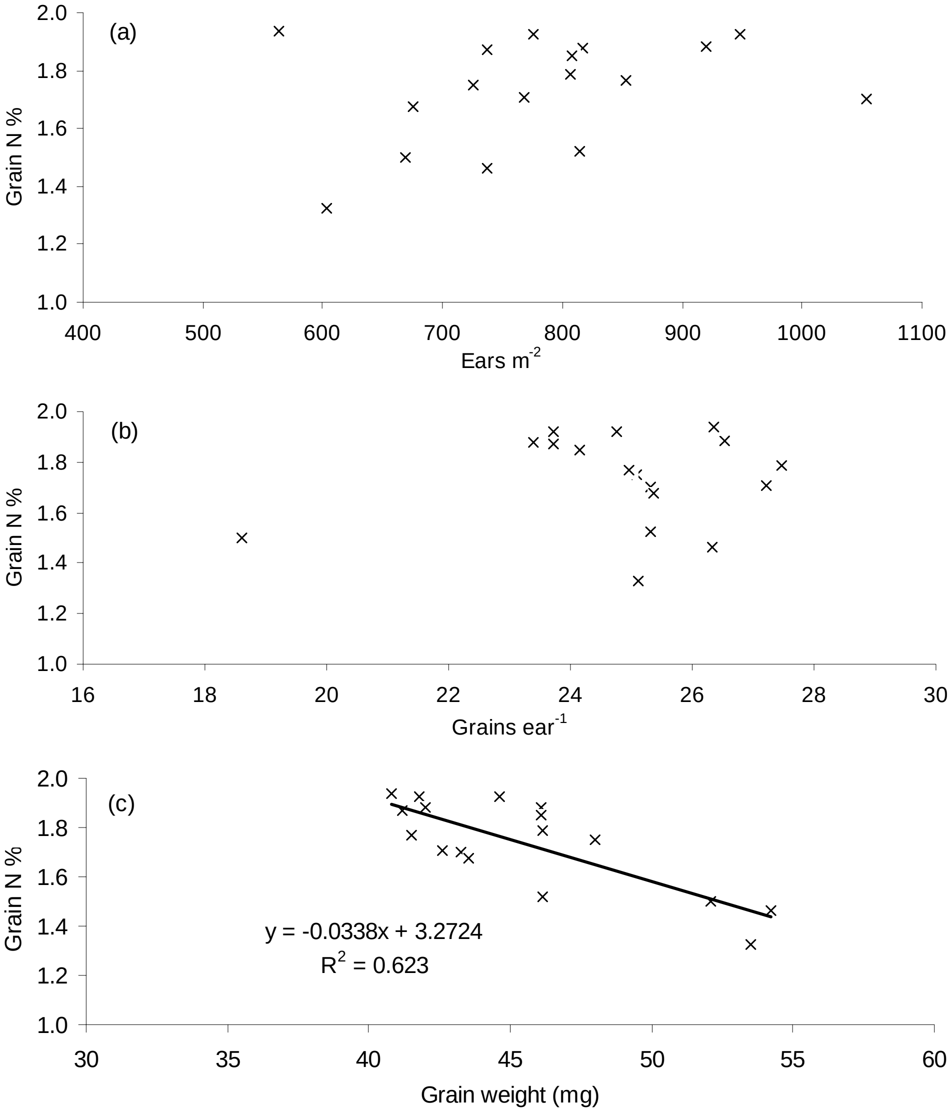


Fig. 4.25. Relationship of grain N % with (a) ears m^{-2}, (b) grains ear^{-1} and (c) grain weight (mg), across all sites and seasons.

No clear relationship existed between grain N % and ear number m^{-2} ($R^2 = 0.098$) (Fig. 4.25a) or grain number ear^{-1} ($R^2 = 0.017$) (Fig. 4.25b). There was a significant relationship between grain weight and grain N% ($p=0.0024$) (Fig. 4.25c). Increases in grain weight were associated with reductions in grain N %. Grain weight accounted for 62.3% of the variation in grain N%.

Grain N % and the source:sink balance

Yield formation can be considered in terms of the storage capacity of the ear (sink), and the ability of the crop to fill the ear (source) (see Appendix 3). In barley it is considered that yield is usually restricted by the storage capacity of the crop rather than its ability to fill the grains. By calculating the potential source and comparing this with the eventual yield, it is possible gauge the extent to which source and sink are in balance. There was a relationship between the degree of sink:source imbalance and grain N% at Aberdeen, High Mowthorpe, Rosemaund and King's Lynn (Fig. 4.26). No relationship existed at Sutton Bonington due to a minimal amount of variation grain N% between seasons. It was not possible to conduct any comparisons at Edinburgh as grain was harvested in only two seasons. Grain N appeared to be lower where sites had a closer balance between sink and source.

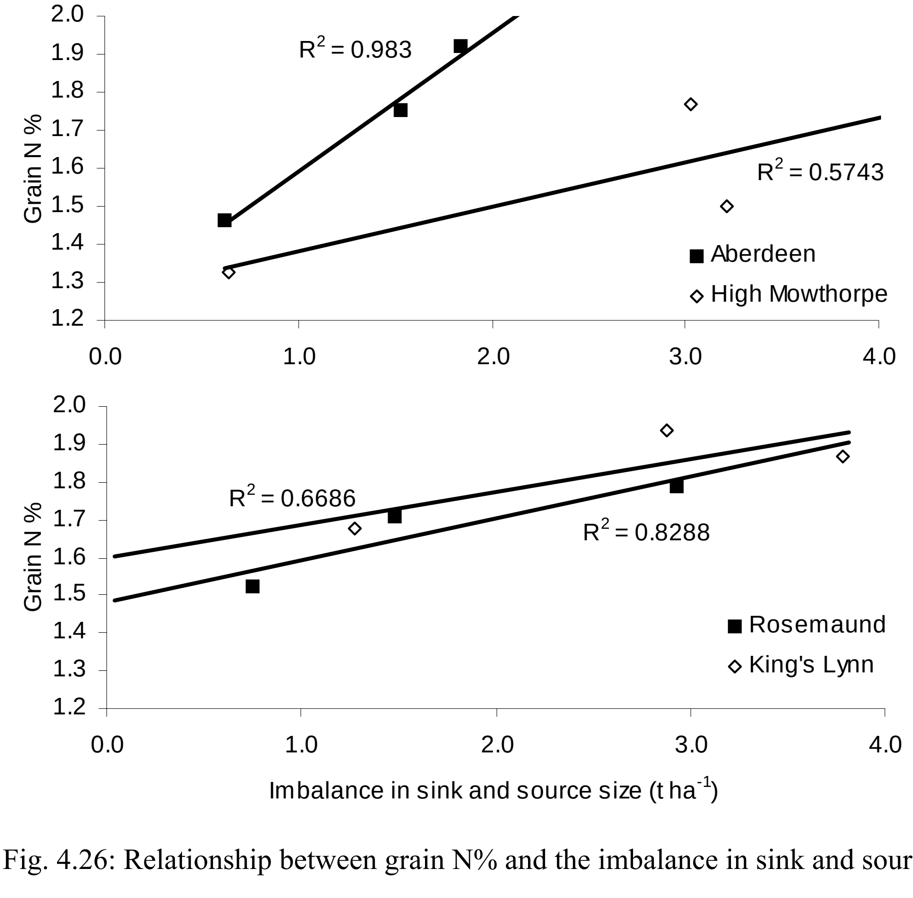


Fig. 4.26: Relationship between grain N% and the imbalance in sink and source (t ha^{-1}).

Discussion

Autumn and Spring N uptake

Despite some crops only achieving 10 to 20 kgN ha^{-1} uptake by mid February, crops at other sites achieved up to 75 kgN ha^{-1} uptake, and this high early N uptake was associated with high yields. However, where total N uptake by mid February was low, this was not due to low N availability during this period. In both early February, and at GS39, correlations between N uptake and concentrations of N per unit of GAI, indicated that where a low total N uptake occurred, the concentration of N in each unit of green area was higher than where early N uptake was high. This implies that slow growing crops, as observed at several sites including King's Lynn and Sutton Bonington in 2003, and Aberdeen in 2004, may not have been restricted by poor N availability. The poor total N uptake observed may have been a symptom rather than a cause of poor growth at these sites.

These data imply that, despite the relationship between early N uptake and yield, site selection and management to promote and protect early growth may be more important than applications of autumn N.

Across the whole season, crops required an average of 27.6 kgN ha^{-1} to form each unit of green area. However, the amount of N present in each unit of green area did vary widely with site, season (Table 4.4) and crop component (stems in general containing twice as much N compared to leaves per unit of green area).

The most rapid period of N uptake occurred between GS31 and growth stage 39. During this period N was taken up on average at a rate of 3.14 kgN ha^{-1} day^{-1} though this varied widely between sites and seasons. N uptake was slowed in this period at several sites, possibly as a result of dry soils. Such conditions were apparent at High Mowthorpe, Sutton Bonington and King's Lynn in 2003 and King's Lynn in 2002. For these crops, N offtake at GS39 as a percentage of the total N offtake was just 30.8%, 44.2%, 34.5%, and 35.6% respectively, compared to 67% where N uptake was unrestricted.

This did not appear to adversely affect total N uptake and was associated with continued uptake post GS59 (Table 4.5). Despite the perception that this would increase grain N%, increases in late N uptake were not associated with high grain N%.

By GS59, on average crops had taken up 90.1% of their total N uptake at harvest. Most of the N reaching the grain resulted from retranslocation, mainly from the stems which contained a greater proportion of the N, but also from the leaves.

Yield and Quality

Total N uptake at harvest did not appear to be in any way associated with the yield differences observed. It might be expected that a close relationship between yield and grain N would exist, such that where a high yield is achieved, grain N concentration would be diluted by high yields. No direct relationship was present, due to high variation between sites and seasons in both yield and grain N concentrations. Low grain N values were however associated with high individual grain weights (Fig. 4.25). This suggests that where low grain N% is required, producing large grains may be the most effective way of reducing grain N%.

The lowest grain N% values were recorded in 2003, a season characterised by a dry February and March period. This limited early spring uptake of applied N, and prevented the pattern of excessive tillering followed by tiller death, seen in both 2002 and 2004. This caused a small reduction in total grain number. However, in late spring, N uptake was rapid and the crop compensated with greater thousand grain weight and yield than the other two seasons. In addition, grain N% was considerably lower than that in other seasons (Table 4.6).

Table 4.6. Combine yield, yield components and grain N% at harvest for each season (Edinburgh data excluded due to lack of data in 2004).

Harvest year	Grains ear^{-1}	Ear number m^{-2}	Grain number m^{-2}	TGW @ 85%DM	Yield t/ha @85% DM	Grain N %
2002	25.4	763	19323	44.0	8.55	1.86
2003	25.3	727	18359	47.8	8.72	1.57
2004	24.2	764	18682	45.2	8.31	1.74

In 2002 and 2004 crops were generally more sink limited, with more post anthesis supply of assimilates than could be used in grain filling (Appendix 3). As a consequence, their rate of dry weight gain was reduced, but grain N uptake by the ear appeared unaffected. In the 2003 harvest season, sink and source were closest to being in balance. Thus, it appears that whereas grain dry weight gain may be restricted in some seasons by a sink-source imbalance, grain N uptake by the ear appears to be less influenced by this. As such, where source and sink were most in balance, as in 2003, ear dry weight gain matched N uptake patterns, resulting in a low grain N concentration.

APPENDIX 5: DATA SETS

Table 5.1, Growth stage 21(GS21), date of attainment, fertile shoots, biomass and green area index (GAI), calculated by interpolation between sampling dates.

GS 21	year	date	Fertile shoots m^{-2}	Biomass (t ha^{-1})	Total GAI	Plants m^{-2}
Aberdeen	2002	19-Nov	508.6	0.12	0.33	319.68
	2003	20-Nov	502.0	0.14	0.34	281.72
	2004	13-Nov	947.6	0.22	0.53	380.09
	Average	17-Nov	652.7	0.16	0.40	327.16
Edinburgh	2002	28-Nov	626.1	0.13	0.28	367.53
	2003	11-Nov	638.3	0.20	0.37	335.65
	2004	17-Nov	1485.9	0.62	1.29	343.06
	Average	18-Nov	916.8	0.32	0.65	348.74
High Mowthorpe	2002	12-Nov	333.0	0.08	0.19	215.28
	2003	13-Nov	390.7	0.14	0.30	305.40
	2004	31-Oct	*	*	*	*
	Average	08-Nov	361.8	0.11	0.24	260.34
Kings' Lynn	2002	30-Oct	*	*	*	*
	2003	11-Nov	430.1	0.08	0.17	188.89
	2004	17-Nov	589.6	0.17	0.27	286.57
	Average	09-Nov	509.9	0.12	0.22	237.73
Rosemaund	2002	19-Oct	*	*	*	*
	2003	16-Nov	493.0	0.13	0.25	310.49
	2004	17-Nov	483.3	0.14	0.23	276.85
	Average	07-Nov	488.1	0.14	0.24	293.67
Sutton Bonington	2002	12-Nov	490.7	0.10	0.16	270.83
	2003	13-Nov	390.5	0.10	0.19	277.78
	2004	13-Nov	893.4	0.30	0.49	334.26
	Average	12-Nov	591.5	0.17	0.28	294.29

* Missing data due to sites reaching GS21 prior to first sampling date.

Table 5.2, Growth stage 30 (GS30), date of attainment, fertile shoots, biomass, green area index (GAI) and Total Crop N content, calculated by interpolation between sampling dates.

GS 30	year	date	Fertile shoots m^{-2}	Biomass t ha^{-1}	Total GAI	Total crop N kg ha^{-1}
Aberdeen	2002	15-Apr	2122.5	1.85	2.36	62.6
	2003	04-Apr	1208.6	1.34	1.39	46.1
	2004	01-Apr	1264.9	1.17	0.89	45.6
	Average	06-Apr	1532.0	1.45	1.55	51.4
Edinburgh	2002	15-Apr	1847.9	1.64	1.60	49.5
	2003	14-Apr	961.9	1.25	1.20	28.8
	2004	05-Apr	1488.2	2.25	3.16	104.8
	Average	11-Apr	1432.7	1.71	1.99	61.1
High Mowthorpe	2002	02-Apr	1210.0	0.87	0.99	26.6
	2003	06-Apr	986.9	1.36	1.24	36.0
	2004	22-Mar	1158.3	1.21	1.37	59.5
	Average	30-Mar	1118.4	1.15	1.20	40.7
Kings' Lynn	2002	02-Apr	835.5	0.39	0.55	12.6
	2003	31-Mar	641.5	1.14	1.09	60.4
	2004	05-Apr	977.8	1.16	1.88	70.7
	Average	02-Apr	818.3	0.90	1.17	47.88
Rosemaund	2002	04-Mar	1392.2	2.36	3.30	70.7
	2003	22-Mar	1265.9	1.89	2.49	24.2
	2004	22-Mar	1319.0	1.89	2.30	54.0
	Average	16-Mar	1325.7	2.05	2.70	49.7
Sutton Bonington	2002	01-Apr	1141.4	1.12	1.15	35.4
	2003	14-Apr	778.5	1.20	0.87	32.8
	2004	22-Mar	1079.1	1.89	1.96	63.5
	Average	02-Apr	999.7	1.40	1.32	43.9

Table 5.3, Growth stage 31 (GS31), date of attainment, fertile shoots, biomass, green area index (GAI) and Total Crop N content, calculated by interpolation between sampling dates.

GS 31	year	date	Fertile shoots m^{-2}	Biomass t ha^{-1}	Total GAI	Total crop N kg ha^{-1}
Aberdeen	2002	22-Apr	2041.18	2.61	3.10	86.3
	2003	15-Apr	1181.58	1.66	2.09	59.8
	2004	10-Apr	1235.12	1.77	1.50	63.1
	Average	15-Apr	1514.24	2.01	2.06	69.7
Edinburgh	2002	24-Apr	1822.26	2.66	2.91	74.6
	2003	22-Apr	971.50	1.95	1.79	45.3
	2004	19-Apr	1338.28	3.98	5.03	131.2
	Average	21-Apr	1377.35	2.86	3.24	83.7
High Mowthorpe	2002	17-Apr	1148.71	1.70	1.41	36.0
	2003	16-Apr	1053.26	1.91	1.63	42.6
	2004	14-Apr	1198.06	2.61	3.25	113.2
	Average	15-Apr	1133.35	2.07	2.10	63.9
Kings' Lynn	2002	17-Apr	658.03	1.88	1.72	56.5
	2003	25-Apr	517.96	1.72	1.33	40.8
	2004	17-Apr	1058.51	2.55	4.05	103.8
	Average	19-Apr	744.83	2.05	2.37	67.0
Rosemaund	2002	15-Mar	1232.37	2.73	3.66	66.7
	2003	31-Mar	1184.56	2.62	2.81	79.2
	2004	05-Apr	1324.31	3.04	3.57	92.7
	Average	27-Mar	1247.08	2.83	3.34	79.6
Sutton Bonington	2002	12-Apr	1043.25	1.73	1.72	40.1
	2003	24-Apr	711.85	2.08	1.62	56.9
	2004	05-Apr	1401.31	2.96	3.19	87.7
	Average	13-Apr	1052.14	2.26	2.18	61.6

Table 5.4, Growth stage 31 (GS31), date of attainment, fertile shoots, biomass, green area index (GAI), total crop N content, Water Soluble Stem Carbohydrates (WSC) and Photosynthetically Active Radiation (PAR) intercepted reflected and absorbed by the crop. Values calculated by interpolation between sampling dates.

GS 39	year	date	Fertile shoots m^{-2}	Biomass t ha^{-1}	Total GAI	Total crop N kg ha^{-1}	% PAR intercepted	% reflected	% absorbed	WSC t ha^{-1}
Aberdeen	2002	13-May	1606.9	5.89	5.64	140.4	89.8	2.8	87.0	1.22
	2003	14-May	1138.9	6.49	5.48	146.0	90.0	2.9	87.1	1.65
	2004	07-May	1134.8	4.62	4.25	139.5	87.3	2.9	84.4	0.53
	Average	11-May	1293.5	5.67	5.13	142.0	89.0	2.9	86.2	1.14
Edinburgh	2002	16-May	1272.8	5.90	6.62	138.5	94.75	3.38	91.37	1.00
	2003	09-May	777.6	3.14	2.34	92.3	66.2	2.6	63.7	0.74
	2004	06-May	1221.1	7.25	8.36	209.9	98.0	2.7	95.3	*
	Average	10-May	1090.5	5.43	5.77	146.9	82.1	2.6	79.5	0.87
High Mowthorpe	2002	10-May	1209.5	4.40	3.85	122.9	73.3	3.7	69.6	0.84
	2003	01-May	942.1	3.06	2.37	58.3	68.9	1.5	67.4	0.76
	2004	04-May	971.3	5.64	6.82	125.6	93.4	5.4	88.0	1.23
	Average	05-May	1041.0	4.37	4.35	102.3	78.5	3.5	75.0	0.94
Kings' Lynn	2002	03-May	472.3	3.45	2.35	77.4	64.6	3.8	60.8	0.87
	2003	06-May	384.5	2.20	1.49	57.4	66.2	6.3	60.0	0.43
	2004	08-May	831.2	5.21	6.99	161.4	92.8	3.0	89.8	0.81
	Average	05-May	562.7	3.62	3.61	98.7	74.5	4.4	70.2	0.71
Rosemaund	2002	23-Apr	662.8	7.33	5.56	118.9	98.0	3.4	94.6	1.48
	2003	30-Apr	1001.3	6.93	7.76	148.8	96.7	4.0	92.7	1.32
	2004	08-May	1010.8	6.76	6.84	137.9	96.3	3.3	93.1	0.65
	Average	30-Apr	891.6	7.00	6.72	135.2	98.0	3.4	94.6	1.15
Sutton Bonington	2002	07-May	770.1	4.39	4.24	114.0	92.3	2.9	89.4	0.81
	2003	03-May	700.0	2.77	2.16	78.6	69.3	4.2	65.1	0.51
	2004	30-Apr	773.4	5.12	4.75	144.2	*	*	*	0.59
	Average	03-May	747.9	4.09	3.72	112.2	80.8	3.6	77.2	0.64

Table 5.5, Growth stage 59 (GS59), date of attainment, fertile shoots, biomass, green area index (GAI), total crop N content, Water Soluble Stem Carbohydrates (WSC) and Photosynthetically Active Radiation (PAR) intercepted, reflected and absorbed by the crop. Values calculated by interpolation between sampling dates.

GS 59	Year	Date	Fertile shoots m^{-2}	Biomass t ha^{-1}	Total GAI	Total crop N kg ha^{-1}	% PAR intercepted	% reflected	% absorbed	WSC t ha^{-1}
Aberdeen	2002	31-May	890.2	9.76	6.40	160.4	95.99	3.37	92.62	1.28
	2003	31-May	783.8	9.57	5.39	128.3	94.90	5.63	89.26	1.74
	2004	28-May	855.1	9.08	5.26	163.7	93.74	3.33	90.41	1.51
	Average	30-May	843.0	9.47	5.68	150.81	94.88	4.11	90.77	1.51
Edinburgh	2002	07-Jun	978.2	10.07	6.77	179.6	97.84	2.57	95.27	2.57
	2003	29-May	859.5	7.14	4.82	135.9	90.03	3.12	86.91	1.05
	2004	31-May	1059.2	12.88	9.53	270.4	97.79	2.62	95.16	1.18
	Average	01-Jun	965.6	10.03	7.04	195.33	95.22	2.77	92.45	1.60
High Mowthorpe	2002	30-May	1028.9	8.15	5.62	172.5	96.49	2.57	91.76	0.89
	2003	25-May	643.1	7.73	4.01	76.3	86.34	2.65	83.69	1.53
	2004	21-May	838.8	9.93	7.60	161.7	98.35	3.27	95.08	1.14
	Average	25-May	836.9	8.60	5.74	136.82	93.73	2.83	90.18	1.19
Kings' Lynn	2002	17-May	494.3	5.19	3.31	104.7	84.66	3.82	80.85	0.95
	2003	15-May	515.6	4.73	2.65	102.0	75.48	5.19	70.29	0.73
	2004	27-May	737.7	9.98	6.62	164.0	97.14	3.40	93.73	1.63
	Average	19-May	582.5	6.63	4.19	123.57	85.76	4.14	81.62	1.10
Rosemaund	2002	20-May	941.0	11.88	8.34	181.0	97.15	5.23	91.92	1.71
	2003	20-May	834.8	11.60	8.27	175.1	97.79	3.59	94.20	1.68
	2004	16-May	877.3	10.18	7.32	155.3	97.66	3.55	94.12	0.67
	Average	18-May	884.4	11.22	7.98	170.47	97.53	4.12	93.41	1.35
Sutton Bonington	2002	24-May	755.9	7.98	5.58	142.1	95.18	3.35	91.83	1.25
	2003	27-May	949.9	6.97	3.61	164.2	87.61	3.02	84.59	1.09
	2004	17-May	949.0	9.60	6.07	170.5	*	*	*	0.97
	Average	22-May	885.0	8.19	5.08	158.96	91.40	3.18	88.21	1.10

Table 5.6, Growth stage 71 (GS71), date of attainment, fertile shoots, biomass, green area index (GAI), total crop N content, Water Soluble Stem Carbohydrates (WSC) and Photosynthetically Active Radiation (PAR) intercepted, reflected and absorbed by the crop. Values calculated by interpolation between sampling dates.

GS 71	Year	date	Fertile shoots m^{-2}	Biomass t ha^{-1}	Total GAI	Total crop N kg ha^{-1}	stem N kg ha^{-1}	leaf N kg ha^{-1}	Ear N kg ha^{-1}	WSC t ha^{-1}
Aberdeen	2002	19-Jun	846.2	13.23	3.77	190.9	93.6	30.9	66.3	2.01
	2003	11-Jun	732.5	12.21	4.92	166.1	84.6	38.4	55.8	2.41
	2004	09-Jun	863.0	10.79	4.62	178.8	88.2	47.3	28.2	2.09
	Average	13-Jun	813.9	12.08	4.43	178.6	88.8	38.9	50.1	2.17
Edinburgh	2002	21-Jun	864.3	10.73	6.21	185.3	89.7	35.6	60.0	1.75
	2003	13-Jun	995.7	11.75	6.20	161.9	65.3	33.2	63.4	1.51
	2004	10-Jun	1088.8	15.22	8.58	260.3	123.8	59.9	76.6	0.97
	Average	14-Jun	983.0	12.57	6.99	202.5	92.9	42.9	66.7	1.41
High Mowthorpe	2002	17-Jun	942.0	12.81	5.02	194.8	86.4	33.1	75.4	1.49
	2003	06-Jun	573.9	8.78	3.35	79.3	36.6	9.0	33.6	1.73
	2004	07-Jun	799.8	13.62	5.52	195.5	85.1	53.3	57.1	3.05
	Average	10-Jun	771.9	11.74	4.63	156.5	69.4	31.8	55.4	2.09
Kings' Lynn	2002	07-Jun	579.3	8.80	3.12	121.6	52.8	19.1	49.6	1.36
	2003	09-Jun	577.9	7.35	2.54	122.1	43.8	12.2	66.0	0.73
	2004	07-Jun	730.1	11.95	4.96	167.6	70.3	35.5	61.7	2.47
	Average	07-Jun	629.1	9.37	3.54	137.1	55.7	22.3	59.1	1.52
Rosemaund	2002	31-May	929.8	15.43	8.02	190.5	76.8	44.4	69.3	2.28
	2003	09-Jun	951.0	15.52	4.34	203.3	75.9	34.1	93.3	1.47
	2004	01-Jun	840.1	14.58	4.99	180.1	71.0	40.1	69.0	2.34
	Average	03-Jun	907.0	15.18	5.78	191.3	74.6	39.6	77.2	2.03
Sutton Bonington	2002	05-Jun	874.3	12.71	5.38	163.5	70.6	27.4	65.5	2.85
	2003	02-Jun	1166.2	9.10	4.55	178.8	81.4	34.9	62.5	0.86
	2004	24-May	956.0	10.93	5.82	167.5	83.1	42.8	41.6	1.75
	Average	31-May	998.8	10.92	5.25	169.9	78.4	35.0	56.6	1.82

Table 5.7, Growth stage 87 (GS87), date of attainment, fertile shoots, biomass, green area index (GAI), Water Soluble Stem Carbohydrates (WSC), total crop N content, and N content in the stems, leaves and ears. Values calculated by interpolation between sampling dates.

GS 87	year	date	Fertile shoots m^{-2}	Biomass t ha^{-1}	Total GAI	Total crop N kg ha^{-1}	stem N kg ha^{-1}	leaf N kg ha^{-1}	Ear N kg ha^{-1}	WSC t ha^{-1}
Aberdeen	2002	27-Jul	749.2	14.83	0.02	173.1	30.9	10.6	131.6	0.149
	2003	17-Jul	674.2	16.70	0.09	176.8	43.7	13.2	109.4	0.191
	2004	19-Jul	1236.1	16.13	0.37	206.5	64.8	19.7	122.0	0.313
	Average	21-Jul	886.5	15.89	0.16	185.5	46.5	14.5	121.0	0.218
Edinburgh	2002	20-Jul	881.7	17.17	3.72	192.4	45.2	14.8	132.4	1.098
	2003	18-Jul	931.2	16.24	1.69	202.0	42.8	8.7	150.5	0.427
	2004	19-Jul	910.0	15.34	1.37	248.5	83.0	23.9	141.6	*
	Average	19-Jul	907.6	16.25	2.26	214.3	57.0	15.8	141.5	0.762
High Mowthorpe	2002	13-Jul	776.0	15.08	0.94	174.8	35.3	13.7	125.8	0.471
	2003	05-Jul	561.1	11.93	0.35	105.5	22.8	7.0	75.8	0.466
	2004	04-Jul	814.7	17.50	0.91	174.3	43.1	14.6	116.7	1.332
	Average	07-Jul	717.3	14.84	0.73	151.6	33.7	11.8	106.1	0.756
Kings' Lynn	2002	05-Jul	553.2	9.97	0.13	140.7	27.6	6.2	106.9	0.174
	2003	03-Jul	564.5	10.75	0.14	136.9	20.6	5.5	109.6	0.125
	2004	28-Jun	639.2	13.08	0.43	193.3	44.2	7.0	109.8	0.445
	Average	02-Jul	585.6	11.27	0.24	157.0	30.8	6.2	108.7	0.248
Rosemaund	2002	10-Jul	803.0	17.37	0.40	229.8	*	*	*	0.476
	2003	26-Jun	962.1	17.27	0.65	216.0	47.1	15.6	153.3	0.289
	2004	22-Jun	781.6	15.70	0.14	183.6	46.3	14.7	122.6	0.173
	Average	29-Jun	848.9	16.78	0.40	209.8	46.7	15.2	137.9	0.313
Sutton Bonington	2002	01-Jul	859.7	14.58	0.33	177.7	30.1	8.8	138.9	0.401
	2003	30-Jun	950.3	15.80	1.40	219.8	32.4	9.0	178.4	0.607
	2004	23-Jun	852.5	15.82	0.21	216.3	41.7	13.6	160.9	0.116
	Average	28-Jun	887.5	15.40	0.65	204.6	34.7	10.4	159.4	0.374

Table 5.8, Crop harvest date, yield, specific weight, Thousand Grain Weight (TGW), and grain N %.

Harvest	year	date	Yield t/ha @ 85% DM	Specific weight kg hl^{-1}	TGW	Grain N %
Aberdeen	2002	06-Aug	8.57	67.1	44.6	1.92
	2003	28-Jul	10.52	71.8	54.3	1.46
	2004	08-Aug	8.73	64.8	48.0	1.75
	Average	03-Aug	9.27	67.9	48.9	1.71
Edinburgh	2002	16-Aug	9.40	64.4	41.8	1.92
	2003	04-Aug	11.54	64.1	43.3	1.70
	2004	*	*	*	*	*
	Average	10-Aug	10.47	64.3	42.5	1.81
High Mowthorpe	2002	30-Jul	8.83	63.9	41.5	1.77
	2003	21-Jul	8.11	65.2	53.6	1.33
	2004	26-Jul	6.49	67.2	52.1	1.50
	Average	25-Jul	7.81	65.4	49.1	1.53
Kings' Lynn	2002	26-Jul	6.07	60.6	40.8	1.94
	2003	16-Jul	7.46	63.5	43.5	1.68
	2004	26-Jul	7.21	64.3	41.2	1.87
	Average	22-Jul	6.91	62.8	41.9	1.83
Rosemaund	2002	18-Jul	10.45	69.2	47.1	1.79
	2003	15-Jul	8.56	67.7	41.5	1.52
	2004	23-Jul	8.90	65.9	42.6	1.71
	Average	18-Jul	9.30	67.6	43.7	1.67
Sutton Bonington	2002	22-Jul	8.81	63.0	46.1	1.88
	2003	14-Jul	8.99	68.8	46.1	1.85
	2004	13-Jul	10.25	65.0	42.8	1.88
	Average	16-Jul	9.35	65.6	45.0	1.87

* Crop not harvested

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