HGCA

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EFFECTS OF SITE AND NITROGEN MANAGEMENT ON GROWTH AND GRAIN QUALITY FOR MALTING OF WINTER BARLEY

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EFFECTS OF SITE AND NITROGEN MANAGEMENT ON GROWTH AND GRAIN QUALITY FOR MALTING OF WINTER BARLEY

by

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Contents

Further information about the database and its manipulation can be obtained from Ethel White at the above address.

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Summary

The project 'Interpretation of site/treatment effects on growth and N uptake of winter barley in relation to quality criteria, particularly %N in barley for malting' (0080/2/87) was funded by the Home-Grown Cereals Authority from 1988 to 1990. The programme of 17 experiments with two nitrogen treatments at six sites over three years was carried out by Rothamsted Experimental Station, Newcastle University, Queen's University Belfast, Nottingham University and ADAS Soil Science. Preliminary analysis and interpretation of the data on dry matter production and its partitioning, N uptake and its partitioning, phenological development, leaf area production and shoot production, were reported in Project Report No. 48 (Leigh, 1992). Further analysis of the database was funded by the HGCA in 1992 (0007/1/92) and output from this is presented and discussed in this report.

Partitioning of dry matter (DM) and nitrogen to the grain, i.e. DM harvest index and nitrogen harvest index, together with %N in the grain, were highly conserved characteristics of crops. Grain yield, total DM production and nitrogen offtake were very responsive to the availability of nitrogen and the effects of site and year. The contribution of stored carbohydrate reserves to grain yield was very variable from experiment to experiment and nitrogen had no clear influence on it. The contribution from nitrogen taken up before anthesis to the nitrogen content of the grain was much more consistent from experiment to experiment.

A database was constructed from the data collected on all characteristics at each centre. Verification of the data involved checking for outliers and examining residuals. The time series of data on dry weights were summarised using the Gompertz[*] function and the parameters from these functions used to calculate variates describing the patterns of growth. Variates describing the patterns of nitrogen uptake were derived using fitted dry weights and actual nitrogen concentrations. Site x Year matrices for the variates were analysed using ANOVA with corrected variance ratios and standard errors.

Fitting of the Gompertz function provided reliable and valuable summaries of the time series of total and ear dry weights. The agreement between the modelled and the observed data was

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[*] Gompertz Function: $y = A + C^{-(-b^{(x-m)})}$
This function allows the Relative Growth Rate to decrease exponentially with time and with growth achieved.

substantial, giving confidence in the fitting procedures adopted. However, the fitted growth patterns did not correlate with either stages in crop development or calendar date.

◆

Influence of Nitrogen, Site and Year on yield, carbohydrate production and partitioning and nitrogen uptake and partitioning

- **Economically-important characteristics:**

Grain yield

Grain yields varied in response to nitrogen and from site to site and year to year. Differences in ear numbers/m^2 accounted for variation in grain yield from year to year. The effect of nitrogen on grain yield was attributable to differences in both ear number/m^2 and grain number per ear. Various combinations of the components contributed to differences in grain yield amongst the sites. Variation in total dry matter production rather than harvest index accounted for the effects of year and nitrogen on the components and grain yield. Harvest index as well as total dry matter production varied from site to site.

%N in the grain

Nitrogen concentration in the grain (%) varied between 1.17 and 1.88% in 32 of the 34 experimental treatments. The two remaining samples, which were from Sutton Bonington, had nitrogen concentrations of 2.18 and 2.54%. Although nitrogen harvest index was much lower, total N and grain N offtakes were markedly higher at Sutton Bonington than at the other sites resulting in these high %N's in the grain. Application of nitrogen resulted in increases in %N in the grain of up to 0.43% in most experiments, greater increases of 0.60-0.77% being obtained at Sutton Bonington. Total N and grain N offtakes both increased in response to nitrogen application but nitrogen harvest index was lower in the fertilised than in the unfertilised crops.

- **Physiological characteristics:**

Total dry weight

The beginning and end of the phase of rapid increase in total dry weight as derived from the fitted Gompertz functions was not consistent from experiment to experiment either in calendar date or in relation to development. Approximately 10-15% of the final dry weight was produced prior to the main phase of growth. By anthesis 60% of the final dry weight was present with the remaining 40% being produced during the grain filling period. Application of nitrogen usually increased the rate of growth. Growth rates in the fertilised crops were much less variable than in the unfertilised crops.

Ear dry weight

The large effect of nitrogen on ear dry weight varied to some extent from site to site in each year. The contribution of stored reserves to the increment in ear dry weight was very variable from crop to crop. In eight out of 13 experiments, utilisation of reserves was greater in the unfertilised than in the fertilised crops.

Total N content

Application of nitrogen had a significant effect on the total N content of the crop at harvest but the responses to nitrogen varied from site to site and from year to year. In the unfertilised crops 34-63% and in the fertilised crops 12-88% of the final total N content, was present at ZGS 30/31. The fertilised crops took up 6.3-9.3g/m^2 and the unfertilised crops 0.3-3.5g/m^2 nitrogen between the time when nitrogen was applied to the fertilised crops and anthesis. Two of the unfertilised crops and six of the fertilised crops lost 0.6-2.0g/m^2 nitrogen between anthesis and harvest whilst the remaining crops, both fertilised and unfertilised, took up between 0.6 and 8.0g/m^2 nitrogen during grain filling.

Ear N content

Although application of nitrogen had variable effects on ear N contents at anthesis and harvest from experiment to experiment, the increment in ear N content and the contribution from pre-anthesis N uptake were markedly consistent in their response to nitrogen from site to site and year to year. Pre-anthesis uptake of nitrogen supplied 45% of the increment of 5.2g/m^2 in ear N content during grain filling in the unfertilised crops. In the fertilised crops there was a much greater contribution, 80%, from pre-anthesis uptake to the increment of 8.5g/m^2 in ear N content.

Shoot production and survival

In many crops most of the shoots were already present when nitrogen was applied. Maximum shoot number was not consistently reached at any particular growth stage. Final shoot number was very variable but the proportion of shoots surviving was reasonably constant from experiment to experiment. Both dry weight per shoot and N content per shoot were very variable from site to site and from year to year. Application of nitrogen had a variable effect on maximum shoot number but consistently increased survival by 15% so increasing final shoot number.

◆ **Mechanisms explaining carbohydrate production and partitioning**

A number of approaches were used to describe and explain carbohydrate production and partitioning:

(1) The **components of yield** provided a more detailed picture of the structure of the crop but are themselves net results of complex processes. The components confer a flexibility to cereal crops which allows them to respond continuously to and to exploit fully the variable weather conditions and supply of resources encountered in every cropping situation. Although the overall total dry matter production of the crop may be determined by the quantity of light intercepted, the crop's capacity to intercept all the available light over a long period of its life cycle and to utilise it depends on its ability to 'keep all its options open' until very late in the life cycle. In doing so it can avoid being severely limited by short term shortfalls and can capitalise on surpluses to produce what in effect is a relatively stable yield from situation to situation.

(2) The **rates and durations of production of dry weight** as derived from the fitted growth functions were related to grain yield via a simple model and a preliminary analysis of the effects of limiting factors was conducted. Application of nitrogen increased the rate of growth, thereby increasing total dry matter production and as a consequence increasing yield. Site and Year had large effects on both the rate and duration of growth, and therefore, on total dry matter production. Harvest index varied from year to year and from site to site but was only minimally affected by nitrogen. Site and Year both had marked effects on grain yield.

(3) The **status of the crop at anthesis** was considered as a pivotal point in growth and development, ear numbers and grain numbers having been finalised and crop capacity for photosynthesis and supply of stored reserves for remobilisation during grain filling having been established. The status of the crop at anthesis as shown by total dry weight, shoot number and dry weight per shoot, was not strongly associated with either the numbers of grain present at this stage, the grain productivity per shoot at harvest or the extent to which stored reserves contributed to grain yield. Stored reserves were utilised to a varying extent in grain growth, particularly when compared with the large and consistent effect of nitrogen on ear dry weight.

It was not possible to determine if reserves were fully utilised in grain-filling, i.e. exhausted, or if some reserves were left unused because there was insufficient demand from the grains.

(4) The relationship between **total dry weight and nitrogen offtake** was examined. Monteith's relationship (Monteith, 1977) between light interception and dry matter production was extended to include the influence of nitrogen on production of the light capturing capacity of the crop, i.e. its green area. Total dry weight was not strongly related to N offtake at any stage of growth although the nitrogen content of the unfertilised crops was more highly correlated with their dry matter production than was the nitrogen content in the fertilised crops. The unfertilised crops were also much more effective than the fertilised crops in utilising the nitrogen they took up to produce dry weight.

◆ Mechanisms explaining nitrogen uptake and partitioning

Although **apparent recovery** of the applied nitrogen varied between 20 and 79% in those crops where it could be determined, **uptake** between the time when nitrogen was applied and anthesis was similar in all crops within each treatment. During grain filling the behaviour of the crops varied greatly, some losing nitrogen whilst others had uptakes of up to 8.0g/m^2. However, the increments in ear N content and the amounts of nitrogen remobilised from pre-anthesis N uptake were similar in most crops within each nitrogen treatment.

Significant differences between the sites and variation from year to year in characteristics associated with grain yield and with nitrogen uptake of the crops only rarely led to high %N's in the grain. Consistent site differences in %N were not detected. The remarkably low sensitivity of %N in the grain to nitrogen availability to the crop is apparent from the small effect of the applied nitrogen on %N relative to its large influence on grain yield.

◆ Implications for crop management

Prediction of %N in the grain at earlier stages in the life cycle was shown to be unlikely to be reliable using results from this programme. Although remobilisation of nitrogen taken up before anthesis was the major source of nitrogen for the grain, variation in uptake and other processes influencing losses of nitrogen from the crops during grain filling resulted in variation in grain N offtake and therefore, in %N in the grain.

Crops maximise their production of dry matter using the nitrogen taken up, therefore, management for grain with low %N is consistent with management for optimum grain yields, i.e. maximum efficiency in utilisation of nitrogen.

◆ Future work

- Further analysis of green area, nitrogen concentration and nitrogen:area ratio in this database.
- Further analysis of the relationships between dry matter production and meteorological variates in this database.
- Development of concepts and experimental techniques for understanding flexibility of cereal crops.
- Methods of definition of sites using weather and soil data and including an investigation of the implications of the scale of definition on modelling of crop behaviour.
- The nitrogen economy of crops during grain filling - an investigation of processes influencing uptake and loss of nitrogen by crops and internal factors governing the remobilisation of nitrogen to the grain.

Chapter 1

Introduction

Cereal growers producing barley for malting want both to maximise yield and optimise %N in the grain. To do this, they have to modify their nitrogen fertilisation strategy from that employed for feed barley crops where the objective is to maximise yield with no concern for %N in the grain, lodging being the main qualifying limitation to this strategy. Thus the rates of nitrogen fertiliser applied to crops producing barley for malting are reduced compared with those applied to crops being grown solely for feed purposes, especially in the spring. The result is that the risk of producing high N concentrations in the grain is reduced. However, yield is also reduced. At present there is no way of knowing whether or not yield has been maximised and %N in the grain optimised. Therefore, the aim of any research should be to obtain knowledge upon which to base advice concerning the amount and timing of nitrogen applications so that yield is maximised and %N in the grain is optimised in each crop.

What research has been done?

Advice upon which management decisions have been made has traditionally been obtained from agronomic experiments looking mainly at the effects of factors on outputs from the crop such as yield and %N in the grain. The concern has been to clearly and accurately identify the magnitude of the effect which will be produced consistently in most years at most locations. To identify the effect results from a number of experiments are averaged and statistical measures (standard errors and significance levels) derived to describe consistency of the effect. The effects of weather and soil in introducing variation into these effects are considered as undesirable noise and have usually been ignored when giving advice.

The certainty of obtaining an effect of a specific magnitude should be an important consideration in making management decisions. Therefore, it would be desirable to know:

1. the relative magnitudes of the variation due to the (a) factor under consideration and (b) the environment,
2. the magnitude of the variation due to location, i.e. soil type, which is consistent from year to year, and
3. the magnitude of the variation due to year, which is highly inconsistent and unpredictable.

What do we know about physiology of cereal crops?

Our knowledge about the physiology of cereal crops has been usefully summarised in recent years by Hay and Walker (1989) in their book 'An introduction to the physiology of crop yield' and by Sylvester-Bradley, Scott and Wright (1990).

Essentially we know about:

1. Development in cereals, i.e. how their external morphology changes through the course of the life cycle, for example, E.J.M. Kirby's work on apical development (Kirby and Appleyard, 1984) and the Zadoks' growth Stage Key,
2. The mean effects of agronomic factors such as variety, sowing date, seed rate, nitrogen fertilisation regime, disease/fungicide, plant growth regulator, on yield and to a lesser extent on quality.

Attempts to understand the formation of yield have focused on:

1. The components of yield, i.e. ear number per unit area, grain number per ear and grain weight,
2. The linear relationship between the quantity of light intercepted and the production of dry weight.

These approaches have given a fuller picture of how cereal crops function but both have failed to yield information which can be used to manage the crop. The component approach is limited because the components themselves are the net results of a number of processes which have also been found to be extremely variable, i.e. with considerable noise due to environmental factors. Therefore, they are not easily managed. The light interception model is a summation over time and is not therefore, sensitive enough to events and influences occurring during the growing season.

What do we need to learn -

(a) About the crop?

1. What aspects of crop functioning influence yield formation and determine quality?
2. The relative effects of both agronomic and environmental factors on these processes.

(b) About using knowledge in formulating management advice?

1. How do we determine the expected effect of a factor in the context of individual crops, i.e. in relation to the conditions in which they are growing and their state of growth and development?
2. Since we cannot either adequately manage or predict the effects of weather and soil, how do we incorporate knowledge of their effects into management decisions -

   how do we determine to what extent such environmental effects outweigh, negate or override the effects of manageable factors?
3. Can we develop new ways of manipulating crops based on an improved understanding of their functioning?

Brief statement of physiology of cereal crops in relation to nitrogen

Crops utilise nitrogen to increase their capacity to produce carbohydrate, which constitutes most of the yield. Yield initially increases in direct proportion to the quantity of nitrogen applied. At higher rates of nitrogen, yield increases are much smaller and decreases may even occur. As yield increases the concentration of nitrogen in the grain remains low and constant. When yield increases begin to decline, nitrogen concentration in the grain begins to increase. Thus it appears that nitrogen in the plant which is surplus to the crop ‘requirement’ is likely to end up in the grain.

The amount of applied nitrogen at which yield is maximised and %N in the grain begins to increase will vary because some of the crop requirement for nitrogen will be met by residues from previous crops mineralised in the soil. The crop requirement for nitrogen and the supply of nitrogen by the soil are areas under active investigation and discussion by agronomists and physiologists (Bradbury, Tuck, Whitmore and Jenkinson, 1993; Sylvester-Bradley, 1993a).

Recent work producing new knowledge of the nitrogen economy of cereal crops

Guidance on the amounts and timing of nitrogen for crops has been the goal of much agronomic research including various HGCA-funded projects in recent years (Project Report Nos. 70, 73, 74 and 94). The influence of environmental factors, i.e. soil and weather, and the functioning of the crop have begun to be examined in greater detail in these projects.

Garstang, Vaughan and Dyer (1993) examined the effects of soil type, defined in terms of Available Water Capacity, and nitrogen source on yield and %N in autumn-sown barley. However, the behaviour of the crop during the growing season was not examined. The erratic and unpredictable effects of weather on yield and %N in the grain and therefore, on the regional availability and premia offered for malting barley were identified as major and uncontrollable factors.

In a wide-ranging review of nitrogen usage on cereal crops, Sylvester-Bradley (1993b) presented a hypothesis about how nitrogen influences crop growth to increase yield. The asymptotic response of yield to nitrogen could be attributed to the asymptotic pattern of light interception shown by the crop as its green area increases. Based on evidence from a limited data-set from one experiment in one year (Sylvester-Bradley, Scott and Stokes, 1990), it was concluded that the quantity of green area produced by crops is directly related their nitrogen content, 30 kg of nitrogen being required to produce one hectare of green area. Although green area continues to be produced as the quantity of nitrogen increases, once a green area of three to six ha per ha of land is produced there is little further increase in interception of light and therefore, little further increase in yield. From this hypothesis it is possible to predict the crop requirement for nitrogen based on its requirement for green area to intercept light. This hypothesis requires validation from other experiments.

The supply of nitrogen by the soil was modelled by Bradbury *et al.* (1993). Soil type influenced the minimum quantities of nitrogen which were retained by the soil and unavailable to all biological processes. Clay content of the soil played a role in determining the decomposition of organic carbon. The authors were satisfied with the agreement between the model predictions and observed soil mineral N levels and crop N offtakes at three locations over four years. However, when used as a management tool it requires expected yield from the field given an average season. Sensitivity to variation in expected yield was not reported.

Within-crop variation in partitioning of dry matter and nitrogen in spring barley, i.e. both between tillers and within shoots, was investigated by Marshall and Ellis (HGCA Report No. 94, 1994). Implications for a number of grain characteristics playing a role in malting behaviour were discussed. Their experimental programme took place mainly under controlled environmental conditions to permit control and regularisation of the supply of nitrogen and to allow easier identification of the effects of nitrogen. A model was developed to explain the role of nitrogen in determining growth, in which the concentration of nitrogen in the photosynthesising tissues is related to the intensity of light incident on the tissue. This contributed to a fundamental restructuring of the approach to physiology, i.e. the concepts used in understanding the controlling mechanisms and the driving variables.

Aims of the continued analysis and interpretation of the 1988-1990 database undertaken in this project

Yields of barley crops and %N in the grain vary. Nitrogen application as fertiliser and other management strategies have known effects on yield and %N in the grain. However, the size and direction of these effects are not entirely predictable because season and site modify their influence on the growth and development of crops.

In the experimental programme, 1988-1990, variation in yield, %N in the grain, growth and development of 17 crops was monitored. Site, season, genotype, sowing date, residual nitrogen in the soil and timing of the nitrogen application all varied from experiment to experiment. Control of disease, application of a growth regulator and some standardisation of the amount of nitrogen applied as a fertiliser removed some sources of variation from the crops. A major part of the project is descriptive but traditional and novel hypotheses about the functioning of crops will be examined in the discussion.

Our objectives were:

1. To find accurate, practical and biologically meaningful ways of interpreting growth analyses data from experiments.
2. To describe and understand the processes involved in crop utilisation of nitrogen and how the environment modifies these processes:
    - to describe the patterns of dry matter production and its partitioning and nitrogen uptake and its partitioning in crops;
    - to examine how nitrogen affects these processes;
    - to determine the extent to which year and location produce variation in these processes and their response to nitrogen application.
3. To consider how this knowledge will contribute towards refining guidance about how much nitrogen to apply to crops and when it should be applied, so removing some of the uncertainty about its effects on yield and %N in the grain.

Dry matter production in crops

Green plants use light energy to make carbohydrate from carbon dioxide and water in the biochemical process of photosynthesis. Since most of a plant's dry matter comprises carbohydrate, the supply of light, water and carbon dioxide are vitally important to the macro-process of growth. Proteins, a class of compounds which includes many chemicals indispensable to the functioning of the plant, are also a major constituent of the dry matter. Nitrogen is necessary for protein production and so the supply of nitrogen is also an important determinant of growth. In practice we find that growth of crops is mainly limited by the supply of light, nitrogen and, to a lesser extent, water with carbon dioxide not considered to be a practical constraint on productivity.

The extent to which the plant can make use of the supply of these raw materials relates to its development which is largely dependent on temperature. Where plants are grown together as a population, a crop, the time course of their growth will inherently follow a sigmoidal pattern. The rate of growth is slow to begin with, then it speeds up and finally it slows down as individual plants reach their maximum size as determined by competition with their neighbours. In cereal crops the first of these phases coincides with cooler temperatures and poorer light conditions over winter in autumn-sown crops and in spring with spring-sown crops. These conditions exaggerate the length of the phase, particularly in autumn-sown crops. The second phase, when there is rapid growth, coincides with late spring and early summer when light and temperature are most favourable for growth and development. The third phase also coincides with a time of the year when environmental conditions favour growth but the crop is being driven towards maturity by its inherent development pattern, having achieved maximum capacity to utilise the available light.

The mathematical descriptions of growth derived from the results of this experimental programme will be examined in relation to what might be expected from the development pattern of the crop. The modification of this pattern of growth by the supply of light, water and nitrogen and the influence of site and year on this will then be considered.

Pattern of dry matter production as determined by development

The development of the crop defines both the time course of growth and its magnitude. Organs are produced according to a genetically determined sequence and, in classical physiological terms, can be considered to act as both sinks and sources, usually sequentially but also, depending on the organ, simultaneously. Development of winter barley will be described and a pattern of dry matter production derived from this will be presented.

Barley plants produce leaves, tillers, stem internodes and inflorescences in an orderly sequence. The timing and rate of **production** of these organs is primarily controlled by temperature, daylength and vernalisation, the influence of these factors varying during the life cycle.

The **potential** numbers and size of each of the organs are also determined by these environmental factors. The **realisation** of these numbers and sizes is dependent on the availability of carbohydrate, nutrients and water when they are growing. Phenological development plays an important role by determining the phasing of growth in relation to the supplies of light, water and nutrients which are controlled by climate and weather. Thus phenological development indirectly influences the final numbers and sizes of organs and the grain yield of crops.

Up to ZGS30, leaves and tillers are being produced but they comprise little dry matter at this stage. Once stem elongation begins, more or less synchronously in all shoots, dry matter increases rapidly. The ear is also increasing in size and differentiating during this phase up to ear emergence and anthesis. After anthesis, dry matter production continues to increase for some time as the grains fill with carbohydrate which has been produced throughout the plant. The rate of dry matter production declines as the plant senescences from the lower leaves upwards and the grain dries out prior to harvesting.

The following phases of dry matter production can be defined in relation to growth stage:

- **Sowing - ZGS30** - very low rate of dm production (approx. 10% final dw)
- **ZGS30 - ZGS65** - very high rate of dm production (approx. 60% final dw)
- **ZGS65 - ca. ZGS87** (hard dough) - high rate gradually decreasing to zero (approx. 30% final dw)
- **ZGS87 - ZGS92** - dry weight constant or decreasing due to respiration

Sowing to ZGS 30

This is an important phase for subsequent growth of the crop although only a small proportion of the total dry matter produced by the crop is present at the end of this phase. leaves are produced, their size being dependent on temperature and nitrogen supply. Tiller buds in the axils of the oldest leaves may or may not succeed in emerging and continuing growth. Leaves and grain are initiated at the apical meristem hidden deep within the shoot.

ZGS 30 - ZGS 65

Most of the biomass of the crop is produced in the period between ZGS 30/31 and anthesis. The crop is producing tillers which in turn are producing leaves, the stem is elongating and the ear is growing rapidly and differentiating. Leaf area is produced which absorbs radiation and carbohydrate is produced for further growth. Nitrogen, water and radiation are the resources being used which will determine the amount of growth which takes place. Research to date has tended to focus on one of these resources to the exclusion of the others in individual programmes.

ZGS65 - ca. ZGS87 and ZGS87 - ZGS92

Under ideal conditions during grain filling ie. adequate water and non-high temperatures, dry matter production will continue. However, if drought and/or high temperatures curtail photosynthesis or hasten senescence, less dry matter will be produced and pre-anthesis dry matter will constitute a greater proportion of the final crop dry weight. Therefore, the crop has to rely on its reserves if the grain filling period is shortened.

Parameters of the pattern

For any crop the pattern of growth may be defined and summarised by the following parameters:

- Date of ZGS30
- Date of ZGS65
- Date of ZGS87
- Duration of dm production Sowing-ZGS30
- Duration of dm production ZGS30-65
- Duration of dm production ZGS65-87
- Rate of dry matter production ZGS30-65
- Rate of dry matter production ZGS65-87
- Total crop dry weight
- % total dry weight at ZGS30
- % total dry weight at ZGS65

Chapter 2

Materials and Methods

(a) Experimental phase

A total of 17 experiments was conducted at five to six sites throughout England and Northern Ireland over three years, 1988 to 1990 (Figure 2.1). At each site, detailed assessments of development, dry matter production and crop nitrogen content were conducted on two nitrogen treatments:

(i) **N0 crops,** where no nitrogen was applied - to look at the supply and effect of soil supply of nitrogen and compare this with

(ii) **Ns crops,** where the amount of nitrogen applied was designed to produce malting quality grain.

Details of the sites and management at each are given in Table 2.1

In 12 of the 17 experiments the cultivar grown was Magie, with Pipkin grown in another three and Halcyon and Igri each in one experiment. The use of several cultivars in the programme creates major difficulties with interpretation of the results but there was no other option given the guidelines and limited budget of the project.

The following measurements were made on each crop:

- Total crop and ear dry weights and N contents of the whole crop and ears fortnightly from N application to anthesis and weekly thereafter.
- Grain yield, components of yield and grain % N.

Optional measurements of shoot numbers, projected green area index, patterns of grain growth and intercepted radiation.

Mean data for the time series from each site available at the beginning of this project are presented in Appendix 2.1

Table 2.1 Site and management details 1988-1990

Sites

Belfast
Newcastle
Sutton Bonington
Rothamsted
Blunham
Potton

Years

1988
1989
1990 (Potton was not included)

Cultivars

	Belfast	Blunham	Newcastle	Potton	Rothamsted	Sutton Bonington
1988	Pipkin	Magie	Magie	Pipkin	Magie	Igri
1989	Magie	Magie	Magie	Magie	Magie	Magie
1990	Magie	Pipkin	Magie	-	Halcyon	Magie

N Application (kg/ha)

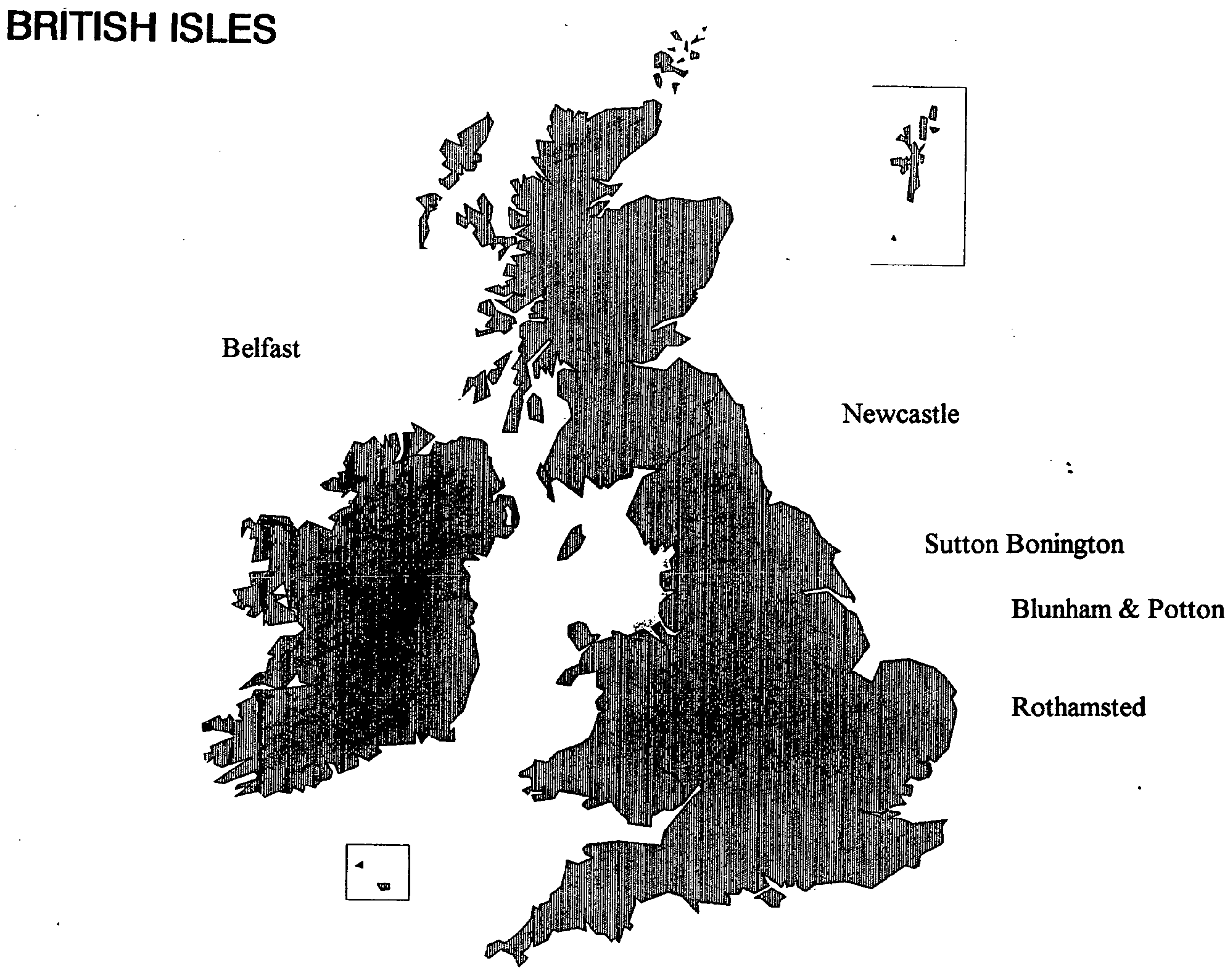
	Belfast	Blunham	Newcastle	Potton	Rothamsted	Sutton Bonington
1988	0, 120	0, 120	0, 100	0, 120	0, 125	0, 120
1989	0, 120	0, 120	0, 100	0, 120	0, 85	0, 120
1990	0, 120	0, 120	0, 100	-	0, 100	0, 120

PGR (if used)

	Belfast	Blunham	Newcastle	Potton	Rothamsted	Sutton Bonington
1988	Terpal	Terpal	Terpal	Terpal	-	-
1989	Terpal	Chlormequat	-	Terpal	-	-
1990	Terpal	Chlormequat	Terpal	-	-	-

Figure 2.1

Sites where data were collected 1988-1990



(C) George Philip & Son Limited

(b) Data handling

2.1 Nature of task

The treatment and handling of data derived from this collaborative multi-centre winter barley project was a complex task because of:

- The large number of data pieces (≥20,000 original data pieces).
- The need to transfer data from five centres to one.
- A variety of methods of storage and initial handling had been used at different centres/sites.
- Storage and retrieval of information contained in and derived from combined data was required.
- Formation/construction of a database with specific characteristics was an objective.

Prior to the interpretative stage of the project the following steps were required to deal with the above scenario:

1. Transfer of original data
2. Verification of original data
3. Calculation of derived data

The aim of the data handling part of the project was the construction and interrogation of a large database. In addition to the size and dimension aspects of such a database (year, site/centre, cultivar, N application, cultivar, variate), the objectives and practicalities of database construction were considered:

- Database should be error free.
- Outliers were to be identified and removed.
- Database must be organised and structured in time and space.
- Database must yield results (derived data).
- All steps in construction phase must be accurately recorded.
- Database must be easy to use (logical) and accessible to others, i.e. a valuable resource.
- The database must be secure (cross referenced and incorruptible).

2.2 Tools

Data was handled using both mainframe and PC software tools. The database was constructed using the Digital VAX mainframe at Rothamsted, and at DANI/Queen's University, Belfast. The major statistical package used was Genstat 5.22. Display, tabulation and calculation was also carried out using PC based Microsoft Excel software.

2.3 Database construction

(i) Data transfer

During the experimental phase of this project, 1988 to 1990 (Project 0080/2/87), data collection was controlled at the centre level. Therefore, a centralised destination at Rothamsted for collated data had been established. The interpretative or secondary phase of the project funded in 1992 (0007/1/92) had no control over either data collection or collation. At the beginning of the second phase in March 1992, the collated data was transferred by electronic mail in bulk in DATATRIEVE format to the VAX mainframe at Belfast. All data files where edited to remove extraneous text codes and symbols which had been inserted during e-mail.

(ii) Data extraction

The DATATRIEVE format for the collated data ensured that all data pieces were correctly aligned with any associated text. DATATRIEVE operates in a row and column format like a spreadsheet unlike GENSTAT which reads data in either serial or parallel format. The extraction process allowed data to be read to a set of logically named files in a standard format while ensuring the association of data with owner details, e.g. a certain number with a certain year+site variate name. The format was standardised so that the way the database could be read by GENSTAT, i.e. the serial/parallel order of each file was standardised. The end result of extraction was a set of "original" data derived from all centres/collaborators. At this stage problems with the data (such as missing replicates, etc.) were sorted out by personally contacting each collaborator. The extraction phase involved a considerable amount of file editing to enable GENSTAT to read the data, e.g. adding the colon symbol which GENSTAT recognises as an end mark.

(iii) Verification

This particular phase was carried out using four subdivisions of the data as follows:

- Dry matter production
- Nitrogen uptake
- Shoot production
- Final harvest characteristics

This structure provided a practical and logical structure for verification. The aim of verification was to obtain a reliable and compatible set of data.

Prior to verification the (raw) collated data contained a number of unusual data pieces that did not appear to be similar to data from other experiments. Exclusion of such data pieces made the database more reliable and ensured that interrogation of the database was carried out using comparable datasets and was not confounded by suspect data. The verification processes can be summarised thus:

Original Datasets ➔ Verified Datasets
➘
Outliers/Errors

Outlier/error types identified can be summarised as follows:

- Input errors or sampling errors.
- Calculation errors.
- High residuals.

To verify the database simple GENSTAT programs were devised (Appendix 2.2) to read, sort, print, graph and tabulate all data pieces. Outliers and residuals derived from ANOVA were shown. The graphs from these outputs were manually examined for unusual data and residuals. A number of basic errors in the data were identified as simply input mistakes (e.g. input 1300 instead of 1.3) and these data pieces were removed from the database immediately and easily. An example of an input error is shown in Appendix 2.3. This first analysis enabled the following basic information to be examined.

1	2	3	4	5	6
Day	Block	Treatment	Variate	Residuals	Graphs

Since all the data were capable of being tabulated and graphed in the same format and had a parallel set of residuals, all "large" residuals were marked in each dataset. Corresponding data pieces were checked on graphs in the previous report (Leigh, 1993) on the experimental phase.

(iv) Fundamental errors

In addition to data input errors calculation errors were encountered, for example:

		Treatment	
	Urea Fertiliser	Ammonium Nitrate Fertiliser	Nil Fertiliser
Data in Initial Database	728	641	614
	↙	↘	
After Recalculation	641	728	614

Data pieces assumed to be due to calculation errors were removed from the database.

(v) Residuals

Residuals for all variates were obtained by conducting Analysis of Variance using Genstat. High residuals were identified as those which were greater than the mean ± standard error (Table 2.2). The data pieces contributing to the mean were then examined to determine which one was extreme. This data piece was then removed.

Table 2.2 Extract from GENSTAT output file showing residuals

* the following units have large residuals

Site	Year	Block	Unit	Data
Belfast	1990	2	1	151
Belfast	1990	2	2	-151
Newcastle	1989	3	1	151
Newcastle	1989	3	2	-151
Sutton Bonington	1990	2	1	-113
Sutton Bonington	1990	2	2	113
Sutton Bonington	1990	3	1	243
Sutton Bonington	1990	3	2	-243
Sutton Bonington	1990	4	1	-157
Sutton Bonington	1990	4	2	157
Rothamsted	1989	1	1	-155
Rothamsted	1989	1	2	155
Rothamsted	1989	4	1	130
Rothamsted	1989	4	2	-130

Residuals were removed from the database in the following proportions (across all 3 years):-

Data Type	Number	%
Total dry weight	49	7.3
Ear dry weight	62	9.3
Shoot number	31	4.6
% N total	41	6.1
% N Ear	44	6.6
% N Straw	18	2.7
Grain dry weight	14	2.1
Total N uptake	11	1.6
Grain N uptake	29	4.3

Of the total of 670 data pieces with high residuals removed from the database over half of these were from 1988 datasets (55%) while the other two years had approximately a quarter of the data pieces with high residuals each (24% - 1989; 21% - 1990).

2.4 Database manipulation

Once a standardised set of data was available, new variates, known as derived variates, were calculated using a number of methods:

Dry Matter	Total and Ear	New variates derived from curve fitting exercises
Nitrogen Uptake	Total and Ear	New variates calculated using dry weight and % N data
Shoot Production		New variates derived by visual examination of graphed data

(i) Dry matter production

The derivation of calculated variates is common to most areas of scientific research. Such variates can be defined as being:

- mathematically related to the original data, e.g. a result of division, multiplication, summation, subtraction or some other mathematical function;
- additional to, not instead of, original variates;
- useful, as they enable forecasting, prediction and extension of data limited by sampling.
- meaningful (sometimes with more meaning than original data), for example, rates of change can be more meaningful than a static sample result.

For example: A fitted curve will give rise to additional information regarding the total dry weight of a crop at any point in the development of the crop. This would not be possible unless derived variates are obtained.

In the case of the database it was highly desirable to statistically compare data sets which were limited by the practicalities of labour intensive sampling programs. Derived or calculated variates were obtained through curve fitting using mathematical functions for dry weights of the crops.

The process can be simply summarised thus:

1. Modelling of original datasets (curve fitting)
2. Production of a mathematical function describing the curve
3. Acceptace or rejection of new variates/information
4. Calculation of derived variates using curve parameters
5. Statistical comparison of sites/years based on new derived variates

Curve fitting procedure

Genstat programs devised to handle and analyse the database, were amended to fit curves to time series of dry weights of the whole crop and ears.

The first stage was to fit several curves to the data with the aim of selecting a curve fitting procedure which most accurately reflected the original data and gave rise to few rejections of datasets. The Genstat function FITCURVE with option parameters GLOG and GOMP provided two curve fitting procedures based on biological growth functions. Both curves are LOGISTIC: GLOG is a generalised logistic curve and GOMP is the Gompertz logistic fitted curve. These curves can be described thus:

Generalised Logistic [GLOG]

$$y = 1 + C / (1 + t^{-b^{(x-m)}})^{1/t}$$

Gompertz [GOMP]

$$y = A + C^{-(-b^{(x-m)})}$$

where

A = lower asymptote
m = point of inflection for explanatory variable
b = slope parameter
t = power law parameter
C = upper asymptote

A good fit of the GLOG curve requires data both for the steep central part of the curve and for the lower and upper asymptotes.

The Gompertz curve is non-symmetrical about the inflection point, $x = m$, and has asymptotes at $y = A$ and $y = A + C$. The Genstat program is shown in Appendix 2.4.

Results of Fitting GLOG

When Generalised Logistic (GLOG) functions were fitted to the data, many datasets gave problems which appeared on the output as:

- Approaches Gompertz fit
- Fatal fault
- Approaches arrested exponental
- Residual variance exceeds variance of Y variate
- Optimisation out of bounds

Twenty out of 30 datasets had such problems. When Gompertz functions were fitted to the same datasets, all but two had no problems. Therefore, it was decided to fit Gompertz functions to all datasets (102 in total).

Results of Fitting GOMPERTZ

The general aim was a curve of best fit which could give rise to meaningful parameters such as area under the curve from which growth rates could be calculated.

Total Dry Weight:

Two methods were used.

(1) No modification of the original data.

(2) Since there were often large differences in dry weight between samples during grain filling, the upper asymptote was 'forced' to increase the likelihood of an asymptote being produced. This was achieved by using an extra day added at the end of each dataset (replicate + treatment). A value was inserted based on the mean dry weight over the last two dates in each replicate, at an interval of 5 days after the last sample date.

For example:

Replicate	Nitrogen	Total dry weight at 4 Julian dates				New value
1	0	140	148	152	165	159
2	0	141	145	153	160	157
3	0	145	146	150	155	153
1	120	150	158	165	170	168
2	120	153	159	163	171	167
3	120	149	155	159	169	164

Mean

Genstat output based on the two methods outlined above was produced. Table 2.3 shows data for Belfast 1988 with and without modification. This procedure improved the fit of the function to the data and the derived curve functions (Maximum, time 1, etc.) were more realistic. All datasets were subsequently modified to add an extra data piece at a "sampling" date of five days after the last actual sample date.

Table 2.3

(a) Total dry weight: parameters and derived variates based on no modification of data (Belfast, 1988)

Replicate	Nitrogen	B	M	C	A	Max	Time 1	Time 2	Duration	Growth Rate
1	0	0.0978	156.9	424.2	41.1	466	149	180	32	6060
2	0	0.4410	145.4	331.1	49.4	381	144	151	7	963
3	0	0.0861	147.3	287.0	30.6	318	138	174	36	473
1	120	0.1136	147.4	1216.4	131.1	1348	140	167	27	15101
2	120	0.0808	143.2	1145.3	67.7	1212	133	171	38	22212
3	120	0.0684	146.5	1391.5	53.1	1445	134	180	65	33072

(b) Total dry weight: parameters and derived variates based on modification of data by addition of extra sample day (forced upper asymptote)

Replicate	Nitrogen	B	M	C	A	Max	Time 1	Time 2	Duration	Growth Rate
1	0	0.0888	157.5	450.7	41.1	491	148	183	35	7434
2	0	0.4959	145.3	322.3	49.5	372	144	149	6	816
3	0	0.0918	147.1	279.5	31.1	311	138	172	34	4259
1	120	0.1205	147.2	1194.3	132.0	1326	140	166	26	13924
2	120	0.0870	143.4	1119.8	71.5	1191	134	169	36	19824
3	120	0.0729	146.3	1355.7	56.6	1412	135	177	42	29952

Ear Dry Weight

The same procedure for fitting GOMP curve was applied across all Ear Dry Weight datasets. However, for Ear Dry Weight the number of available data points influenced the fitting of the curve. Four methods of handling the data were attempted:

(1) No modification of data.

(2) Upper asymptote forced (as per Total Dry Weight)

(3) Upper and lower asymptotes forced using zero mg m^{-2} at date of sowing.

(4) Upper and lower asymptotes forced using zero values for missing measurements prior to earing.

The following examples are based on data from Rothamsted 1989.

	Replicate	N	B	Time 1	Duration
• Without modification	1	0	0.03177	140	97
• Upper asymptote forced	1	0	0.04614	139	67
• Upper and lower asymptotes forced using 0g/m^2 at date of sowing	1	0	0.05205	145	59
• Upper and lower asymptotes forced using 0g/m^2 for early dates	1	0	0.05023	140	62

In all cases where Method 2 (upper asymptote forced) was used there was a small improvement in the shape of fitted curves and consequently an improvement in the curve parameters and derived variates. Where the lower asymptote was also forced using a zero value, Method 3, (based on the assumption that the initial contribution of the seed towards ear weight can be regarded as being very close to zero), poorly fitted curves were produced, the lower part of the curve being considerably weighted. The curves from the modification of the data just prior to existing data, Method 4, resulted in much better fitted curves and realistic curve parameters and derived variates. It was decided to force the lower part of Ear Dry Weight datasets using a 0g/m^2 for the first value and missing values for the remaining values, as follows:

Ear Dry Weight Modification

Julian Day	Measurement	
78	0	← (ZGS 30)
84	*	
90	*	← missing values
94	*	
99	*	
105	37	
109	45	
116	110	

Derived parameters

A growth rate for Total Dry Weight in each replicate was calculated from the parameters B, M, C and A (curve gradient, point of inflection, upper asymptote and lower asymptote respectively) obtained from the fitted Gompertz curves. Genstat was used to calculate functions of the B, M, C, A parameters as follows:

1. Obtain B, M, C, A by fitting Gompertz to Total Dry Weight data
2. Obtain maximum value from original data (g m^{-2})
3. Calculate TIME 1 as 10% of growth, i.e. start of growth proper (day)
4. Calculate TIME 2 as 90% of growth, i.e. end of growth (day)
5. Calculate DURATION to be TIME 1 - TIME 2 (day)
6. Calculate GROWTH RATE (g m^{-2} day^{-1}) using Genstat which assumes that the curve is linear
7. Calculate CURVE AREA (g m^{-2} days), i.e. *Increase in total dry weight between TIME1 and TIME2,* using MATLAB, a Maths software package. The area under the curve is calculated using a numerical method based on the Gompertz function.
8. Calculate WEIGHTED MEAN ABSOLUTE GROWTH RATE (g m^{-2} day^{-1}), i.e. *Mean weight increase per* m^2 *per day during period TIME1...TIME2 (=AREA UNDER CURVE/DURATION*^{2}*)* using MATLAB

Calculation of the Weighted Mean Absolute Growth Rate using MATLAB was satisfactory as it took into account the slower rate of growth at the beginning and end of the growth period in barley crops. Genstat was capable of estimating the growth rate basing its calculations only on a linear curve with no lag phases at the start or end of crop growth.

Worked example:

Genstat parameters

Replicate	Code	Nitrogen	B	M	C	A
1	A	0	0.02837	138.6	780.5	99.97
2	B	0	0.03448	130.2	1028.9	60.64
3	C	0	0.03318	105.8	736.5	-7.73
1	D	120	0.04146	123.7	1270.4	82.67
2	E	120	0.12619	118.8	903.8	146.23
3	F	120	0.11075	116.8	986.7	151.62

Genstat Derived Variates

Replicate	Code	Maximum value ($g\ m^{-2}$)	Time 1 (day)	Time 2 (day)	Duration (days)	Estimated* growth rate ($g\ m^{-2}\ day^{-1}$)	Curve** ($g\ m^{-2}$ days)	Weighted mean absolute growth rate** ($g\ m^{-2}\ day^{-1}$)
1	A	880	109.2	218.0	108.72	5.74	58896	4.98
2	B	1090	106.0	195.0	89.45	9.20	57386	7.17
3	C	729	80.7	173.6	92.95	6.34	37963	4.40
1	D	1353	103.6	178.0	74.40	13.66	59595	10.77
2	E	1050	112.1	136.6	24.44	29.58	16051	26.87
3	F	1138	109.3	137.2	77.85	28.34	19831	25.57

* Using Genstat

** Using Matlab

Summary of total and ear dry weight data

Original data ➔ B C M A ➔ Max Growth
Time 1
Time 2
Duration
Growth Rate

↑ Curve Parameters (under B C M A)

↑ Derived Variates (under Max Growth … Growth Rate)

Quality control of fitted functions

When curves had been fitted, parameters extracted and derived variates calculated for all datasets of Total and Ear Dry Weights, checking was carried out prior to collation of the site/year matrices for selected variates. The criteria used were:

1. Goodness of fit as indicated by the % variance accounted for. 70% was the limit for acceptance.

2. Physiologically realistic derived variates, such as durations of growth and the comparison of Time 2 with date of harvest.

3. Comparison of the maximum growth calculated from the fitted function with the maximum dry weight in the actual dataset and the maximum determined visually from a plot of the data.

Where fitted curves accounted for less than 70% of the variance, had unrealistic derived variates and deviated from either the maximum dry weight in the dataset and/or the curve maximum, their derived variates were not included in the sites/years matrices.

(ii) Nitrogen content

N content of crops was calculated by using modelled values for dry weights and N concentrations in the crops on actual dates. The following variates were derived:

Total N content:

- Total N content at harvest
- Total N content at ZGS 30/31
- Proportion of the final total N content in the crop at ZGS 30/31
- Total N content at date of N application
- Proportion of the final total N content in the crop at N application
- Total N content at anthesis
- Proportion of the final total N content in the crop at anthesis
- Increment in total N content between ZGS 30/31 and anthesis
- Proportion of final total N content taken up between ZGS 30/31 and anthesis
- Increment in total N content between N application and anthesis
- Increment in total N content during grain filling
  = Total N in crop at maturity - total N in crop at anthesis
- Proportion of the final total N content taken up or lost during grain filling

Ear N content:

- Ear N content at harvest
- Ear N content at anthesis
- Increment in ear N content during grain filling
- Contribution of N uptake prior to anthesis to final ear N content
  = (increment in ear N content during grain filling
  - increment in total N content during grain filling)

(iii) Shoot production

Original shoot data from the experimental phase were graphed against the dates at which samples were taken. The approximate numbers of shoots at critical stages in development were estimated from these graphs. The derived variates were:

Shoot number at date of N application
Shoot number at anthesis
Mean shoot number after maturity
→ final shoot number
Maximum shoot number
Date of maximum shoot number
Tiller productivity

$$= \frac{\text{Maximum shoot number - Shoot number at N application}}{\text{Shoot number at N application}} \times 100$$

Note: (Shoot numbers were not available for Sutton Bonington)

(iv) Meteorological Variates

All meteorological data were provided by Rothamsted (Met. Office data). The following variates were examined:-

Variate	**Notes**
Evaporation	Over grass (mm)
PSMD	Potential soil moisture deficit (mm)
Rainfall	(mm)
DDA	Temperature in degree days above zero
Radiation	kj/m^2
Phase Length	(days)

Means, totals, maxima and minima for sites and seasons were obtained, tabulated and graphed.

2.5 Database organisation and retrieval

The database was organised so as to allow users access to all stages of database construction should they so wish. For example, a user may enter the mail facility and retrace step-by-step all the stages described in this report or a user may simply access whatever type of data she/he is interested in. The DIRECTORY held by DANI/QUB is subdivided into sub-directories (Figure 2.2).

1. Input MAIL
    LIS
    HGCA
    CALC
    GEN
    ANAL

Files held in MAIL, LIS, ANAL, GEN and CALC subdirectories have logical filenames and a further subdirectory (GRAPH) contains easy to use Genstat programs for producing graphical output (DGRAPH command in Genstat 5). Graphs can be viewed using a high definition graphics terminal.

2. Output HARV
    SHOOT
    DWT
    NITROGEN
    MET

Each subdirectory contains Data and Genstat programs. Derived variates are accessible in a data file with their associated Genstat program as follows:-

Harv Subdirectory

HARVEST.DAT
HARVEST.GEN
HARVESTA.GEN
HARVESTB.GEN

Figure 2.2

Organisation and retrieval of the database

Directory

GBDG - Mail (all original E-mail data files transferred from Rothamsted)

Tools (Input)			DATABASE STAGE 1				Results (Output)		
ANAL	HGCA	LIS	GEN	CALC	HARV	SHOOT	MET	NITROGEN	DWT
Model Programs for Genstat Analysis	Original Files	List Output (Text + Data) From original data	Genstat Programs	Verified Data files	Final Harvest	Shoot Data	Meteorological Files	N Content Data	Site x Year Matrix

Shoot Subdirectory

SHOOTDATA.DAT
SHOOTDATA.GEN

DWT Subdirectory

TOTALDWT.DAT
TOTALDWT.GEN
EARDWT.DAT
EARDWT.GEN
BMCATOT.DAT
BMCATOT.GEN
BMCAEAR.DAT
BMCAEAR.GEN
CALCDWT.DAT
DALCDWT.GEN

Nitrogen Subdirectory

SITEYEAR.DAT
SITEYEAR.GEN
MODUNIT.GEN

Met Subdirectory

Three file types containing meteorological variates can be accessed as follows:-
Files with file extension .DOC
Files with file extension .DAT
Files with file extension .GEN

Files listed as .DOC contain original data extracted for various time periods from Met. Office data. Each file contains summary information such as max, min and mean as well as dates. The data is arranged in chronological order, e.g. 1988, 1989, 1990. Three phases are accessible:-

Phase 1 Filename P1.DOC Sowing to ZGS 30/31

Phase 2 Filename P2.DOC	ZGS 30/31 to anthesis
Phase 3 Filename P3.DOC	Anthesis to maturity

Files containing the file extension .DAT contain the meteorological data in a form readable by Genstat, i.e. data with no header or foot text. Again the data is arranged in 3 blocks, 1988, 1989 and 1990, each dataset being separate by a colon.

Files with the .GEN extension refer to the Genstat program which corresponds to each data file. Each program reads the relevant data file and produces an annotated graphical output for each variate for each year, i.e. five graphs per year for evaporation, PSMD, rainfall, DDA and radiation. The x axis of each graph produced will be in days beginning with the date which starts the phase and ending the date which finished the phase.

The meteorological files are listed below:-

METBELP1.DOC/DAT/GEN
METBEL882.DOC/DAT/GEN
METBEL892.DOC/DAT/GEN
METBEL902.DOC/DAT/GEN
METBELP3.DOC/DAT/GEN

METNEWP1.DOC/DAT/GEN
METNEW88P2.DOC/DAT/GEN
METNEW89P2.DOC/DAT/GEN
METNEW90P2.DOC/DAT/GEN

METSUTP1.DOC/DAT/GEN
METSUIT88P2.DOC/DAT/GEN
METSUT89P2.DOC/DAT/GEN
METSUT90P2.DOC/DAT/GEN
METSUTP3.DOC/DAT/GEN

METPOTP1.DOC/DAT/GEN
METPOTP3.DOC/DAT/GEN

METBLUNP1.DOC/DAT/GEN
METBLUNP3.DOC/DAT/GEN

METRESP1.DOC/DAT/GEN
METRES88P2.DOC/DAT/GEN
METRES89P2.DOC/DAT/GEN
METRES90P2.DOC/DAT/GEN
METRESP3.DOC/DAT/GEN

METBLUNPOT88P2.DOC/DAT/GEN
METBLUNPOT89P2.DOC/DAT/GEN
METBLUNPOT90P2.DOC/DAT/GEN

Chapter 3

Results

3.1 Statistical aspects of the interpretation of the results

In standard agronomic and physiological experiments, treatment factors are replicated within the experiment to obtain an estimate of variation due to random and unknown factors, for example, fertility or moisture availability disuniformities across fields. However, in this programme of experiments we are interested in the nature and magnitude of site effects and variation from year to year, neither of which can be replicated. Therefore, to give an estimate of the significance of these factors the error variance used is that of an interaction. The nitrogen treatment and the site factor are regarded as fixed factors in that they are not variable whilst year is a random factor because it does vary. The status of the factor affects their statistical comparison, so that variance in the fixed factors, nitrogen and site, is compared with variance in the combination of factors which includes years rather than the smaller 'error' variance.

Table 3.1 Corrected variances for determining significance of the effects of nitrogen, site and year and their interactions

	Variance for significance		
	P<0.05	P<0.01	P<0.001
Sites (5df) v Sites x Years (8df)	3.69	6.63	13.49
Years (2df) v Error(a) (40df)	3.23	5.18	8.25
Sites x Years (8df) v Error(a) (40df)	2.18	2.99	4.21
N (1df) v N x Years (2df)	18.51	98.50	998.5
N x sites (5df) v N x Sites x Years (8df)	3.69	6.63	13.49
N x Years (2df) v Error(b) (40df)	3.23	5.18	8.25
N x Sites x Years (8df) v Error(b) (40df)	2.18	2.99	4.21

Since year effects are random, their significance primarily tells us that synoptic weather affects the characteristics. However, significant **year x site** and **year x N** interactions show that site and N effects are not consistent from year to year and cannot be used with confidence to guide in developing crop management advice. Significant **N x site** interactions are indicative of differences in response to N at the various sites but if the **N x site x year** interaction is also significant then these differences are not observed consistently from year to year and are less valuable in providing guidance in crop management. Given the degrees of freedom for the comparison of N with its appropriate error variance, 1 v 2, the effect of N would have to be very large to show up as significant. Simply put, the comparisons of greatest value for developing advice for crop management are significant site and N effects and **N x site** (N x S) interactions. A non-significant year effect and non-significant **N x year** (N x Y) and **N x site x year** (N x S x Y) interactions are desirable.

Since the factors and their interactions frequently show highly significant variation for many of the characteristics, the variance ratios will also be used in comparing their influences.

3.2 Life cycles/Development (Table 3.2, Appendix 3)

Dates of sowing, ZGS 30/31, anthesis and harvest

Sowing of most of the experiments did not take place within the optimum period, i.e. before the end of September. Newcastle and Rothamsted were first to be sown, usually towards the end of September, but others, and in particular Belfast, were sown later with 24 November 1989 being the latest date amongst the 17 experiments.

Accurate determination of **ZGS 30 or 31** was not possible because growth stage was examined at fortnightly intervals when the samples for dry weight determination were being collected. However, these data indicate that generally ZGS 30/31 was reached towards the end of March and during the first week of April. Belfast reached ZGS 30/31 later in all three years and Newcastle was earlier in 1989 and 1990.

Anthesis was more accurately determined as sampling became weekly at this stage. In 1988 and 1989, anthesis was reached at a wide range of dates between 8 May and 10 June, but in 1990 all experiments reached anthesis within a very short period, 21 to 24 May. The variable timing of anthesis did not reflect differences in sowing date between the sites.

Harvest of the experiments took place between 10 July and 2 August. The sites did not show any consistent trends towards either early or late harvest dates.

Dates of Nitrogen application

Nitrogen fertiliser was usually applied between 12 and 19 March in each year although in some experiments application was as late as 27 April. In 12 of the 17 experiments the nitrogen was applied 14-21 days before ZGS 30/31. In the remaining five experiments, application was at ZGS30/31.

Durations of stem elongation and grain-filling

The **duration of the stem elongation phase** between ZGS 30/31 and anthesis varied between 34 and 70 days. Even allowing for inaccuracy in determining ZGS 30/31, there is still a considerable degree of variation with no apparent pattern emerging either amongst the sites or between the years.

The duration of the **grain filling period** varied between 41 and 72 days. Some trends between the sites could be discerned although they did not occur in all three years. Belfast and Sutton Bonington had shorter grain filling periods than the other sites.

Maximum shoot number occurred between 37 days before and 25 days after ZGS 30/31 in most of the N0 crops. In five of the 14 experiments where information was available, maximum shoot numbers in the NS crops were observed on the same dates as in the N0 crops. In most of the remaining NS crops, maximum shoot number was observed between 13 and 56 days later than in the N0 crops, i.e. between ZGS 30/31 and anthesis.

Conclusion

Development is a relatively stable aspect of crop functioning compared with dry matter production which is primarily governed by interception of radiation (Monteith, 1977) and which is therefore, very variable. As the life cycle progresses from sowing to harvest, crops sown on very different dates tend to synchronise in their development. This occurs because the influence of vernalisation and daylength over-rides that of temperature in determining rates and durations of development during the various phases. Also, as the life cycle progresses, development is taking place in warmer conditions where temperature is accumulated at a faster rate and therefore, the number of days during which key stages such as anthesis are likely to be observed will be fewer than for events at cooler times of the year.

The results for both dates of stages and durations of phases observed in this programme show that development, far from synchronising in each year, was highly erratic. The major developmental stages did not occur at particular calendar dates with any consistency. Therefore, the crops will have received very different quantities of radiation during the main growing periods defined by development.

3.3 Meteorological variates

The growing season was divided into three phases using the data on development from each experiment. Total rainfall, total radiation and mean temperature are presented for Sowing to ZGS 30/31 in Figure 3.1. Total rainfall, total radiation and maximum potential soil moisture deficit are presented for ZGS 30/31 to anthesis in Figure 3.2 and for anthesis to maturity in Figure 3.3.

Sowing to ZGS 30/31: Potton 1988 was cooler and had lower receipts of radiation than other experiments. Newcastle tended to have lower receipts of radiation and to be warmer than other sites. Belfast and Rothamsted tended to have higher receipts of radiation.

ZGS 30/31 to Anthesis: Sutton Bonington had high total receipts of radiation and in 1989 had high total rainfall. Higher maximum potential soil moisture deficits were obtained at Newcastle than at other sites although rainfall was not as low as at Belfast, Rothamsted or Blunham/Potton.

Anthesis to Maturity: No site had consistently low or consistently high maximum potential soil moisture deficits, total rainfalls or total radiation receipts.

Figure 3.1

Meteorological Variables: Sowing to ZGS 30/31
[Mean temperature (Celsius) as labels]

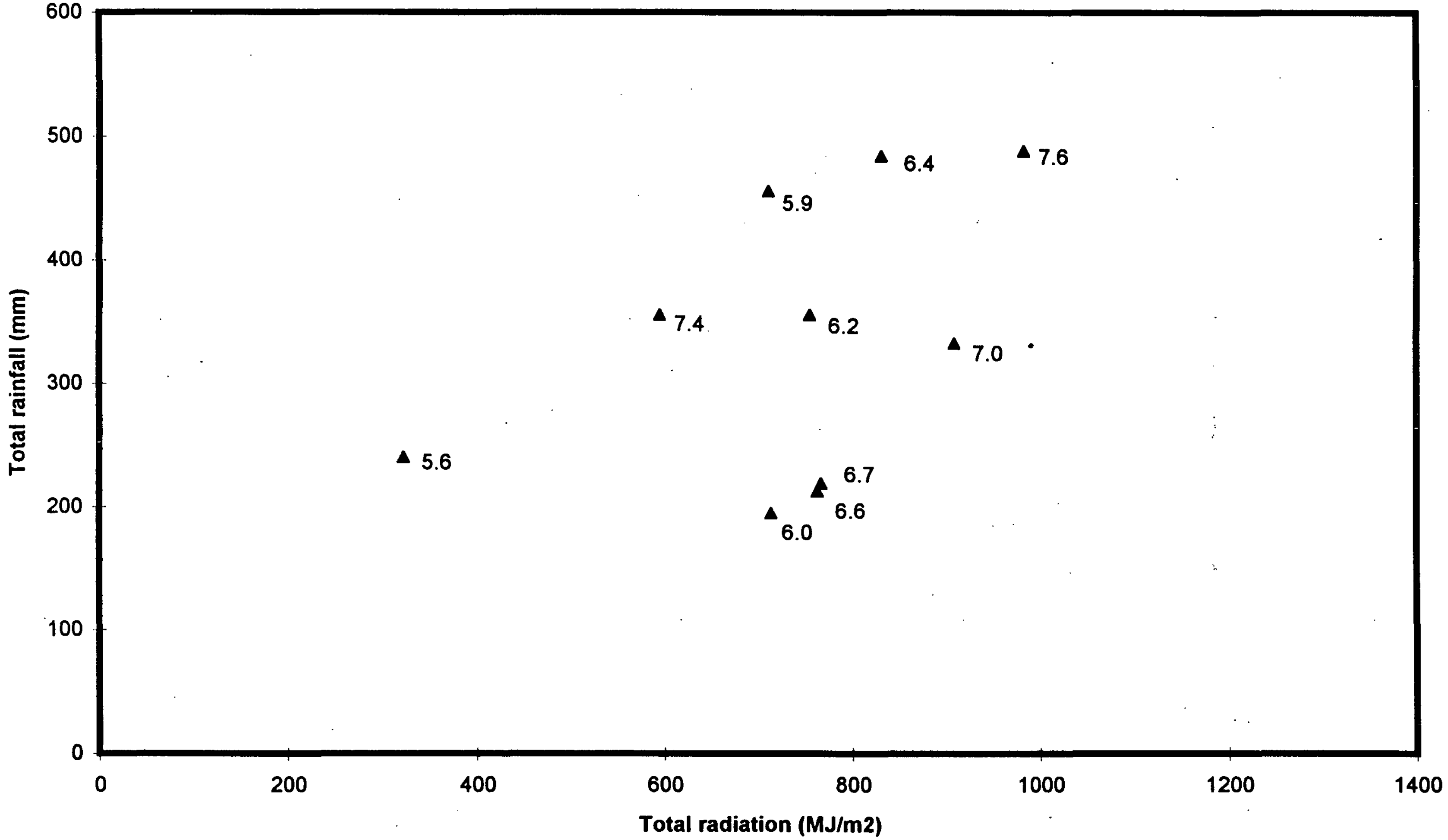


Figure 3.2

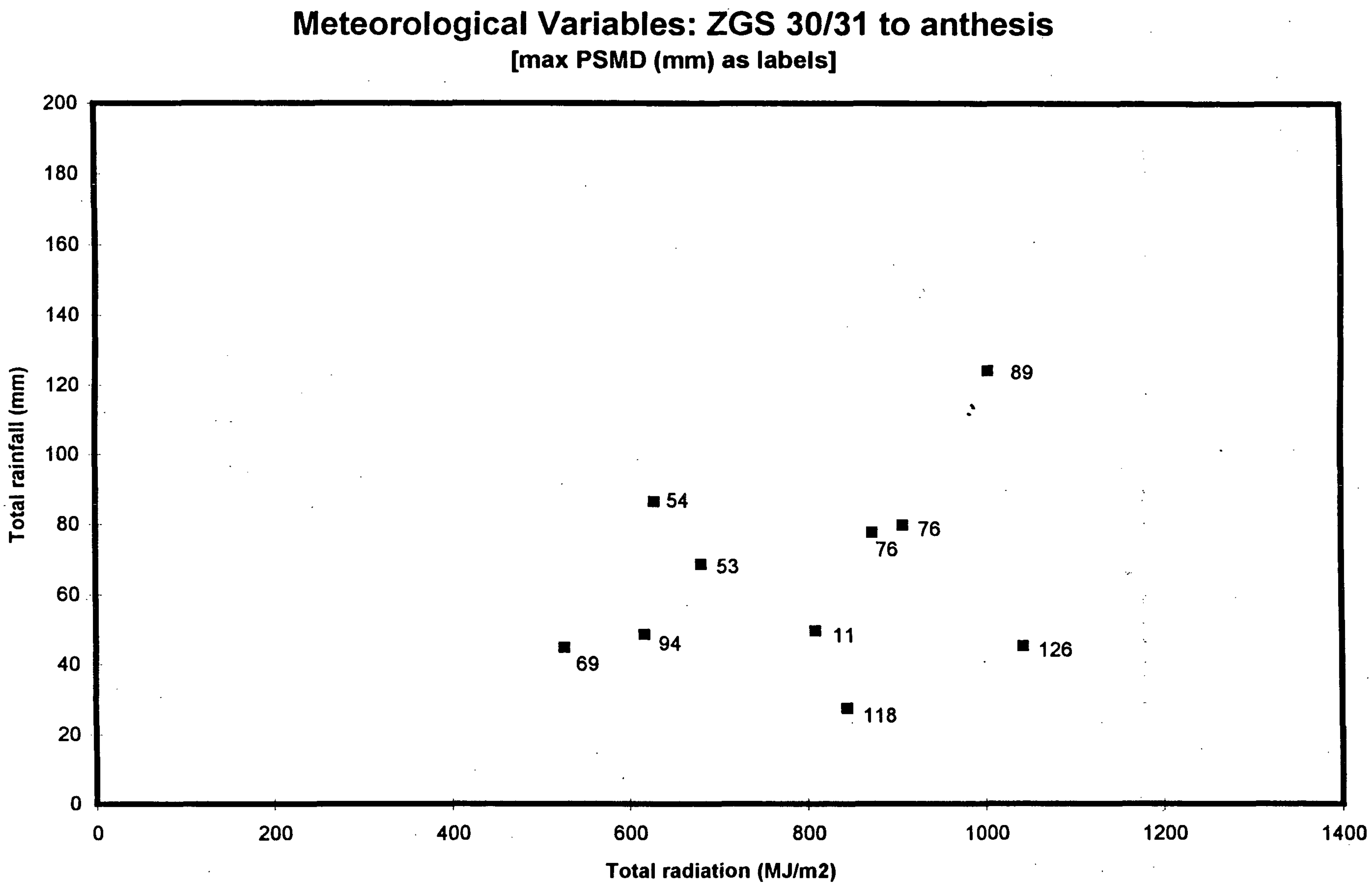
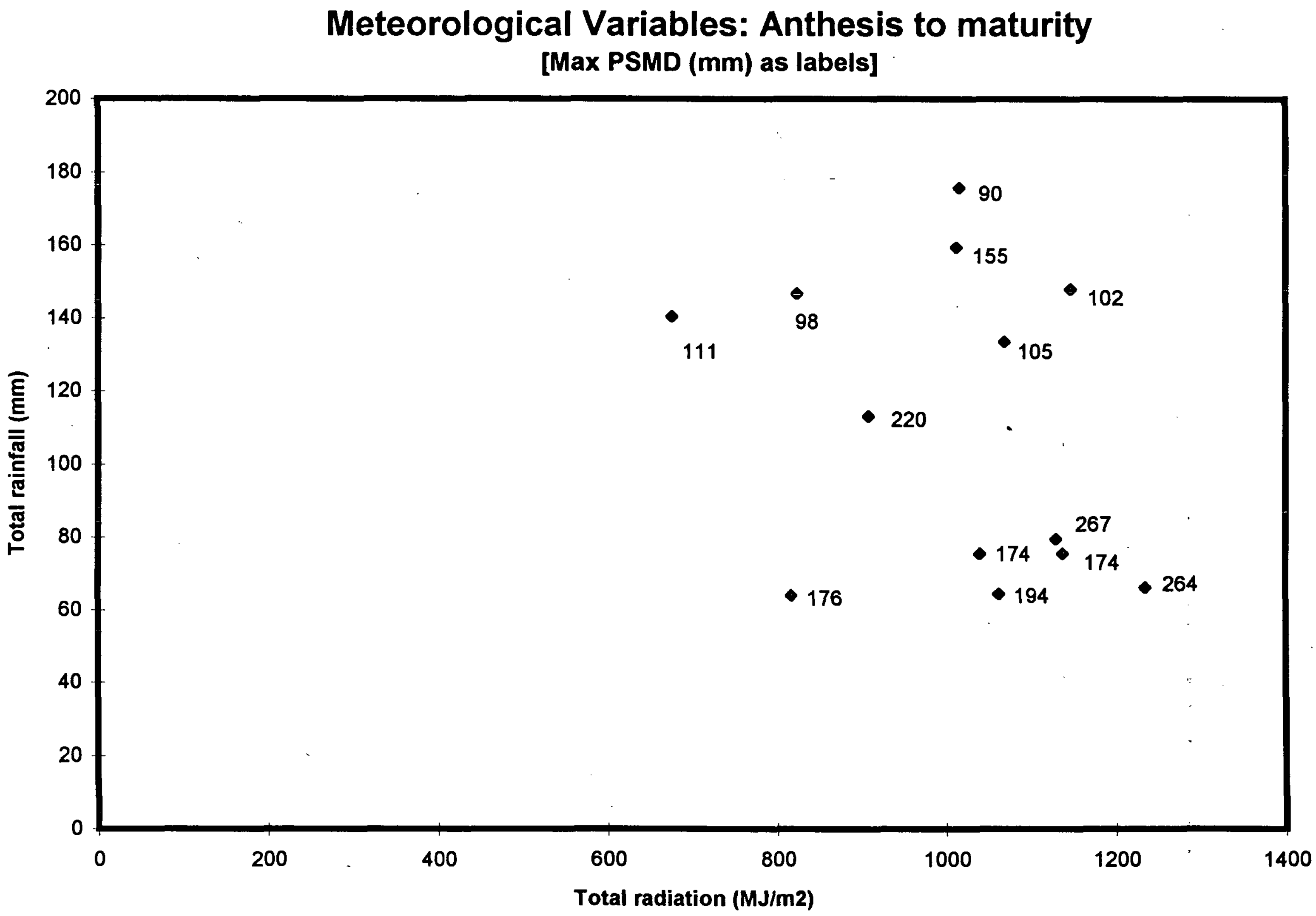

Meteorological Variables: ZGS 30/31 to anthesis
[max PSMD (mm) as labels]
Total rainfall (mm)
200
180
160
140
120
100
80
60
40
20
0
Total radiation (MJ/m2)
0
200
400
600
800
1000
1200
1400
89
54
76
76
53
11
94
69
126
118

Figure 3.3


Meteorological Variables: Anthesis to maturity
[Max PSMD (mm) as labels]
Total rainfall (mm)
200
180
160
140
120
100
80
60
40
20
0
Total radiation (MJ/m2)
0
200
400
600
800
1000
1200
1400
90
155
102
98
111
105
220
267
174
174
264
176
194

3.4 Harvest

Characteristics:

- Combine grain yield (t/ha at 15%mc)
- Ear number per m^2
- Grain number per ear
- Individual grain dry weight (mg)
- Total dry weight (g/m^2)
- Harvest index (%)
- %N in the grain
- %N in the straw
- Grain N offtake (kg/ha)
- Total N offtake (kg/ha)
- Nitrogen harvest index (%)

Significance of the effects of year, site and nitrogen on all characteristics (Table 3.3, Appendix 3)

All harvest characteristics were greatly affected by the year (Y) in which the experiment was grown. Site and nitrogen effects were usually inconsistent from year to year (S x Y and N x Y). Nitrogen (N) affected most characteristics to a significant degree but differences between sites in their response to nitrogen were usually inconsistent from year to year (N x S x Y).

Grain yield (Table 3.4, Appendix 3)

Yields in 1989 and 1990 were much higher than in 1988 ($p<0.001$). Rothamsted and Potton tended to produce the lowest yields and Newcastle the highest yields ($p<0.05$).

Applying nitrogen increased grain yield by 2.65t/ha on average above the yield of 3.86t/ha produced without nitrogen over all experiments. However, the response to nitrogen varied significantly from year to year and site to site. In 1988, when yields were lower, the response to N was greater, 3.3t/ha, than in 1989 and 1990 when yields were higher and increases in yield of 2.6 and 2.0t/ha in response to N were obtained. Larger responses to N were usually obtained at Belfast and Newcastle and smaller responses at Sutton Bonington.

Ear number/m^2 (Table 3.5, Appendix 3)

Ear number/m^2 was very variable from site to site in each year ($p<0.001$). In most of the experiments 100 - 300 more ears/m^2 were produced in response to nitrogen application (N x S x Y: $p<0.001$).

Grain number per ear (Table 3.6, Appendix 3)

Although number of grains per varied greatly from from site to site in each year ($p<0.001$), nitrogen application produced a consistent increase of 2.4 grains per ear ($p<0.05$).

Grain mass (mg) (Table 3.7, Appendix 3)

The weight of individual grains was highly variable from site to site in each year ($p<0.001$). The response to nitrogen application was erratic with decreases of up to 5.2 mg in six experiments and increases of up 5.6 mg in the remaining 11 experiments (N x S x Y: $p<0.05$).

Influence of year, site and nitrogen on yield formation in terms of its components

General trends in yield can be related to consistent trends in the components for the major effects noted for year and nitrogen but not for differences between the sites.

Year: The higher grain yields in 1989 and 1990 compared with 1988 were largely attributable to higher numbers of ears/m^2. Grain numbers per ear and grain mass were similar in all three years.

Nitrogen: Nitrogen applications led to higher yields by increasing both ear number and grain numbers, grain weight not being affected.

Site: High yields at Newcastle were attributable to very high grain weights and high grain numbers per ear despite the low numbers of ears produced. High ear numbers at Blunham were accompanied by average grain numbers per ear and very low grain weights to produce intermediate grain yields. Low yields at Potton were attributable to low grain numbers per ear and low grain weights despite the high ear numbers produced. At Rothamsted very low ear numbers led to very low yields despite high grain numbers per ear and high grain weights.

Total dry matter production (Table 3.8, Appendix 3)

Total dry matter production was much greater in 1989 and 1990 than in 1988, as with grain yield ($p<0.001$). Response to nitrogen varied significantly from year to year ($p<0.001$) and site to site ($p<0.05$). In 1988, when total dry matter production in the N0 treatment was lower, the response to N was greater, 6.15t/ha, than in 1989 and 1990 when total dry matter production in the N0 treatment was higher and increases in total dry matter production of 4.18 and 3.73t/ha in response to N were obtained. Generally larger responses to N were obtained at Belfast, Potton and Newcastle and smaller responses at Sutton Bonington (N x S x Y: $p<0.05$).

Harvest index (Table 3.9, Appendix 3)

The proportion of the total dry matter harvested as grain varied between 36.5 and 58.6% across all crops. As with grain yield and total dry matter production, harvest index was greater in 1989 and 1990 than in 1988 ($p<0.001$). Nitrogen usually resulted in a decrease in harvest index but in a few experiments, for example Sutton Bonington in 1988 and Belfast in 1990, harvest index increased in response to nitrogen (N x S x Y: $p<0.001$).

%N in grain (Table 3.10, Appendix 3)

%N in the grain varied between 1.17% and 1.88% in all but two of the total of 34 samples from both nitrogen treatments in all experiments. The two remaining samples from the NS crops at Sutton Bonington in 1988 and 1989 had nitrogen contents of 2.18% and 2.54% respectively.

Application of nitrogen resulted in increases in %N in the grain of up to 0.43% in most experiments. In a few experiments, namely Belfast in 1988 and 1990 and Blunham in 1990, %N in the grain decreased by up to 0.26%. At Sutton Bonington increases in %N in the grain of 0.60 and 0.77% were observed in 1988 and 1989 respectively. It is notable that in these two years at Sutton Bonington, %N in the grain in the N0 treatment was higher than in the other experiments.

Of the 34 grain samples obtained from all treatment combinations, six had %N in the grain of greater than 1.75% which has been taken as the maximum acceptable content for malting purposes (Cranstoun and Wiseman, 1994). Five of these were from the NS treatment and one from the N0 treatment. Thus 'informed' decision-making about the appropriate amount of nitrogen to apply to achieve acceptable N contents was less than successful in nearly one-third of the crops. On the other hand, keeping N application rates low did not ensure that N contents were always acceptable.

Grain N offtake (Table 3.11, Appendix 3)

Grain N offtake in 1988 was much lower than in 1989 and 1990 ($p \leq 0.001$). Grain N offtakes were lowest at Belfast and highest at Sutton Bonington ($p<0.001$). Application of 85 to 125 kg/ha nitrogen increased grain N offtake by between 28 kg/ha at Blunham and 62 kg/ha at Potton (N x S: $p<0.05$).

Total N in crop at maturity (Table 3.12, Appendix 3)

Data on the content of nitrogen in the straw at harvest were not collected at several sites and therefore, discussion of the responses of total N offtake and nitrogen harvest index is limited.

The pattern of variation in total N in the crop at maturity due to site, nitrogen and year was similar to that shown by grain N offtake.

Total N offtake in 1988 was much lower than in 1989 and 1990 ($p<0.001$). Total N offtake was much greater at Sutton Bonington than at the other sites, Blunham, Potton and Rothamsted. Application of nitrogen increased total N offtake by between 47 kg/ha at Blunham and 84 kg/ha at Potton (N x S: $p<0.05$).

Nitrogen harvest index (Table 3.13, Appendix 3)

The proportion of nitrogen in the crop harvested in the grain varied between 57 and 88% across all crops. When nitrogen was applied, nitrogen harvest index was generally lower and more stable. At Rothamsted and Sutton Bonington nitrogen application had little effect on the proportion of N recovered in the grain whilst at Blunham and Potton, the nitrogen harvest index (NHI) was reduced by 5 to 8% when nitrogen was applied.

Influence of year, site and nitrogen on yield formation in terms of dry matter production and partitioning

Year: Grain yield was much lower in 1988 than in 1989 and 1990. This was mainly due to reduced total dry matter production in 1988 compared with 1989 and 1990 although harvest index was also lower, by 3-4%, in 1988. Total and grain N offtakes and nitrogen harvest index were also lower in 1988 than in 1989 and 1990. Since both grain yield and grain N offtake were lower in 1988, %N in the grain was only marginally lower in 1988 compared with the two later years.

Site: The high yields at Newcastle were attributable to both high dry matter production and a high harvest index. High dry matter production at Blunham and Sutton Bonington did not lead to high grain yields because harvest indices at these two sites were low. The low grain yields at Potton and Rothamsted were primarily a result of lower dry matter production. Total N and grain N offtakes were markedly higher at Sutton Bonington than at the other sites (four sites only for total N offtake). Although nitrogen harvest index was much lower at Sutton Bonington, %N in the grain was still very high.

Nitrogen: Nitrogen application, as expected, increased grain yield dramatically. This was attributable to its effect on total dry matter production as harvest index was only 2% lower when nitrogen was applied. Total and grain N offtakes were both greater when nitrogen was applied but more of the nitrogen was found in the grain in the N0 treatment as shown by the higher nitrogen harvest index. However, %N's in the grain were marginally higher in the NS treatment.

3.5 Total dry weight

Characteristics derived from the fitted Gompertz functions:

- Total dry weight at maturity
- Beginning of the phase of rapid growth, i.e. Day when growth = A + 0.1C
- End of the phase of rapid growth, i.e. Day when growth = Total - 0.1C
- Duration of growth, i.e. length of the phase of rapid growth
- Dry weight at the beginning of the rapid phase of growth, i.e. A
- Rate of growth during the phase of rapid growth
- Total dry weight at anthesis
- Proportion of total dry weight at maturity produced by anthesis
- Increment in total dry weight during grain filling =
  (total dry weight at maturity - total dry weight at anthesis)

Goodness of fit to data for total dry weight by the Gompertz function (Table 3.14, Appendix 3)

Datasets in which less than 70% of the variance in the data was accounted for by the fitted Gompertz function were excluded from the over-experiments ANOVA analyses. Of the 106 functions fitted to the data for total dry weight, only five sets had less than 70% of the variance accounted for by the fitted function. Of the remaining 101 datasets, 63 had over 90% of their variance accounted for by the functions.

The major phase of growth in the fitted curves is defined by C, the difference between the lower asymptote, A, and the final total dry weight of the crop, (C + A). The beginning and end of this phase have been defined as (A + 0.1C) and (Total dry weight at maturity - 0.1C, i.e. [C + A] - 0.1C) respectively. Variation in total dry matter production will be related to variation in the rate and/or the duration of this phase of growth and in the dry weight of the crop at the beginning of the phase, i.e. A.

Most of the total dry matter would be expected to be produced between the beginning of stem elongation and when complete green area senescence occurs. It would therefore, be expected that the beginning of the phase of rapid growth should coincide with a growth stage about ZGS 31-33 fairly consistently and the end of the rapid phase should occur during grain-filling prior to senescence at about ZGS 71-75. It would also be expected that dry weight at the beginning of the phase of rapid growth would also be small since stem elongation has not begun, the larger upper leaves have yet to emerge and expand and the ear has yet to grow and develop.

Significance of the effects of year, site and nitrogen on all characteristics
(Table 3.15, Appendix 3)

Parameters describing the production of dry matter by the crops were greatly affected by year and site. Nitrogen affected all parameters but in most cases different responses found at the sites varied from year to year. The exceptions were (1) the dry weight at the beginning of the phase of rapid growth and the date when this phase began, where differences between the sites were consistent in each year, and (2) the proportion of total dry weight at maturity present in the crop when that phase of rapid growth began, where the crops did not differ in their response to nitrogen from site to site.

Beginning of the rapid phase, i.e. Time when growth = A + 0.1C
(Table 3.16, Appendix 3)

In the NS treatment the phase of rapid growth began between 12 April and 16 May. In the N0 treatment, the phase of rapid growth generally began over a longer period, from 5 April to 22 May. The date of the beginning of the phase of rapid growth in the N0 treatment would be less well-defined than in the NS treatment because, having smaller total dry weights, the curves of dry matter production had much shallower slopes.

Rapid growth tended to begin later at Belfast than at the other sites especially when nitrogen was applied ($p<0.01$). This may be due to the later sowing at Belfast and the later time of reaching ZGS 30/31.

Rapid growth began much later than either the date of application of nitrogen or ZGS 30/31 with the exception of Belfast in 1990. Regression analysis showed that there were no clear relationships between the dates of the beginning of the phase of rapid growth and developmental parameters (Table 3.17).

Table 3.17 Relationships between the date of the beginning of rapid phase of growth and major stages in the life cycle and development

	N0		Ns	
	% variance	regression coefficient	% variance	regression coefficient
Dates of:				
• Sowing	0	0.17	4.3	0.17
• N application	7.7	0.35	15.5	0.35
• ZGS 30/31	1.7	0.24	4.3	0.21
• Anthesis	11.4	0.52	14.2	0.46
Length of phase:				
• Sowing - ZGS30/31	0	-0.05	0	-0.07

Generally, however, where nitrogen was applied both early and well before ZGS 30/31, rapid growth began earlier than in the N0 treatment. Where nitrogen was applied late and/or at ZGS 30/31, it had little effect on when rapid growth began.

End of rapid growth, i.e. Time when growth = (C + A) - 0.1C (Table 3.18, Appendix 3)
Compared with the beginning of rapid growth, the date when this phase ended was much more erratic and much more variable in response to nitrogen at individual sites. Rapid growth ended as early as 30 May in 1988 at Sutton Bonington but continued until 9 August in 1988 at Newcastle. The date when growth ended at individual sites varied greatly from year to year. The end of growth was both delayed and advanced in the NS crops compared with the N0 crops, so that the period of growth was extended by up to 24 days in some crops, shortened by up to 46 days in others and no different in a few cases.

There was no relationship apparent between the end of rapid growth and the dates of anthesis, ZGS 30/31 or the date of N application (Table 3.19). However, there was a slight tendency for rapid growth in the N0 treatment to end later when it had begun earlier and when the length of time between sowing and ZGS 30/31 was greater. This was not apparent when nitrogen was applied.

The poor definition of the end of the phase of rapid growth obtained in these fitted curves may be primarily due to the frequent occurrence in many datasets of wildly fluctuating values for dry weight during the grain-filling period. Also growth does not end as abruptly as it begins but slows down gradually as senescence progresses up the plant.

Table 3.19 Relationships between the date of the end of the phase of rapid growth and major stages in the life cycle and development

	N0		Ns	
	% variance	regression coefficient	% variance	regression coefficient
Dates of:				
• Sowing	0	-0.19	0	-0.06
• N application	0	-0.23	0	-0.29
• ZGS 30/31	0	0.25	0	-0.20
• Anthesis	0	0.36	0	0.15
• Harvest	0	0.03	0	-0.003
• Beginning of rapid phase				
N0	12.2	-0.79		
Ns n			0	-0.02
Length of phase:				
• Sowing - ZGS30/31	9.5	0.61	0	-0.11
• ZGS 30/31 - Anthesis	0	-0.14	0.8	0.40
• Anthesis - Harvest	0	0.02	0	-0.01

Duration of growth = length of period between beginning and end of the phase of rapid growth (Table 3.20, Appendix 3)

The variation already noted in the date of the end of the phase of rapid growth had an overriding influence on the duration of the phase of rapid growth. Thus the phase of rapid growth varied in length from as short as 20 days at Sutton Bonington in 1988 to as long as 108 days at Newcastle in 1990 and was not consistent from year to year at individual sites. Nitrogen also had a variable effect on duration, in some crops having no effect, in some increasing but in others decreasing the duration of growth.

Rate of growth during the phase of rapid growth (Table 3.21, Appendix 3)

Growth rate during the phase of rapid growth was very variable. The most strikingly anomalous growth rate was that of 36.1 g/m^2/day in the N0 treatment at Blunham in 1989. This was much higher than the highest growth rate found in the rest of the programme which was 23.6 g/m^2/day recorded at Belfast in 1988.

In most experiments, nitrogen increased the rate of growth. Growth rates in the N0 treatment were much more variable than when nitrogen was applied. There were no consistent site effects from year to year except at Sutton Bonington where growth rate in all three years tended to be very high in both the N0 and NS treatments.

These growth rates were calculated from the parameters of the fitted Gompertz functions. Given that the derived values for the end of the phase of rapid growth were so variable, it is not surprising that the derived values for growth rate were so erratic.

Dry weight of the crop at the beginning of the phase of rapid growth, i.e. A (Table 3.22, Appendix 3)

At the beginning of the phase of rapid growth, dry weights of the crops varied between 22.5 and 396.8 g/m^2. Crops at Belfast and Potton were usually small at this stage and Sutton Bonington crops very heavy. Nitrogen did not have a consistent effect on dry weight at this stage although in most experiments it had been applied at least 30 days earlier and therefore, would have been begun to have an influence on crop growth.

The dry weights of the crops at the beginning of the phase of rapid growth would be affected by many factors influencing growth and development of the crops prior to this time. These would include the earliness of sowing, the warmth of the winter and the availability of nitrogen in the soil. Comparison of the dry weights at this stage with date of sowing (Table 3.2) suggests that there is a reciprocal relationship between sowing date and this characteristic so that dry weight at the beginning of the phase of rapid growth was greater where sowing was earlier.

Proportion of total dry weight at maturity present at the beginning of the phase of rapid growth (Table 3.23, Appendix 3)

The proportion of growth which had taken place before rapid growth began, A/(C + A), was usually much lower where nitrogen was applied than in the N0 treatment because the total amount of growth was greater in the NS treatment.

Total dry weight at anthesis (Table 3.24, Appendix 3)

By anthesis nitrogen had begun to exert a considerable influence on the production of dry matter by the crops ($p<0.01$), although there was significant variation in its effect from site to site and from year to year ($p<0.001$). In most experiments the increase in dry weight attributable to nitrogen was between 250 and 500g but in a few, in particular the Sutton Bonington experiments, the response to nitrogen was minimal. Belfast, Newcastle and Sutton Bonington tended to be more productive than Blunham, Potton and Rothamsted, especially in 1989.

Proportion of total dry weight at maturity produced by anthesis
(Table 3.25, Appendix 3)

The marked effect of nitrogen on the size of the crop at anthesis was not so apparent when its weight at this stage was compared with its weight at maturity. However, the proportion present at anthesis varied greatly, from 39% to 97%. At some sites the proportion was smaller in response to nitrogen in one year yet larger in another. It might have been expected that a high proportion, say 80%, of the total dry weight would have been produced prior to anthesis but in these experiments, only seven of the 32 crops had produced more than 75% of their final dry weights by this stage.

Increment in total dry weight during grain filling =

total dry weight at maturity - total dry weight at anthesis

(Table 3.26, Appendix 3)

In most experiments the increment in total crop dry weight during grain filling was greater in the NS than in the N0 treatment but this response varied greatly from site to site and year to year ($p<0.001$). In the N0 treatment, between 1 and 565 g/m^2, with a mean of 290 g/m^2, was produced during this period. With nitrogen, between 70 and 865 g/m^2 with a mean of 530 g/m^2, was produced. It is surprising that during grain-filling dry weights of this magnitude could be accumulated and that they are so variable.

Summary

The pattern of production of total dry matter by the crops is defined by their dry weights at the beginning of the phase of rapid growth and at anthesis and by the increment in total dry weight during grain filling. On average about 10-15% of final dry weight had been produced prior to the main phase of growth. By anthesis about 60% of final dry weight was present, which means that 40% on average was produced during grain-filling.

Year: More of the final dry weight had been produced at the beginning of rapid growth and at anthesis in 1989 than in 1988 and 1990.

Site: At Sutton Bonington higher proportions and at Potton lower proportions of final dry weight had been produced at the beginning of rapid growth and anthesis than at the other sites.

Nitrogen: Although nitrogen application had a dramatic effect on the final dry weight produced, it had only a small effect on the proportion of dry weight present at the beginning of rapid growth, reducing it from 17 to 12% on average. The lower proportion in the NS treatment was primarily a consequence of the greater final dry weight produced in this treatment, dry weights of the two treatments at the beginning of rapid growth being similar in most crops. The proportion of dry weight present at anthesis was affected by nitrogen to a small extent, being reduced by 4-8% in 1988 and 1989 on average and increased by 9% in 1990. Therefore, the increase in final dry weight attributable to nitrogen arises from effects on the processes of dry matter production during both stem elongation and grain filling, broadly similar dry weights being produced in each of these phases.

Although nitrogen had a marked effect on growth rate, and the variance ratio is greater for this parameter than for any of the others relating to the duration and timing of growth, there is still a lot of variation in growth rate which is not explained by nitrogen.

3.6 Ear dry weight

Characteristics:

- Final ear dry weight at maturity
- Ear dry weight at anthesis
- Increment in ear dry weight during grain-filling
  = final ear dry weight - ear dry weight at anthesis
- Contribution of stored carbohydrate reserves to ear dry weight
  = increment in ear dry weight during grain filling
  - increment in total dry weight during grain filling

Goodness of fit to ear dry weight data by the Gompertz function (Table 3.27, Appendix 3)

Data on ear weights were not obtained at Belfast in 1988 or at Potton, Blunham, Newcastle or Sutton Bonington in 1990. Of the 94 datasets to which functions were fitted, four had lower % variances accounted for than the 70% limit and were therefore, excluded from the sites x years analyses. Seventy-six of the remaining 90 datasets had over 90% of their variance accounted for by the fitted functions.

Ear dry weight at anthesis and **final ear dry weight** were derived from the fitted curves in order to calculate the **increment in ear dry weight during grain filling**. Since dry weights of the parts of the ear, namely lemmas, paleas, rachises and awns, would remain constant during grain filling, the change in ear dry weight equates with growth of the grains themselves. The increment in ear dry weight will be derived from assimilation during grain filling and also possibly from relocation of reserves which had been produced and stored in the plant before anthesis.

Significance of the effects of year, site and nitrogen on all characteristics (Table 3.28, Appendix 3)

All parameters describing the growth of the ears varied significantly from year to year at each site. Different responses amongst the sites to nitrogen were only consistent from year to year for ear dry weight at anthesis. Nitrogen had very marked effects on final ear dry weight and the increment in ear dry weight during grain filling but these varied from year to year at each site. The effect of nitrogen on ear dry weight at anthesis and the contribution of stored reserves to the increment in ear dry weight during grain-filling were reasonably consistent from site to site but varied from year to year.

Ear dry weight at anthesis (Table 3.29, Appendix 3)

In most crops ear dry weight at anthesis was low, with weights of less than 110 g/m^2 being interpolated from the fitted functions for 22 of the 26 crops. At Sutton Bonington they were much heavier, particularly in 1989.

Nitrogen application led to higher ear dry weights in 1988 and 1990 but not in 1989 ($p<0.001$). Although the increase in ear dry weight due to nitrogen was significantly different at each of the sites ($p<0.05$), there was much variation between experiments, differences of less than 10g/m^2 between the two nitrogen treatments occurring in five experiments and increases of up to 80g/m^2 in the remaining experiments.

Final ear dry weight (Table 3.30, Appendix 3)

The large effect of nitrogen on final ear dry weight varied from site to site in each year ($p<0.001$), final ear dry weights of between 189 and 651 g/m^2 being observed in the N0 treatment and 358 and 924 g/m^2 when nitrogen was applied.

Increment in ear dry weight during grain filling
= final ear dry weight - ear dry weight at anthesis (Table 3.31, Appendix 3)

Nitrogen had a marked effect on the increment in ear dry weight during grain-filling. Increments in ear dry weight generally ranged from 185 to 641 g/m^2 in the N0 treatment and from 525 to 859 g/m^2 in the NS treatment but were smaller at Sutton Bonington, where ear weights at anthesis were high, and in 1990, when final ear weights were low ($p<0.001$).

Contribution of stored reserves to ear dry weight
= increment in ear dry weight - increment in total dry weight during grain filling
(Table 3.32, Appendix 3)

The contribution of stored reserves to the increment in ear dry weight was very variable. In some crops more dry matter was produced during grain filling than was used in increasing ear dry weight, i.e. negative values were recorded for the contribution from reserves in these crops. This happened in both nitrogen treatments at Potton in 1988 and when nitrogen was applied at Sutton Bonington in 1988. Between 59 and 341g/m^2 assimilate were provided by reserves to fill the grains in the remaining 23 crops.

In eight of the 13 experiments utilisation of reserves was greater in the N0 treatment than in the NS treatment. The effect of nitrogen on the contribution from reserves varied significantly from year to year ($p<0.05$). Taking into account the dry matter produced during grain filling which was surplus to the requirements of the ears in their growth, application of nitrogen to the crops led to a greater utilisation of stored reserves in 1990, a similar requirement to that in the N0 treatment in 1989 and a smaller utilisation than in the N0 treatment in 1988. The large amounts of reserves supplied by the N0 crops and the small amounts of reserves utilised by the NS crops are both surprising findings in these experiments.

The large and consistent effect of nitrogen on the increment in ear dry weight suggests that the use of reserves is driven by those factors which are determining grain yield rather than by the supply of assimilate either from current photosynthesis or relocation of reserves. In particular, since grain number has been determined by anthesis and since grain size is relatively constant, those factors which control grain size will determine the demand for assimilate and consequently the non-use of post-anthesis assimilates or the use of pre-anthesis stored assimilates.

The constancy or conservatism of grain size relative to the other components of yield (Gallagher *et al*, 1975) has led to this component being ignored as a major determinant of variation in grain yield. However, its constancy should be regarded as conferring a stability to yield which would otherwise have been even more variable.

What is measured as grain weight is an average which masks a truncated normal distribution in the weight of individual grains. This normal distribution arises from the hierarchy in grain size within individual ears and it is truncated because of the sieving operations during combining. When variation in grain weight is detected, this may be attributable to variation in the weight of all grains or to variation in specific size fractions within the grain population such as the small grains or the large grains. Mechanisms controlling grain size within individual ears will determine the overall constancy of grain weight shown by crops. This in turn will result in the erratic utilisation of stored reserves shown in these experiments.

Summary

Year: Ear dry weights at anthesis and at maturity were greater in 1989 than in 1988 and 1990. The increase in ear dry weight during grain-filling was greater in 1989 than in 1988 and 1990. Contributions of stored reserves to ear dry weight were also higher in 1989 and 1990 than in 1988.

Site: Crops at Sutton Bonington had greater ear dry weights at anthesis and lower final ear dry weights than those at the other sites. Consequently the Sutton Bonington crops had an average increment in ear dry weight of 192 g/m^2 compared with between 502 and 625 g/m^2 at the other sites. The contribution from stored reserves to the ear dry weight increment was greater at Newcastle, Blunham, Belfast and Rothamsted than at Sutton Bonington and Potton, sites where, in some crops, more dry matter was produced during grain filling than was used by the ears.

Nitrogen: Ear dry weight at anthesis was increased by 30 g/m^2, 55%, on average following the application of nitrogen earlier in the season. Final ear dry weight was increased by a similar proportion, 51%, 229 g/m^2, by the nitrogen application. Nitrogen therefore, increased the increment in ear dry weight by 199 g/m^2, 51%, which is smaller than its effects of 68% on grain yield and 66% on total dry matter production. The effect of nitrogen on the utilisation of reserves varied dramatically from year to year. Therefore, the effect of nitrogen on ear dry weight cannot be explained as a direct effect of nitrogen on the contribution of stored reserves to grain filling.

3.7 Total N content

Characteristics:

- Total N content at harvest
- Total N content at ZGS 30/31
- Proportion of the final total N content in the crop at ZGS 30/31
- Total N content at date of N application
- Proportion of the final total N content in the crop at N application
- Total N content at anthesis
- Proportion of the final total N content in the crop at anthesis
- Increment in total N content between ZGS 30/31 and anthesis
- Proportion of final total N content taken up between ZGS 30/31 and anthesis
- Increment in total N content between N application and anthesis
- Increment in total N content during grain filling

  = Total N in crop at maturity - total N in crop at anthesis
- Proportion of the final total N content taken up or lost during grain filling

Significance of the effects of year, site and nitrogen on all characteristics (Table 3.33, Appendix 3)

Site-related factors and the weather in each year played an important part in determining both the contents of nitrogen in the crops and also the response to nitrogen application. Nitrogen had a marked effect on the total N contents later in the life cycle but not at the earlier stages as would be expected.

Relating total N contents at ZGS 30/31, N application and anthesis to the final content of the crops, diminished differences between the years so that responses to nitrogen application varied from year to year only at ZGS 30/31. The sites differed significantly only at N application. Nitrogen application had a very marked effect on the proportion of the final total N content of the crop at N application and also at anthesis.

The influence of nitrogen application on the increment in total N content between ZGS 30/31 and anthesis varied from year to year and from site to site. The proportion of the final total N content taken up in this period varied from year to year but was similar at all the sites. The influence of nitrogen on the increment in total N content between N application and anthesis again varied from year to year but was similar at all the sites. The application of nitrogen had no effect at all on the increment in total N content during grain filling. However, when considered in relation the final total N content, there was an effect of N treatment on the proportion taken up or lost during grain-filling.

Total N content at harvest (Table 3.34, Appendix 3)

Application of nitrogen had a significant effect on the total N content of the crop at harvest ($p<0.01$) but the responses to nitrogen varied from site to site and from year to year ($p<0.001$). Total N content ranged from 2.49 to 18.05 g/m^2 in the N0 crops and from 7.77 to 23.76 g/m^2 where nitrogen was applied. Application of nitrogen increased total N content by between 2.17 and 10.14 g/m^2.

The total N content of the crop in the N0 treatment can be considered as an indicator of the amount of nitrogen which the soil could supply. Therefore, the proportion of the total N content in the fertilised crops which could have been supplied by the soil varied between as little as 20% at Potton in 1988 and as much as 80-82% at Belfast in 1990 and Sutton Bonington in 1989 and 1990. Conversely, the proportion of the total N content supplied by uptake of applied nitrogen ranged from 18 to 80%.

Total N content in the crop at ZGS 30/31 (Table 3.35, Appendix 3)

In the N0 treatments at ZGS 30/31, total N content ranged from 0.85 to 4.35 g/m^2. Where nitrogen was applied before ZGS 30/31, total N content at ZGS 30/31 varied between 1.91 and 11.94 g/m^2. In seven of the eight crops where nitrogen was applied before ZGS 30/31, the total N content of the crop was between 2.65 and 7.88 g/m^2 higher than in the unfertilised crops at this stage. At the other site, Rothamsted in 1988, and at the three sites in 1988 where nitrogen was applied at ZGS 30/31, total N contents of the fertilised and unfertilised crops differed by a maximum of 2.17 g/m^2 at ZGS 30/31.

Proportion of the final total N content present in the crop at ZGS 30/31 (Table 3.36, Appendix 3)

In the N0 treatment between 34 to 63% of the final total N content was present at ZGS 30/31. Therefore, between 37 and 66% of the crop's total N content was taken up after stem elongation had begun, the soil continuing to be the source of nitrogen during this period.

Where nitrogen was applied, two of the crops, those at Belfast in 1990 and at Rothamsted in 1989, had more than 88% of their total N content present at ZGS 30/31, the other fertilised crops having between 12 and 63% of their total N content taken up at this stage. It was surprising that crops could have taken up most of their final total N content so soon after nitrogen application and as early in their life cycle as ZGS 30/31. The Rothamsted 1989 fertilised crop was not unusual in its development or date of nitrogen application compared to the other crops that year. However, it entered the phase of rapid growth much earlier than the other crops and this may be a consequence of its early uptake of nitrogen. The Belfast 1990 crop, like the Belfast crops in the other years, was very late in reaching ZGS 30/31. However, in 1990 the Belfast crop began the phase of rapid growth earlier and reached anthesis earlier than in 1988 and 1989, which may be a consequence of its earlier uptake of fertiliser nitrogen. The information available about development and about growth in the N0 crops provides no indication why N uptake before ZGS 30/31 was so high in some of the crops.

Total N content in the crop at N application (Table 3.37, Appendix 3)

With the exception of Sutton Bonington in 1989, where total N content of the crop at the time when nitrogen was applied was 8.3-9.2 g/m^2, total N contents varied between 0.73 and 5.30 g/m^2 at this point. Crops at Blunham had higher total N contents at this time compared with the other sites. As expected there were no differences between the two N treatments.

Proportion of the final total N content present in the crop at N application (Table 3.38, Appendix 3)

Although the amounts of nitrogen in the two treatments were similar at the time when nitrogen was applied, because more nitrogen was taken up from the applied fertiliser, the proportion of the final total N content present would be expected to be lower in the treatment receiving N fertiliser. On average 44% of the final total N content was present at the time of N application in the N0 treatment. In the fertilised treatment 26%, on average, was present. Sutton Bonington had high proportions of its final total N content already taken up by the time of N application whereas Belfast had low proportions taken up at this time compared with the other sites.

Total N content in the crop at anthesis (Table 3.39, Appendix 3)

At anthesis total N content ranged from 1.56 to 10.97 g/m^2 in the N0 treatment and from 8.00 to 19.36 g/m^2 where nitrogen was applied. Application of nitrogen resulted in an increase in total N content of between 4.80 and 11.00 g/m^2, the increase being 6.58 g/m^2 on average. Newcastle and Sutton Bonington had considerably higher total N contents of 11.1-11.2 g/m^2 at anthesis than the other sites where N contents ranged from 6.0 to 8.5 g/m^2.

Proportion of the final total N content present in the crop at anthesis (Table 3.40, Appendix 3)

In eight of the 30 crops up to 17% more nitrogen was present at anthesis than at harvest, i.e. there was a loss of nitrogen from the crop during grain filling. This occurred in both fertilised and unfertilised crops. Potton was the only site where none of the crops behaved in this way.

Other workers have reported losses in crop N content in the latter part of the growing season (Greenwood and Draycott, 1988; Nielsen, Schjorring and Jensen, 1988; Mary, Recous and Machet, 1988). These losses have been attributed to leaf drop, which is not likely in this programme since all plant material was recovered, to translocation to roots and soil and to volatilisation.

Increment in total N content between ZGS 30/31 and anthesis (Table 3.41, Appendix 3)

In the N0 crops the maximum amount of nitrogen taken up during stem elongation was 2.53 g/m^2 at Belfast in 1989, most crops taking up between 0.1 and 1.0 g/m^2. Where nitrogen was applied most crops took up much more nitrogen, between 0.5 and 9.3 g/m^2, with an average of 4.1 g/m^2. Nitrogen uptake during stem elongation in the NS crops was markedly higher in 1988 than in 1989 and 1990.

Proportion of final total N content taken up between ZGS 30/31 and anthesis (Table 3.42, Appendix 3)

The proportions of the final N content taken up during stem elongation were quite small, less than 39% in all crops except in 1988 when the fertilised crops took up much higher proportions, 64-90%. In 1989 and 1990, some fertilised crops took up a smaller proportion of their final total N contents between ZGS 30/31 and anthesis than unfertilised crops.

Increment in total N content between N application and anthesis (Table 3.43, Appendix 3)

The amount of nitrogen taken up by unfertilised crops in the period between N application and anthesis varied between 0.3 and 3.5 g/m^2. The fertilised crops took up between 6.3 and 9.3 g/m^2, showing remarkable consistency at all sites within each year in the amount taken up, with most being taken up in 1988 and least in 1990.

When these uptakes between N application and anthesis are compared with those between ZGS 30/31 and anthesis it would seem that the growth stage of the crop does not exert a strong influence on nitrogen uptake and that as soon as nitrogen is applied the crop will take it up irrespective of its growth stage. The amount of nitrogen in the fertilised crops is remarkably consistent relative to the amounts in the unfertilised crops which suggests that when the supply of nitrogen is limited, uptake is determined by availability but that when nitrogen is plentiful, variation in supply does not lead to variation in uptake.

Increment in total N content during grain filling (Table 3.44, Appendix 3)

During grain filling two of the unfertilised crops lost 0.6 to 0.8 g/m^2 but most of the N0 crops gained between 0.6 and 7.1 g/m^2 nitrogen. Thus, during grain filling, soil nitrogen was still available to the crops and the crops were still able to take it up.

The fertilised crops showed a greater tendency than the unfertilised crops to lose nitrogen with six of them losing up to 2.0 g/m^2. Otherwise, with the exception of Sutton Bonington in 1990 where 8.0 g/m^2 were taken up during grain filling, less than 3.0 g/m^2 was taken up by the fertilised crops. Therefore, although nitrogen was available from the soil and their roots were capable of taking it up, the fertilised crops either did not require it or could not use it to the same extent as the unfertilised crops.

Proportion of the final total N content taken up or lost during grain filling (Table 3.45, Appendix 3)

In the 13 unfertilised crops where there was uptake of nitrogen during grain filling, up to 56 % of the final total N content was obtained by these crops during this period. This is remarkably high and unexpected. In the fertilised crops, given that these contained more nitrogen at anthesis, the amounts taken up constituted smaller proportions of their final N contents, yet up to 37% of their final total N content was obtained during this latter part of the life cycle.

Losses of nitrogen by both fertilised and unfertilised crops were up to 17% of the total in the crop.

Summary

The pattern of nitrogen uptake by the crops is described by their N contents at ZGS 30/31, N application, anthesis and maturity and also by the increments during phases of the life cycle as defined by these stages. In the unfertilised crops 42% on average (maximum - 51%) of the final N content had been taken up by ZGS 30/31, 29% on average during stem elongation and 29% during grain filling. In the fertilised crops 48% (maximum - 95%) of the final N content had been taken up by ZGS 30/31, this proportion being higher than that in the unfertilised crops because nitrogen had usually been applied and had begun to be taken up before ZGS 30/31. A further 42% of the final N content in the fertilised crops was taken up during stem elongation, a greater proportion than in the unfertilised crops. During grain-filling the fertilised crops, on average, took up only 9% of their final N content, a much smaller proportion than in the unfertilised crops.

Year: A greater quantity of nitrogen was present in the crops at maturity in 1989 and 1990 than in 1988, a similar pattern to that found in dry matter production. At the other principal stages where results on N content are presented, the same pattern is found with less nitrogen being present in the crops in 1988 than in 1989 and 1990. Despite these qualitative similarities from year to year, the proportions of nitrogen present in the crops relative to their final N contents still differed significantly at ZGS 30/31 and at anthesis but not at the time of nitrogen application when 35-36% was present in all years. At ZGS 30/31 in 1988 a smaller proportion, 39%, of the final total N content was present than in 1989 and 1990 when 48-49% was present. At anthesis this pattern was reversed with the highest proportion being present in 1988, 92%, and lower proportions of 82 and 69% being present in 1989 and 1990 respectively. This is reflected in the increments in total N content between ZGS 30/31 and anthesis which were 4.3 (50%), 2.2 (22%) and 2.3 (23%) g/m^2 in 1988, 1989 and 1990 respectively. The increments in total N content between N application and anthesis were very similar, 4.4 to 4.6 g/m^2, in the three years. The 1988 crops took up very little nitrogen during grain filling, 0.4 (9%) g/m^2, the 1989 crops 2.0 (18%) g/m^2 and the 1990 crops 4.2 (31%) g/m^2.

Site: The sites had similar total N contents at ZGS 30/31 but at the time of N application, Sutton Bonington crops had markedly higher N contents. At anthesis crops at both Sutton Bonington and Newcastle had much higher N contents than the other sites but by maturity the other sites had largely caught up. When considering total N contents at earlier stages in relation to those at maturity, crops at Sutton Bonington had a much higher proportion of the final total N content, 63%, present at the time of N application than at the other sites where 18 to 40% was present. At anthesis both Sutton Bonington and Newcastle had taken up over 90% of their final total N contents, crops at Potton only having taken up 63% of their final total N content. The increments in total N content during the various phases were similar at all sites.

Nitrogen: Applying nitrogen obviously had a marked effect on the patterns of nitrogen uptake but its effect varied significantly from year to year. Total N content at maturity was 6.0 g/m^2 higher in those crops where nitrogen had been applied. At ZGS 30/31, applying nitrogen resulted in increased uptakes of 4.7 and 3.0 g/m^2 in 1989 and 1990 respectively but only 1.1 g/m^2 in 1988. At the time of N application there were differences of less than 0.68 g/m^2 between the two N treatments in their N contents. At anthesis the fertilised crops had 6.6 g/m^2 more nitrogen on average than the unfertilised crops.

A lower proportion of the final total N content was present at ZGS 30/31 in the fertilised crops, 31%, in 1988 than in the unfertilised crops, 46%, compared with 1989 and 1990 when the fertilised crops had higher proportions of their final total N contents present at this stage. At the time of N application more of the final total N content was present, 44%, in the unfertilised crops than in the fertilised crops, 26%. At anthesis this was reversed with the fertilised crops having a higher proportion present, 91%, than the unfertilised crops, 71%.

The increments in total N content from ZGS 30/31 to anthesis in the unfertilised crops were less than 1.2 g/m^2 (22%) but varied from year to year in the fertilised crops, being very high in 1988, 7.5 g/m^2 (74%), and much smaller, although still greater than in the unfertilised crops, in 1989, 2.8 g/m^2 (22%), and 1990, 3.6 g/m^2 (29%). When the period between the time of N application and anthesis is considered, the unfertilised crops took up 1.7 g/m^2 on average and the fertilised 7.4 g/m^2, these amounts being less variable from year to year than the increments between ZGS 30/31 and anthesis. During grain filling the unfertilised crops took up 2.5 g/m^2

(29%), a much higher amount and a much higher proportion of their final total N contents than the fertilised crops which took up 1.9 g/m^2 (9%).

3.8 Ear N content

Characteristics:

- Ear N content at harvest
- Ear N content at anthesis
- Increment in ear N content during grain filling
- Contribution of N uptake prior to anthesis to final ear N content

  = (increment in ear N content during grain filling

  - increment in total N content during grain filling)

Significance of the effects of year, site and nitrogen on all characteristics (Table 3.46, Appendix 3)

Site-related factors and the weather in each year played an important part in determining the contents of nitrogen in the ears. The effect of nitrogen varied from year to year at each site but overall there was a marked effect of its application on ear N contents at both anthesis and at maturity. Nitrogen application had a very marked and a highly consistent effect on the increment in ear N content during grain filling and on the contribution from pre-anthesis nitrogen uptake to ear N content.

Ear N content at harvest (Table 3.47, Appendix 3)

Nitrogen content of the ears at harvest ranged from 2.1 to 14.6 g/m^2, with a mean of 6.3 g/m^2, in the unfertilised crops, and from 7.2 to 19.3 g/m^2, with a mean of 10.7 g/m^2, in the fertilised crops. The difference between the two treatments at individual sites ranged from as little as 1.0 g/m^2 at Belfast in 1990 to as much as 8.0 g/m^2 at Potton in 1988.

N content of the ears at anthesis (Table 3.48, Appendix 3)

Since nitrogen present in the ears at anthesis is likely to be structural protein rather than storage protein or surplus nitrogen, the amounts of nitrogen tied up in the ears at anthesis would be expected to be fairly small and constant, being influenced mainly by the number of ears present. At anthesis the ears in the unfertilised crops contained between 0.4 and 4.0 g/m^2 nitrogen, with a mean of 1.5 g/m^2. Ears in the fertilised crops had between 0.8 and 5.6 g/m^2, with a mean of 2.6 g/m^2. Ear N contents were significantly different at the sites being lowest at Belfast and Rothamsted and highest at Newcastle and Sutton Bonington.

Increment in ear N content during grain filling (Table 3.49, Appendix 3)

The amounts of nitrogen taken up by the ears during grain filling averaged 5.2 g/m^2 in the unfertilised crops and 8.5 g/m^2 in the fertilised crops. This response to nitrogen application of an increase in the increment in ear N content of 3.3 g/m^2 was consistent from year to year and from site to site.

Contribution from pre-anthesis nitrogen uptake to ear N content
= increment in ear N content during grain filling - increment in total N content during grain filling
(Table 3.50, Appendix 3)

The contribution from nitrogen uptake prior to anthesis to the increment in ear N content during grain filling was 2.4 g/m^2 on average in the unfertilised crops and 6.9 g/m^2 in the fertilised crops. The mean increase of 4.5 g/m^2 in the contribution from pre-anthesis N uptake in response to nitrogen application was very similar in all three years at the four sites where this assessment was made.

Summary

Year: Ear N content at harvest, like total N content at harvest, was much greater in 1989 and 1990 than in 1988. At anthesis the same pattern was observed but the small differences at these times resulted in the increments in ear N content being greater in 1990, 8.9 g/m^2, than in 1989, 7.4 g/m^2, and smallest in 1988, 4.4 g/m^2. The contribution from nitrogen uptake before anthesis to the increment in ear N content during grain-filling was very similar in all three years, 4.4 to 4.8 g/m^2.

Site: At anthesis and maturity Sutton Bonington had higher and Belfast and Rothamsted lower ear N contents than the other sites. Blunham had the greatest increment in ear N content during grain filling. The contribution from nitrogen uptake before anthesis was very similar at all sites, ranging from 4.3 to 4.9 g/m^2.

Nitrogen: Application of nitrogen increased ear N content from 1.5 to 2.6 g/m^2 at anthesis and from 6.3 to 10.7 g/m^2 at harvest. The increment in ear N content during grain-filling was much greater where nitrogen had been applied. Pre-anthesis uptake of nitrogen supplied 2.4 g/m^2 of the increment of 5.2 g/m^2, 45%, in the unfertilised crops. In the fertilised crops the contribution from pre-anthesis uptake, 6.9 g/m^2, was much greater and also constituted a greater proportion, 80%, of the increment of 8.5 g/m^2.

3.9 Shoot number

Characteristics:

- Shoot number at date of N application
- Shoot number at anthesis
- Maximum shoot number
- Date of maximum shoot number
- Final shoot number = Mean shoot number after anthesis
- Shoot productivity

  = {(maximum shoot number - shoot number at N application) x 100} /shoot number at N application
- Shoot survival

  = mean shoot number after anthesis/maximum shoot number
- Dry weight per shoot at anthesis

  = total dry weight at anthesis/shoot number at anthesis
- N per shoot at anthesis

  = total N content at anthesis/shoot number at anthesis

Significance of the effect of year, site and nitrogen on all characteristics (Table 3.51, Appendix 3)

The effect of nitrogen on shoot numbers at anthesis ($p<0.05$) and harvest ($p<0.001$) was inconsistent from year to year at each site. Unexpectedly, at the date of N application consistent differences between the sites in their response to nitrogen were found ($p<0.05$). The effect of nitrogen on maximum shoot number varied from year to year (**N x Y**: $p<0.001$) but was similar at all sites. The date when maximum shoot number was recorded was affected by nitrogen but inconsistently from year to year at each site (**N x Y x S**: $p<0.001$). The large effect of nitrogen on shoot productivity (**N**: $p<0.05$) was inconsistent form year to year at each site (**N x Y x S**: $p<0.001$). Nitrogen had a large and highly consistent effect on shoot survival (**N**: $p<0.01$). Nitrogen had a minimal effect on dry weight per shoot but it varied from year to year at each site (**N x Y x S**: $p<0.001$). Nitrogen had a very large effect on N content per shoot (**N**: $p<0.01$) but this also varied from year to year at each site (**N x Y x S**: $p<0.001$).

Shoot number at N application (Table 3.52, Appendix 3)

There was a three-fold variation from 509 to 1782 per m^2, in the number of shoots present in the 12 experiments at the date when nitrogen was applied. Shoot numbers at this stage were much higher in 1989 and 1990 than in 1988. Nitrogen had little effect on shoot numbers at this stage as would be expected except at Rothamsted where they were higher in the NS treatment. Blunham and Potton had high and Belfast low shoot numbers at this stage.

Shoot number at anthesis (Table 3.53, Appendix 3)

Shoot numbers at anthesis of between 390 and 1259 per m^2 in the N0 treatment and between 631 and 1415 per m^2 in the NS treatment were obtained. These were higher in 1989 than in 1988 and 1990. Blunham and Potton continued to have high and Rothamsted and Belfast low shoot numbers. Application of nitrogen increased shoot numbers by about 300 per m^2 at most sites except Newcastle where only 200 more shoots were present in the NS treatment than in the N0 treatment.

Maximum shoot number (Table 3.54, Appendix 3)

Maximum shoot numbers varied between 715 and 1782 per m^2 in the N0 treatment and between 962 and 1750 per m^2 in the NS treatment. These were higher in 1989 and 1990 than in 1988. Nitrogen had little effect on maximum shoot numbers in nine experiments and increased them by up to 475 per m^2 in the other five experiments.

Date of maximum shoot number (Table 3.55, Appendix 3)

Maximum shoot number was attained over a very wide range of dates in the experiments, between 27 February and 14 July. There was little consistency in the effect of nitrogen on the date when maximum shoot number was attained, although the most common effect was a delay of about 10-30 days.

Final shoot number, i.e. mean shoot number during grain filling (Table 3.56, Appendix 3)

Final shoot number varied between 372 and 1084 per m^2 in the N0 treatment and between 621 and 1256 per m^2 in the NS treatment. Final shoot numbers were highest in 1990 and lowest in 1988. Blunham and Potton had the highest and Rothamsted the lowest final shoot numbers. Nitrogen generally increased final shoot numbers by about 200 per m^2 although an increase of almost 500 per m^2 was obtained at potton in 1988.

Shoot productivity

= {(maximum shoot number - shoot number at N application) x 100}/shoot number at N application

(Table 3.57, Appendix 3)

In 14 of the 24 crops there was only a small increase of less than 10% in shoot number between the dates of application of nitrogen and maximum shoot number. This includes five of the 12 NS crops. Nitrogen increased shoot number by between 11 and 87% in the other seven NS crops. The N0 crop at Rothamsted in 1988 had an increase of 78% in shoot number compared with that of 36% which was found in the accompanying NS crop.

Shoot survival = (mean shoot number after anthesis x 100)/maximum shoot number

(Table 3.58, Appendix 3)

The proportion of shoots which survived was notably consistent from year to year. Between 55 and 62% in the N0 treatment and 73-75% in the NS treatment survived at Belfast, Blunham, Newcastle and Potton. Survival was lower at Rothamsted, being 40% in the N0 treatment and 57% in the NS treatment. Nitrogen increased the proportion which survived by 15%.

Dry weight per shoot at anthesis = total dry weight at anthesis/shoot number at anthesis

(Table 3.59, Appendix 3)

Dry weight per shoot at anthesis varied between 0.169 and 1.238g in the N0 treatment and between 0.449 and 1.225g in the NS treatment. Nitrogen increased dry weight per shoot by between 0.1 and 0.9g in eight experiments and decreased it by 0.2-0.3g in the other five experiments. There were no apparent trends either amongst the sites or between years or with dry weight per shoot in the N0 treatment. Since these are mean dry weights per shoot for the whole shoot population, the proportion of small shoots present will have a major effect on the mean dry weight.

N per shoot at anthesis = total N content at anthesis/shoot number at anthesis

(Table 3.60, Appendix 3)

N content per shoot was very variable, ranging from 2.13 to 16.01g in the N0 treatment and from 8.08 to 31.30g in the NS treatment. Nitrogen increased N content per shoot by between

0.4 and 15g per shoot. Newcastle was consistent in having the largest N contents per shoot and Potton tended to have very low N contents

Summary

The data extracted on shoot numbers at N application and anthesis and the maximum and final numbers show that shoot numbers increased and decreased as would be expected. However, in many crops the vast majority of the shoots were already present when the nitrogen was applied (Table 3.57). Maximum shoot number was not consistently attained at any particular growth stage. The final shoot number was very variable but the proportion of shoots surviving was reasonably constant. Survival did not appear to be inversely proportional to the maximum number of shoots produced as might have been expected. Both the dry weight and N content per shoot at anthesis were very variable.

Year: Shoot numbers throughout the life cycle were much higher in 1989 and 1990 than in 1988. As a consequence survival was similar in all three years. Production of new shoots after nitrogen was applied was greater in 1988 than in 1989 and 1990. Dimensions of the shoots, i.e. their dry weight and N content followed a similar pattern to their numbers, being greater in 1989 and 1990 than in 1988.

Site: Blunham and Potton had highest shoot numbers throughout the life cycle. Belfast produced the fewest shoots but lower survival at Rothamsted than at Belfast and the other sites, led to lowest final shoot numbers at Rothamsted. Blunham and Newcastle had the heaviest shoots with the highest N contents and Potton and Rothamsted the lightest shoots with the lowest N contents at anthesis.

Nitrogen: Nitrogen application did not always increase the maximum number of shoots produced by the crops. Final number was increased by nitrogen due its very consistent effect of increasing survival by 15%. Dry weight per shoot sometimes increased and sometimes decreased in response to nitrogen. N content per shoot showed a clear but variable increase in response to nitrogen.

Chapter 4

Discussion

4.1 Critique of experimental and statistical methodology

(a) Fitting of growth functions

The value of fitting Gompertz functions to the data collected in the 17 experiments can be assessed in a number of ways:

(1) the goodness of fit of the Gompertz curves to the data,

(2) comparison of modelled and observed data for particular dates, and

(3) correspondence between the Gompertz curves and patterns anticipated from development.

(1) The goodness of fit of the Gompertz curves to the data.

For total dry weight, 101 of the 106 datasets had over 70% of the variance accounted for by the fitted Gompertz functions (Table 3.14), 63 datasets having over 90% accounted for. For ear dry weight, 90 of the 94 datasets had over 70% of the variance accounted for by the fitted functions and 76 datasets had over 90% accounted for. Standards for judging this extent of the goodness of fit are subjective but having thoroughly verified the data included in this stage of the project, it is considered that fitting the functions has provided very valuable summaries of the time series of dry weights.

(2) Comparison of modelled and observed data for particular dates.

Observed dry weights at anthesis (Table 4.1) can be compared with dry weights determined from the fitted Gompertz functions (Table 3.24). Given the wide range in dry weight at anthesis, from less than 200 g/m^2 to over 1100 g/m^2, the agreement between the observed and modelled dry weights is remarkably good. In 24 of the 32 comparisons the modelled dry weights were within 100 g/m^2 of the observed values and in 14 comparisons, the difference between the two values was less than 50 g/m^2. The agreement found is encouraging, giving confidence in the fitting procedures adopted.

Table 4.1 Actual dry weight at anthesis (g/m^2)

	1988		1989		1990	
	N0	Ns	N0	Ns	N0	Ns
Belfast	155	723	599	1122	499	1010
Blunham	377	801	404	584	-	-
Newcastle	404	832	610	906	512	683
Potton	118	406	373	569	-	-
Rothamsted	165	641	406	837	270	660
S. Bonington	610	847	988	1022	991	1116

(3) Correspondence between the Gompertz curves and patterns anticipated from development.

Changes in dry weight between anthesis and maturity (Tables 4.2 and 4.3) were examined. Dry weight showed tremendous fluctuation during grain filling. Many of the crops, although showing a net increase in weight over this period, first increased in weight and then lost large amounts of weight (Table 4.3). In particular, the crops at Sutton Bonington in 1988 and 1989 all lost weight between anthesis and maturity. Sensitivity of the fully-grown crop to spatial variation in availability of water leading to large differences between samples may contribute to such fluctuating dry weights.

Table 4.2 Change in dry weight between anthesis and maturity (to nearest 10 g)

	1988		1989		1990	
	N0	Ns	N0	Ns	N0	Ns
Belfast	+200	+430	+40	+300	+370	+240
Blunham	+230	+340	+600	+800	-	-
Newcastle	+390	+510	+80	+400	+300	+640
Potton	+170	+740	+410	+640	-	-
Rothamsted	+130	+450	+270	+430	+160	+240
S. Bonington	-160	-40	-160	-40	+670	+670

Table 4.3 Loss in dry weight during grain filling (maximum final to nearest 10 g)

	1988		1989		1990	
	N0	Ns	N0	Ns	N0	Ns
Belfast	-80	-330	-240	-190	0	0
Blunham	-60	-100	-100	0	-	-
Newcastle	-100	-170	-270	-300	-40	-20
Potton	-70	-200	0	0	-	-
Rothamsted	-140	-50	0	0	-30	-300
S. Bonington	-160	-450	-160	-140	0	0

The lack of correspondence between significant points determined on the fitted functions with particular growth stages and events such as application of nitrogen fertiliser, has already been discussed (Tables 3.17 and 3.19). The good agreement between observed and modelled growth and the lack of correlation between development and key points on the fitted patterns of growth suggest that the pattern of growth is not associated with development.

(b) Quality control of data and efficiency of data handling

During the course of construction of the database and subsequent manipulation and analysis, several factors emerged as being important and even critical to the efficiency of management of research programmes:

(1) Data collection - storage - retrieval

Data collection was outside the scope of this project because the data were collected at each individual site under the initial project (0080/2/87). Easy retrieval is dependent on well organised storage, and efficient and effective analysis is dependent on easy retrieval. Whilst there is no criticism of the way data were collected and stored internally at each centre, where a multi-centred project is being undertaken, a common format should be adopted. To achieve highly efficient data storage in a multi-centred project, the final method of analysis should be taken into account prior to data collection and storage, and agreed and implemented from the outset of the project.

(2) House-keeping

Since there are a large number of people involved in a multi-centred project, it follows that there will be an increased likelihood of human error at various stages - sampling, data input and manipulation. Assuming that a common experimental protocol has been used, a helpful contingency in the event of error is good house-keeping, i.e. rigorous and well-organised recording of data and all mistakes and unusual events as well as use of data checking procedures. House-keeping rules must again be devised and agreed at the outset and must be strictly adhered to. When pooling of data occurs after the experimental phase of a project has been completed, or is being done by a person(s) not involved in the experimental phase, house-keeping notes can be consulted in the event of problems in the data. This should enable rapid resolution of the problem avoiding either time-consuming personal contacts and searching for further information or loss of data.

(3) Centralisation

It would be advantageous to appoint a key person with responsibility for monitoring all experiments and checking and storage of data.

(c) Use of several cultivars

The use of four cultivars in different experiments in this programme was outwith the control of the collaborators. Differences between the experiments will be attributable to both environmental and genotypic effects where the cultivars differ. From cultivar trials it is clear that cultivars are very sensitive to weather and soil factors so that their performance varies from field to field and from year to year. Estimates of mean cultivar effects which are obtained from a large number of trials cannot be applied to individual experiments. Therefore it is not possible to attach a magnitude to the cultivar effect on each characteristic. Consequently the cultivar effect cannot be removed from the results.

Comparisons of the cultivars from the results obtained in this programme is not possible given the unequal, and in some cases limited, inclusion of the four cultivars. Therefore the cultivar effect has not been discussed. It is doubtful if use of only one cultivar would have made much difference to the variation found in all characteristics from experiment to experiment.

4.2 Yield and its components

The concept of components of yield has been frequently used to describe and understand what happens in cereal crops during the growing season. It is therefore useful to consider how the components were related to yield in this programme and to examine their value in interpreting crop behaviour.

Relationship between the components and yield

It is generally accepted that grain population density, i.e. ear number/m^2 x grain number per ear, rather than grain weight, accounts for most of the variation in yield (Hay and Walker, 1989). Ear population is considered to be the most sensitive component to environment and management. Grain number per ear is much less variable while individual grain weight, i.e. grain mass, is relatively stable. Dyson (1977) found that in two spring barley varieties, variation in grain number per m^2 accounted for over 90% of the variance in grain yield. Gallagher *et al* (1975) also concluded that grain mass was a relatively conservative component and that grain yield was strongly dependent on grain number per m^2.

In this programme, variation in ear populations alone accounted for yield differences from year to year (Table 3.5). The effects of nitrogen on yield were attributable to both increased ear numbers and grain numbers per ear (Tables 3.5 and 3.6). Variation in grain mass only played a significant role in determining differences in yield between the sites (Table 3.7).

The minor role played by grain mass in determining variation in grain yield relative to the influence of ear number and grain number per ear is illustrated by the regression analyses conducted for each of the components using data from all replicates irrespective of factor level. Ear number per m^2 accounted for 46.0% and grain number per ear 31.0% of the variance in grain yield. Grain mass accounted for 14.8 % of the variance in grain yield. This is very similar to the relationship between grain yield and grain weight in 20 winter barley varieties grown with and without fungicide in 14 trials conducted over six years in N.Ireland which accounted for 16.1% of the variance in grain yield (White, E.M., unpublished).

The correlation matrix (Table 4.4) obtained from a multiple regression of grain yield with ear no/m^2, grain no/ear and grain mass, shows the strong relationships amongst yield and the components. Grain no/ear and grain mass were independent of ear no/m^2. The positive correlation between grain number and grain mass shows that ears with more grains had larger grains.

Table 4.4 Correlation matrix of yield and its components for all data (df=112)

	Yield	Ear no/m2	Grain no/ear
Ear no/m2	0.682***		
Grain no/ear	0.562***	-0.011	
Grain mass	0.394***	-0.159	0.348***

From the multiple regression, ear number and grain number together accounted for 78.6% of the variation in grain yield with grain mass accounting for a further 11%.

Relationships between ear number, grain number per ear and grain mass

Compensation is the mechanism invoked to explain negative correlations amongst the components where higher ear numbers may be accompanied by lower grain numbers per ear and/or lower grain mass in response to the influence of whatever factors are being discussed. Grain mass is frequently expected to decrease at higher ear numbers because, in the later part of the life cycle when this component is being produced, competition for limited resources amongst a greater number of sinks, i.e. grains, results in lower amounts of assimilate being accumulated by each grain.

The common approach to explaining relationships amongst the components has been to consider anthesis as the pivotal growth stage because the number of sinks, i.e. grain population density (ear number/m^2 x grain number per ear) has been finalised by this stage. However, the positive association between grain number and grain mass and the lack of association between either of these and ear population suggests that the components may have a different structure. The crop could be considered to be a population of ears, each with a grain productivity = (grain number per ear x grain mass). Ear population would be determined independently of grain number per ear and grain mass. The magnitudes of these two later components would be linked and would be determined by the growth and development of individual ears. Thus larger shoots would produce both higher grain numbers and larger grains and *vice versa*. The survival of grain primordia to produce florets at anthesis would be determined by the productivity of the green area of the shoot. The magnitude and longevity of this green area would determine the extent of current photosynthesis during grain filling and the production of reserves. It is hypothesised that since both the number of grains and the capacity to fill them are related to the same entity, magnitude of the green area, they are likely to be balanced and therefore, positive rather than negative correlations between them are likely to be observed.

Effect of nitrogen on the components

The components develop sequentially during the life cycle. Tillers are being produced and are growing during the period when applied nitrogen is available to the crop. The ear is also rapidly growing at the same time but survival of the grain primordia to produce florets at anthesis is determined later in the life cycle than survival of tillers to produce ears at anthesis. Therefore, if most of the nitrogen is used to produce tillers, the supply of nitrogen per tiller may be similar in all crops irrespective of the amount of nitrogen applied and competition between the greater number of tillers will lead to reductions in both grain number per ear and grain mass. Tillers in highly fertilised crops would also tend to be smaller because they are produced late. Thus in response to nitrogen, there may be negative correlations of both grain number per ear and grain mass with ear number because of the reduced average size of the shoots.

The availability of nitrogen in the fertilised and unfertilised crops as indicated by the patterns of nitrogen uptake (Tables 3.36, 3.40 and 3.48) influenced the magnitudes of the components. In the fertilised crops where nitrogen was plentiful, ear numbers and grain numbers were both much higher than in the unfertilised crops which were limited to a small but continuous supply of nitrogen from the soil. Grain mass was similar in the fertilised and unfertilised crops.

Relationships between the components and yield in the fertilised and unfertilised crops were examined by conducting multiple regressions on the dataset split into the N0 and NS treatments.

Table 4.5 Correlation matrix of yield and its components in N0 crops (df=55)

	Yield	Ear no/m2	Grain no/ear
Ear no/m2	0.688***		
Grain no/ear	0.435**	-0.166	
Grain mass	0.459***	-0.051	0.378**

Under the N0 treatment (Table 4.5), yield was highly positively correlated with all three components. Grain number/ear and grain mass were independent of ear number/m^2 and were weakly but significantly positively correlated with each other. Ear number/m^2 and grain number/ear accounted for 77.5% of the variation in yield and grain mass contributed only a further 9.7%.

Table 4.6 Correlation matrix of yield and its components in the NS crops (df=55)

	Yield	Ear no/m2	Grain no/ear
Ear no/m2	0.497***		
Grain no/ear	0.518***	-0.177	
Grain mass	0.376**	-0.395**	0.302*

Under the NS treatment (Table 4.6), yield was less strongly correlated with ear number and grain mass than in the N0 crops. In contrast to the N0 treatment, grain mass was significantly correlated with ear number/m^2 and decreased as ear number/m^2 increased. Ear number/m^2 and grain number/ear accounted for a smaller proportion of the variation in grain yield, 61.2%, than in the N0 treatment. Grain mass contributed a further 23.7%, a much larger contribution than in the N0 treatment.

In the fertilised crops competition between ears for light was greater during the grain filling period than in the unfertilised crops because of their higher ear populations. As a result grain mass decreased as ear number increased. In the unfertilised crops, the smaller numbers of ears and numbers of grains which had survived following lower availability of nitrogen earlier in the life cycle, did not inhibit growth of individual grains and no such 'compensation' was observed.

The conservative nature of grain mass

The relatively small contribution of variation in grain mass to variation in grain yield is related to the mechanisms by which assimilate is supplied to the growing grains. Photosynthesis in green tissues present during grain filling provides much of the assimilate but remobilisation of carbohydrate reserves stored prior to grain filling can contribute very significantly to grain yield in some situations. In experiments involving 24 spring barley varieties, Austin *et al*

(1980) found that 54-61% of yield was attributable to photosynthesis in the period from 18 days before to 5 days after anthesis in the drought year of 1976. In the wetter year, 1977, only 16-18% of the yield was produced prior to 5 days after anthesis. Gallagher *et al* (1975), on the assumption that dry weight lost by the stem during grain filling contributed to grain weight, calculated that 2% in 1969, 74% in 1970 and 33% in 1972 of the grain weight was derived from pre-anthesis photosynthesis. The mechanism of remobilisation enables grains to fill to a greater extent than if current photosynthate alone was available. This leads to what is perceived as stability in grain mass. Grain mass is therefore a highly complex characteristic which is dependent on the crop's capacity both to photosynthesise during grain filling and to provide carbohydrate from stored reserves.

Grain mass, although not contributing much to variation in grain yield, varied between 24.8 to 48.1 mg, a two-fold range. This cannot really be considered to be 'stable'. The supply of assimilate to the growing grains by both current photosynthesis during grain filling and translocation of pre-anthesis assimilate may determine grain mass, i.e. it is source-limited. On the other hand it could be argued that grain mass is pre-determined at earlier stages in grain development, i.e. it is sink-limited, and that grain growth ceases at various stages in the utilisation of available assimilate. The variable extent to which reserves were utilised in grain growth (Table 3.32), particularly in relation to the large and consistent effect of nitrogen on ear dry weight (Table 3.31), suggests that grain mass is sink-limited rather than source-limited, at least in some crops. It is hypothesised that nitrogen influenced the processes of growth, i.e. tiller production and survival and grain production and survival, setting up a potential yield which was achieved by remobilisation of reserved of carbohydrate to differing extents depending on the contribution from current photosynthesis during grain filling. The extent to which the reserves were utilised in grain filling in these crops and whether they were exhausted in none, in any or in all crops cannot be determined because there is no knowledge of their maximum amount.

Prediction of yield

Variation in grain yield is therefore largely determined by events in the crop life cycle prior to anthesis which determine both the grain population density, the quantity of stored carbohydrate reserves and possibly also potential grain size. The total dry weight of the crop at anthesis could be used as an indicator of both the sinks available to be filled, i.e. grain population density, and the crop capacity to fill them, i.e. green area available to photosynthesise during grain filling and stored carbohydrate reserves. Dyson (1977) found that the relationship between grain yield and total dry weight at ear emergence explained 92% of the variation in grain yield. In the present study 51% of the variance in grain yield in the full dataset was accounted for by the linear regression of yield on dry weight at anthesis:

grain yield = **1.78** (±0.336) + **0.45** (±0.045) x dry weight at anthesis ($p<0.001$)

When the nitrogen treatments were looked at separately, 57.5% of the variance was accounted for in the N0 treatment but only 16.5% in the NS treatment.

N0 grain yield = **1.40** (±0.339) + **0.44** (±0.056) x N0 dry weight at anthesis ($p<0.001$)

NS grain yield = **3.75** (±0.670) + **0.25** (±0.078) x NS dry weight at anthesis ($p=0.002$)

On the basis of these results it would not be possible to predict grain yield with a sufficient degree of confidence in fertilised crops at anthesis.

Conclusion

The components of yield, through the processes by which they are produced, confer a flexibility to cereal crops which allows them to respond continuously to and to exploit fully the variable weather conditions and supply of resources encountered in every cropping situation. Although the overall total dry matter production of the crop may be determined by the quantity of light intercepted (Monteith, 1977), the crop's capacity to intercept all the available light over a long period of its life cycle and to utilise it depends on its ability to 'keep all its options open' until very late in the life cycle. In doing so it can avoid being severely limited by short term shortfalls and can capitalise on surpluses to produce what in effect is a relatively stable yield from situation to situation.

4.3 Mechanisms explaining variation in carbohydrate production

Grain is 70% carbohydrate, which is a product of photosynthesis, which is a light-dependent process. Yield and dry matter production in cereal crops are primarily limited by the amount of light which the crop intercepts during the course of the growing season. The green area of the crop plays a central role by intercepting incoming radiation. Nitrogen has a major influence on the quantity of green area present and is therefore one of the most important limiting factors in crop productivity.

Nitrogen is known to affect cereal plants by:

producing larger leaves
increasing the production of tillers
increasing the survival of tillers
increasing the length of stems
increasing the survival of grains
increasing grain weight

The production of larger leaves is primarily responsible for all the other effects on the plant.

Scott, Jaggard and Sylvester-Bradley (1994) presented a simple model incorporating the roles of nitrogen and light availability:

(1) grain yield = total dry weight x *harvest index*
(2) total dry weight = total intercepted radiation x *dry matter conversion coefficient*
(3) total intercepted radiation = green area x *extinction coefficient* $(I = Io\ e^{(-kL)})$
(4) green area = nitrogen uptake / *N area ratio* (gN/m^2 green area)

In this model N offtake influences the quantity of green area produced by the crop, which in turn determines the amount of absorbed radiation, which then governs the amount of dry matter produced.

The relationship (1) between grain yield and total dry weight and harvest index can be examined using this database. Intercepted light and green area are not discussed in this report, both because only a few sites collected data on these characteristics and because of lack of time. Therefore only the relationship between N offtake and total dry weight can be examined by combining (2), (3) and (4).

(1) Grain yield = total dry weight x harvest index

Table 4.7 Summary of effects of Nitrogen, Site and Year on grain yield, total dry weight and harvest index

	Grain yield (t/ha)	Total dry weight (t/ha)	Harvest index (%)
N0	3.9	7.1	52
NS	6.5	11.8	50
Belfast	5.2	9.6	47
Blunham	5.5	10.1	50
Newcastle	6.9	10.0	55
Potton	4.3	8.9	53
Rothamsted	4.0	7.7	54
Sutton Bonington	5.2	10.2	46
1988	3.8	7.6	48
1989	5.8	10.6	51
1990	6.0	10.1	53

The effect of nitrogen on grain yield was largely attributable to its effect on total dry matter production, far outweighing the small negative effect that it had on harvest index (Table 4.7).

Variation in grain yield from site to site was related to variation in both harvest index and total dry matter production. At Newcastle high grain yield was attributable to both high total dry matter production and high harvest index. At Rothamsted and Potton lower total dry matter production resulted in lower grain yield despite high harvest indices. At Belfast and Sutton Bonington lower harvest indices resulted in intermediate grain yields despite high total dry matter productions.

Variation in grain yield due to year was largely associated with variation in total dry matter production with similar but smaller variation in harvest index reinforcing this pattern.

- **Conclusion**

Variation in total dry matter production did not fully explain variation in grain yield produced by nitrogen, site and year. Harvest index was not constant and variation in partitioning of the dry matter augmented the influence of total dry matter production due to year but diminished its influence due to site and nitrogen.

(2) Total dry weight = nitrogen uptake x *nitrogen:dry matter conversion coefficient*

i.e. total dry weight = total intercepted radiation x *dry matter conversion coefficient*

total intercepted radiation = green area x *extinction coefficient* $(I = Io\ e^{(-kL)})$

green area = nitrogen uptake / *N area ratio* (gN/m^2 green area)

The relationships between total dry weight and N offtake were looked at separately for the N0 and NS crops since application of nitrogen had a powerful influence on dry matter production of the crops (Table 4.13).

Table 4.8 Relationships between total dry weight (g/m^2) at harvest and N offtake in the N0 and NS crops.

	N0		NS	
	Regression coefficient	% variance accounted for	Regression coefficient	% variance accounted for
N content (g/m^2) at:				
• Harvest	52.2	36.0	29.1	7.7
• ZGS 30/31	138.9	48.8	30.9	17.3
• N application	34.6	15.1	-10.7	-
• Anthesis	37.8	13.0	-7.6	-

The differences in regression coefficients between total dry weight and N offtake at the four stages reflect the course of N offtake during the life cycle (Table 4.8). Total dry weights at harvest in both the N0 and NS crops were more closely related to the nitrogen contents of the crops at ZGS 30/31 than at other stages in the life cycle. In both the N0 and NS crops, the influence of nitrogen on total dry weight became poorer between ZGS 30/31 and maturity.

The N0 crops were much more effective than the NS crops in utilising the nitrogen they took up in producing dry weight as shown by the higher regression coefficients, 52 g/m^2 dry weight being produced for every g/m^2 nitrogen in the N0 crops compared with 29 g/m^2 dry weight for every g/m^2 nitrogen in the NS crops.

The nitrogen content of the N0 crops had a greater influence on their dry matter production than had the nitrogen content of the NS crops, as shown by the higher proportions of the variance accounted for by the relationships. However, the lack of fit, particularly in the NS crops, shows that one or more of the coefficients in the relationships, i.e. nitrogen area ratio, extinction and conversion coefficients, are not constant but vary from crop to crop.

- **Conclusion**

Scott *et al.*'s model (1994) has the virtue of being simple. However, it summarises processes which continue over a period of time into single variates. In order to provide a basis for developing management strategies, these processes require further explanation and, therefore, development of the model.

Using the database produced in this project the factors and characteristics involved in yield formation are examined with a view to:

(i) identifying characteristics potentially useful for prediction of growth and

(ii) describing the effects of Nitrogen, Site and Year.

(A) Total dry matter production

Total dry weight is examined using the parameters derived from the fitting of the Gompertz function:

(3) total dry weight = rate x duration of growth

(4) rate of growth - **light** limited/controlled g/MJ (RUE i.e. Radiation Use Efficiency)

(5) **water** limited/controlled g/mm (WUE i.e. Water Use Efficiency)

(6) **nitrogen** limited/controlled gDW/gN (dwNUE i.e. Nitrogen Use Efficiency, dry weight basis)*

* This relationship is not discussed directly as nitrogen is one of the factors being examined for its influence on all relationships.

(7) duration of growth - controlled by phenological development, i.e. temperature

(3) Total dry weight = rate x duration of growth

Table 4.9 Summary of the effects of Nitrogen, Site and Year on total dry weight, rate and duration of growth

	Total dry weight (t/ha)	Rate of growth ($g/m^2/day$)	Duration of growth (days)
N0	7.1	11.6	60
NS	11.8	15.7	59
Belfast	9.6	13.0	58
Blunham	10.1	18.5	51
Newcastle	10.0	11.7	81
Potton	8.9	10.1	69
Rothamsted	7.7	9.8	65
Sutton Bonington	10.2	18.6	44
1988	7.6	12.2	52
1989	10.6	15.5	60
1990	10.1	13.2	67

Nitrogen has little influence on development and therefore its effect on total dry weight was largely produced by variation in the rate of growth (Table 4.9).

Variation in total dry matter production from site to site and year to year was associated with variation in both the rate of growth and the duration of growth. High total dry matter production at Sutton Bonington and Blunham was attributable to the very high growth rate over a short period of time. On the other hand at Newcastle the high total dry matter production was the result of quite a low growth rate over a very long period.

In 1988, low dry matter production was largely attributable to the short duration of growth. High dry matter production in 1989 was attributable to the high rate of growth. In 1990, the long period for growth led to high dry matter production.

- **Conclusion**

Variation in both rate and duration of growth influenced the total dry weights produced by the crops. The effect of Nitrogen was largely attributable to its effect on growth rate whereas Site and Year influenced both the rate of growth and its duration.

(4) Rate of growth - light limited/controlled (g/MJ)
(5) Rate of growth - water limited/controlled ($g/m^2/mm$)
(7) Duration of growth - controlled by phenological development, i.e. temperature

Preliminary analysis of the relationship between the rates and durations of growth as determined from the Gompertz functions and the summarised meteorological variates during stem elongation, Phase 2, has been conducted. The rates of growth at all sites were regressed with mean radiation per day, mean rainfall per day and maximum Potential Soil Moisture Deficit for the N0 and NS treatments separately (Table 4.10). Durations of growth for the N0 and NS treatments were regressed on the mean temperature during stem elongation.

Table 4.10 Relationships of rate and duration of growth and meteorological variates during stem elongation

	N0		**NS**	
	Regression coefficient	% variance accounted for	Regression coefficient	% variance accounted for
Rate of growth ($g/m^2/day$)				
• Radiation ($MJ/m^2/day$)	-1.07	6.8	0.87	7.5
• Rainfall (mm/day)	-5.06	7.0	-20.56	13.9
• Maximum PSMD (mm)	0.0235	2.4	0.0131	1.2
Duration of growth (days)				
• Temperature (°C)	6.4	3.2	-10.2	13.3

There were no indications of strong relationships of rate and duration of growth with any of these meteorological variates. This may be due to:

(1) the mismatch between the calendar dates for rate and duration of growth, as derived from the Gompertz functions, and the Zadoks' period used in the summation of the weather variates, and/or

(2) the complex relationship between growth and weather. There are two relevant aspects:

 (a) radiation and rainfall can both limit growth, therefore, they should be looked at together in a combined analysis, and

 (b) the time scale is too large. On a day by day basis, and probably even on a much shorter time scale, variation in availability of radiation and rainfall will result in a continuous interchange between the two factors concerning which is limiting growth at any one time.

Even a multivariate analysis combining the meteorological variates may not identify strong relationships simply because the time scale at which light and water limit growth is much shorter than that being used here.

The mechanisms by which meteorological variates limit growth, i.e. where in the plant as it produces and partitions dry matter and which organs are growing and requiring dry matter, are also involved. Events occurring in a very short time determine whether or not an individual shoot survives and therefore will have very significant effects later in the life cycle. Marshall and Ellis (1994) addressed the question of how growth is determined, examining the concepts of cumulative and instantaneous partitioning and the misconception that 'decisions' are made about how growth proceeds.

- **Conclusion**

Rate and duration of growth were not related to radiation, rainfall, soil moisture deficit or temperature on the time scale used in this analysis.

(B) Partitioning of dry matter

Accepting that nitrogen is a major determinant of crop growth by influencing the capacity to produce carbohydrate, i.e. crop green area, because of its primary effect on leaf size, the partitioning of the dry matter produced into various organs at a number of stages in the life cycle can be considered. This will help us to identify particular phases and/or processes to which variation in the final yield due to the effects of Nitrogen, Site and Year can be apportioned. From this analysis it may then be possible to identify features of the crop which could be used as predictors of subsequently-determined parameters.

Partitioning at anthesis

(8) Total dry weight at anthesis = shoot number at anthesis x dry weight per shoot
(9) Grain population density v total dry weight at anthesis
(10) Grain number/shoot v dry weight/shoot
(11) Grain mass v dry weight/shoot

Post-anthesis partitioning

(12) Increment in ear dry weight during grain filling =
increment in total dry weight during grain filling + remobilisation of stored carbohydrate reserves
(13) Increment in total dry weight during grain filling
(14) Remobilisation of stored reserves

Partitioning at anthesis

Anthesis has been identified as a pivotal point in the life cycle in the previous section on components of yield. In the crop at this stage dry matter is distributed amongst a number of shoots of a certain size.

(8) Total dry weight at anthesis = shoot number at anthesis x dry weight per shoot

The effects of nitrogen, site and year were examined using the results from the analyses of variance (Table 4.11).

Table 4.11 Summary of the effects of Nitrogen, Site and Year on total dry weight, shoot number and dry weight per shoot at anthesis

	Total dry weight at anthesis (g/m^2)	Shoot number at anthesis ($number/m^2$)	Dry weight per shoot at anthesis (g)
N0	524	687	0.794
NS	809	971	0.860
Belfast	710	679	0.871
Blunham	720	923	1.085
Newcastle	734	774	1.147
Potton	416	1101	0.465
Rothamsted	507	666	0.566
Sutton Bonington	866	-	-
1988	509	718	0.754
1989	755	945	0.852
1990	735	824	0.874

Lower total dry weights at anthesis in the N0 crops than in the NS crops were mainly attributable to lower shoot numbers, dry weights per shoot being similar (Table 4.11).

Both shoot number and dry weight per shoot were influential in determining the total dry weight present at anthesis at the various sites. High dry weights per shoot led to high total dry weights at Blunham and Newcastle. Low dry weights per shoot led to low total dry weights at Potton and Rothamsted despite very high shoot numbers at Potton.

Lower total dry weights in 1988 than in 1989 and 1990 were attributable to both lower shoot numbers and lower dry weights per shoot.

Regression analysis of the data from all replications of the N0 and NS crops separately showed that there was no relationship in either case between total dry weight at anthesis and shoot number at anthesis. However, variation in the dry weight of individual shoots was important, particularly in the N0 crops. In these crops variation in dry weight of individual shoots accounted for 65.7% of the variance in total dry weight at anthesis:

total dry weight at anthesis = **156** (±46.8) + **411** (±56.7) x dry weight per shoot at anthesis (p<0.001)

In the NS crops variation in dry weight of individual shoots accounted for 44.2% of the variance in total dry weight at anthesis:

total dry weight at anthesis = **447** (±75.5) + **389** (±74.6) x dry weight per shoot at anthesis (p<0.001)

- **Conclusion**

Variation in both shoot number and dry weight per shoot influenced the total dry weights of the crops at anthesis. The effect of Nitrogen was largely attributable to its effect on shoot number. However the size of the shoot in the N0 crops and to a lesser extent in the NS crops has a grreater influence on crop dry matter production at anthesis than the number of shoots present.

(9) Grain population density v total dry weight at anthesis

A crop at anthesis can be considered as comprising a population of sinks, grain population density (grain number/m^2), which are then filled following fertilisation. At anthesis in barley crops, final ear number and grain number per ear, and therefore grain population density, have been determined. The magnitudes of these parameters may be related to the crop's success at producing dry matter up to this stage and therefore, a positive correlation with total dry weight at anthesis could be expected. Total dry weight, as well as indicating sink capacity, might also reflect source capacity, i.e. the green area which the crop has available going into the grain filling phase and the carbohydrate reserves stored in the stem.

The extent to which grain population density was related to total growth at anthesis was examined using regression analysis for all replicates in the N0 and NS crops separately. Grain population density in the N0 crops was associated with total dry weight at anthesis, 50.1% of the variance being accounted for by the relationship:

grain number/m^2 = **4901** (±1008) x **11.1** (±1.66) total dry weight at anthesis (p<0.001)

In the NS crops, there was very little dependency of grain population density on total dry weight at anthesis, the relationship only accounting for 3.3% of the variance in the dataset:

grain number/m^2 = **12617** (±2262) x **4.27** (±2.63) total dry weight at anthesis (p=0.111)

- **Conclusion**

Sink capacity, i.e.grain population density, was dependent on total dry weight to some extent in the N0 crops but not in the NS crops.

(10) Grain number/shoot v dry weight/shoot

(11) Grain mass v dry weight/shoot

The structure of the crop at anthesis can also be viewed as a population of ears each with a grain productivity. The extent to which number of grains and the weight of individual grains on a shoot were related to the dry weight of the whole shoot was examined using regression analysis for all replicates for the N0 and NS crops separately. In the N0 crops increases in grain number per shoot and individual grain mass were associated, to a small extent, with increasing dry weight per shoot:

grain number/shoot = **14.2** (±0.96) + **2.4** (±1.17) x dry weight/shoot (g) (p = 0.054)

grain mass (mg) = **31.1** (±1.69) + **5.8** (±2.04) x dry weight/shoot (g) (p = 0.008)

However, less than 22% of the variance in these two components was explained by variation in dry weight per shoot in the N0 crops.

In the NS crops, grain number per shoot and grain mass showed even less dependency on dry weight per shoot at anthesis, the relationships not accounting for any of the variance in the datasets:

grain number/shoot = **18.1** (±1.26) + **0.16** (±1.25) x dry weight/shoot (g) (p = 0.897)

grain mass (mg) = **34.7** (±2.78) + **2.6** (±2.75) x dry weight/shoot (g) (p = 0.361)

When grain number per shoot and grain mass are combined to give grain yield per shoot, the relationship with dry weight per shoot at anthesis in the N0 crops accounted for 27.8% of the variance but none in the NS crops :

N0 crops

grain yield/shoot (g) = **0.436** (±0.0427) x **0.175** (±0.0517) dry weight/shoot (g) (p=0.002)

NS crops

grain yield/shoot (g) = **0.629** (±0.0714) x **0.053** (±0.0705) dry weight/shoot (g) (p=0.454)

- **Conclusion**

Productivity of individual shoots was influenced by their size to a greater extent in the N0 crops than in the NS crops. Generally, however, there appears to be very little dependency of the productivity of individual shoots measured as either the components individually or combined, on the size of the shoot at anthesis. Therefore, shoot size is not an indicator of source capacity, i.e. green area for photosynthesis and stored reserves for remobilisation.

Post-anthesis partitioning

After anthesis the grains which are present will be filled. Grain yield and the mass of individual grains will be determined by the capacity of the available green area to photosynthesise and, in some circumstances, the capacity of the stems to mobilise and translocate carbohydrate produced and stored prior to anthesis. Thus grain yield is to a large extent equivalent to the increment in ear dry weight during grain filling.

(12) Increment in ear dry weight during grain filling =

increment in total dry weight during grain filling +
remobilisation of stored carbohydrate reserves

The increase in ear dry weight during grain filling produced by the nitrogen application was largely due to the effect of nitrogen on the increment in total dry weight, the contribution by stored reserves being unaffected by nitrogen (Table 4.12).

Table 4.12 Summary of the effects of Nitrogen, Site and Year on the increments in ear and total dry weights and on the remobilisation of stored reserves during grain filling

	Increment in ear dry weight during grain filling (g/m²)	Increment in total dry weight during grain filling (g/m²)	Contribution of stored reserves to ear dry weight (g/m²)
N0	393	290	149
NS	592	530	156
Belfast	514	344	151
Blunham	590	457	185
Newcastle	625	520	259
Potton	510	512	40
Rothamsted	532	344	177
Sutton Bonington	192	281	104
1988	431	362	81
1989	596	402	187
1990	450	464	190

Variation in the increase in ear dry weight during grain filling from site to site was attributable to variation in both the increment in total dry weight over this period and the remobilisation of stored reserves. At Newcastle the large increase in ear dry weight was produced by both a large increase in total dry weight during grain filling and a high remobilisation of stored reserves. At Potton, however, a small contribution from stored reserves resulted in a smaller increase in ear dry weight despite a large increase in total dry weight during grain filling. The higher increase in ear dry weight at Blunham than at Belfast and Rothamsted was attributable to a greater increase in total dry weight during grain filling, the contributions from stored reserves being similar at these three sites.

The results for ear dry weights and contributions from stored reserves for 1990 include only two sites and therefore, are not very helpful to the discussion. Comparison of 1988 and 1989 shows that the higher increase in ear dry weight in 1989 is attributable to both higher increments in total dry weight and increased contributions from stored reserves than in 1988.

- **Conclusion**

Variation in both the increment in total dry weight and the remobilisation of reserves to the ear during grain filling influenced the increment in ear dry weight during grain filling. The effect of nitrogen was largely attributable to its effect on the increment in total dry weight whereas both parameters contributed to the differences between sites and between years in the increment in ear dry weight during grain filling.

(13) Increment in total dry weight during grain filling

The magnitude and longevity of the green area of the crop which is photosynthesising and producing carbohydrate will determine the increase in total dry weight which occurs during grain filling. The green area will be expected to senesce more rapidly under dry conditions and high temperatures than under cool and/or wet conditions. Differences between sites in the availability of light will also be expected to lead to variation in the increment in total dry weight, higher levels of radiation resulting in the production of more dry matter by the green area which is present.

Simple regressions of the relationships between the amount of growth and the total radiation and total rainfall during grain filling showed that for the N0 crops availability of radiation and shortage of water had some influence on growth while in the NS crops, there were no relationships between growth and meteorological parameters (Table 4.13). Lack of data from all the sites and lack of time has meant that availability of green area during grain filling has not been included.

Table 4.13 Relationships of growth and meteorological variates during grain filling

	NO		NS	
	Regression coefficient	% variance accounted for	Regression coefficient	% variance accounted for
Increment in total dry weight (g/m^2)				
• Total Radiation (MJ/m^2)	0.65	40.2	0.22	3.2
• Total Rainfall (mm)	-0.62	2.6	-0.67	1.9
• Maximum PSMD (mm)	0.92	16.6	0.70	5.5
• Temperature (°C)	14.3	0.5	-41.9	2.7

As with the stem elongation period, Phase 2, more rigorous investigation of the relationship between growth and meteorological variates should be undertaken. The increment in total dry weight during grain filling increased as radiation increased. There is no obvious reason why N0 and NS crops should vary in their sensitivity to the availability of radiation. The positive relationship between the increment in total dry weight and maximum PSMD in the N0 crops is surprising since it suggests the growth improves as the risk of drought increases.

- **Conclusion**

The N0 crops are more sensitive and more responsive to variation in weather in this 'coarse' test of such relationships.

(14) Remobilisation of stored reserves

The demand for carbohydrate from the growing grains and the supply of stored reserves available in the stem will determine the contribution from stored reserves to grain yield. Potential grain mass, which is determined during the phase when the ear is differentiating and increasing in size prior to anthesis, and the extent of photosynthesis during grain filling will both determine the demand by the grains for stored assimilate. The supply of stored reserves available for remobilisation and grain filling will be expected to be related to the dry weight per shoot at anthesis and the extent of photosynthesis immediately after anthesis when the cells in the fertilised ovule are dividing and there is little grain growth.

The utilisation of stored reserves by the crop bore no relation to dry weight per shoot at anthesis when a regression model was fitted to these data for the N0 crops:

reserves utilisation = **182.2** (±59.1) - **15.6** (±66.9) x dry weight per shoot at anthesis

(p = 0.819)

In the NS crops dry weight per shoot had a small effect on the utilisation of reserves, the relationship accounting for 10.6% of the variance in the dataset:

reserves utilisation = **-39** (±113) + **228** (±118) x dry weight per shoot at anthesis

(p = 0.066)

In these NS crops utilisation of reserves increased in shoots which had higher dry weights at anthesis.

- **Conclusion**

The size of the shoot at anthesis had little influence on the amount of stored reserves utilised in grain filling in the N0 crops. However, in the NS crops, there is some indication that larger shoots at anthesis provided, or were required to provide, more reserves to fill the grain.

Summary

Neither total dry matter production nor harvest index completely explains the effects of Nitrogen, Site and Year on grain yield. Neither rate nor duration of growth completely explains the effects of these factors on total dry matter production.

Site and Year strongly affected all characteristics associated with yield formation. Nitrogen affected some strongly, namely total dry matter production, rate of growth, shoot number and increment in total dry weight during grain filling, but others weakly, namely harvest index, duration of growth, dry weight per shoot at anthesis and the contribution of stored reserves to the increment in ear dry weight.

Although the total dry weights of the crops at anthesis was found to be dependent on average shoot size at the various sites, neither the productivity at harvest nor the extent to which stored reserves contributed to grain yield was related to this characteristic.

The structure of the crop at anthesis, i.e. the number of shoots present, their size and the numbers and size of florets which have developed, is dependent to varying extents on the amount of carbohydrate supplied by photosynthesis and is therefore related to the green area of the crop. Whilst, for the sake of parsimony, it would be desirable to consider this structure as simply as possible, it is important to take note of the fact that the shoots will vary greatly in size. To some extent an age-related hierarchy in size will have developed so that an average shoot size may not be the most useful parameter describing its status.

Since both the production and survival of individual shoots and their size are dependent on growth, and therefore, on light, it may be possible to identify parameters describing the status of the crop at, for example, ZGS 30, which may be associated with and therefore be useful as predictors of the status of the crop at later stages such as anthesis or even maturity. Clare and Spink (1994) suggested that growth, by which they meant dry weight of the crop at ZGS 31, might be an indicator of final yield in winter wheat but they also went on to show how growth later in the life cycle, such as growth rate during grain filling, also had a major impact on final yield. Murphy (1993) suggested that response to nitrogen fertiliser applications in winter barley was related to the the earliness of canopy development, i.e. the date at which a green area index of 1 was achieved.

Characteristics of the N0 crops, which were deficient in nitrogen, were found to be much more sensitive (as shown by higher %'s of variance accounted for) and more responsive (as shown by higher regressions coefficients) to environmental factors and in relation to each other than the NS crops. The more restricted growth of the N0 crops due to lack of nitrogen seems to have led to more efficient utilisation of available resources both external and internal to the crop. Higher grain yield was produced per unit of nitrogen present in the crop, 52 cf. 29 g/m^2. More grains per unit dry weight at anthesis were produced, 11.1 cf. 4.3 grains per g dry weight. Higher grain yield was produced per unit dry weight of shoot at anthesis, 0.175 cf. 0.053 g/g.

4.4 Mechanism explaining variation in %N in the grain

The concentration of nitrogen in the grain is the crucial characteristic determining whether or not the grain can be sold to the maltster and, once purchased, the use to which the maltster will put the grain.

One relationship which can be used in interpretation of the influence of factors on the concentration of nitrogen in the grain is:

%N in the grain = grain N content/grain mass

This simple mathematical relationship shows that %N may vary because of variation in grain N content and/or variation in grain mass. We already know that grain mass varies, so variation in %N may be a result of this with the amount of nitrogen per grain remaining constant or with the nitrogen content per grain also varying.

Regressions of %N in the grain with individual grain weight (mg) and grain N content (mg) were conducted using results from all replicates in all experiments. %N in the grain varied between 1.12 and 2.94%, grain weight between 24.8 and 48.1mg and grain N content between 0.31 and 0.98mg. There was no relationship between %N and grain mass, i.e. %N's across the whole range were observed as grain mass increased. However, there was a positive relationship between %N and grain N content:

$$\%\text{N in the grain} = \mathbf{0.58}\ (\pm 0.085) + \mathbf{1.78}\ (\pm 0.146) \times \text{grain N content (mg)}\ (p<0.001)$$

This relationship accounted for 56.9% of the variance with %N increasing by 0.178% when grain N content increased by 0.1mg. Therefore, when examining grain from a wide range of sources, the amount of N in the grain plays an important part in determining %N while grain mass is not important. However, for individual crops %N in the grain will always be related to both grain N content and grain mass because of the mathematical relationship between them.

The 3-D relationship presented in Figure 4.1 is more helpful in understanding the relationship between %N and grain N content and grain mass. These show that crops with low grain mass and high grain N content are rare. Conversely crops with high grain mass and low grain N content are also rarely found. Low %N's of less than 1.8% are found across the range of grain mass. High %N's of greater than 1.8% were found mainly at high N contents supporting the conclusion from the correlation analysis that grain N content is a more influential determinant of %N than grain mass.

This relationship focuses on individual grains. The equivalent relationship on a crop basis is:

%N in the grain = grain N offtake/grain yield

Thus %N in the grain may vary because of variation in grain N offtake and/or variation in grain yield. Regressions of %N in the grain with grain yield (t/ha at 15%mc) and grain N offtake (kg/ha) were conducted using results from all replicates in all experiments. There was no relationship between %N and grain yield, i.e. %N's across the whole range were observed as grain yield increased. However there was a positive relationship between %N and grain N offtake:

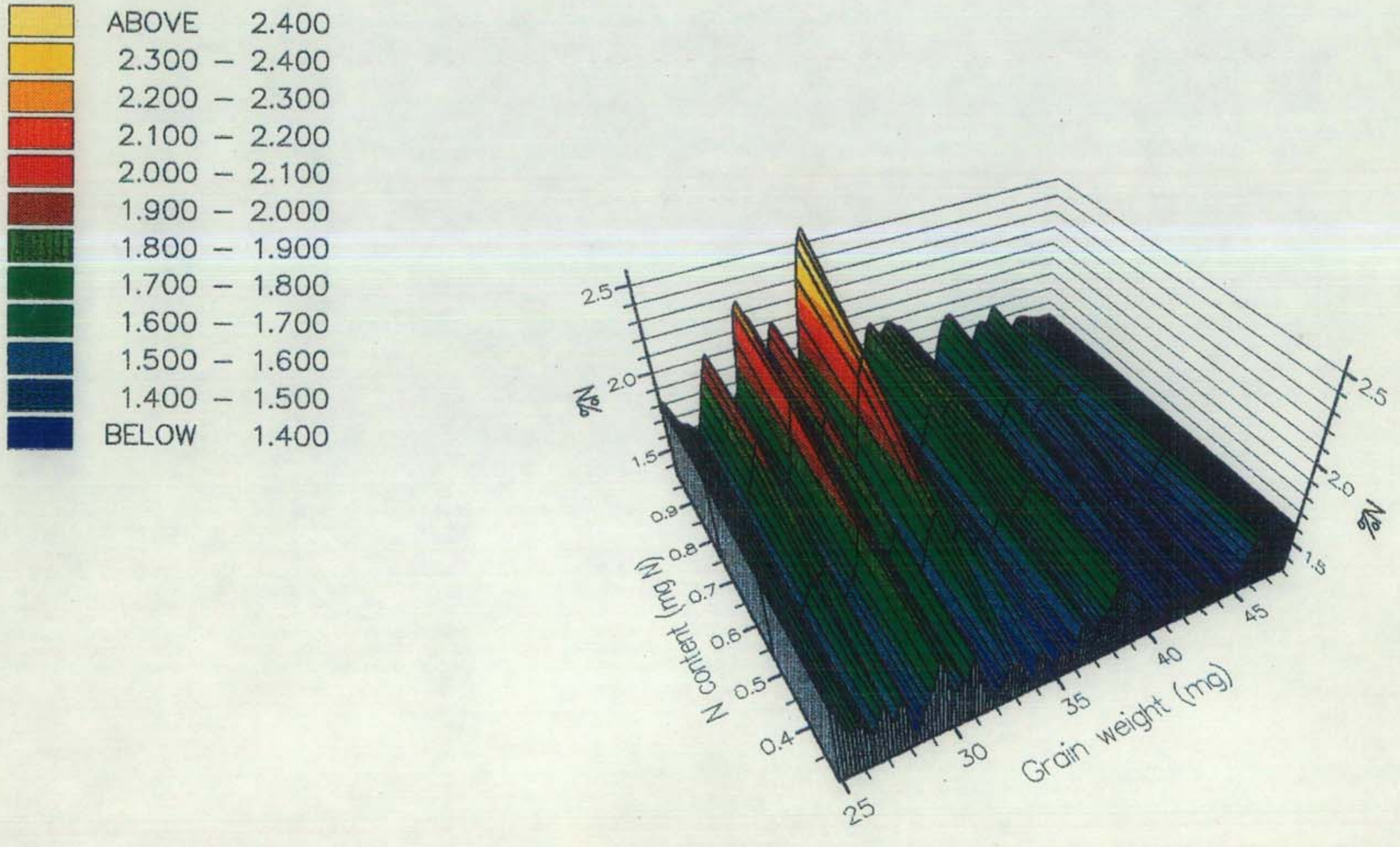
%N in the grain = **1.19** (±0.0582) + **0.00513** (±0.000690) x grain N offtake (kg/ha) ($p<0.001$)

Whilst the relationship between %N in the grain and grain N offtake accounted for 32.5% of the variance, the high value of the constant, 1.19%, and the low value of the response of %N to grain N offtake, 0.1% per 20 kg/ha increase, indicate the strong conservatism of %N in the grain in relation to grain N offtake.

The poor relationship between %N in the grain with grain yield and the quite good relationship with grain N offtake confirms the findings from the testing of the relationship on an individual grain basis that carbohydrate production has a relatively small influence on %N in the grain compared with that of the crop's nitrogen economy. The lack of a strong positive relationship between %N in the grain and grain yield is encouraging, indicating that high yields and low %N's can be readily obtained. Of the 19 crops in this programme which yielded 7t/ha or more, only three had grain with more than 1.7%N. Of the 51 crops which yielded between 4 and 7 t/ha, 15 had grain with more than 1.7%N of which 12 had more than 2.0%N. Therefore high yields do not mean high %N's. However it should be borne in mind that the nitrogen rates were chosen to produce grain with acceptable %N's and therefore may have been lower than would have been chosen to maximise yield.

Figure 4.1

Relationship between %N in the grain
and
grain N content (mg) and grain weight (mg)


ABOVE 2.400
2.300 – 2.400
2.200 – 2.300
2.100 – 2.200
2.000 – 2.100
1.900 – 2.000
1.800 – 1.900
1.700 – 1.800
1.600 – 1.700
1.500 – 1.600
1.400 – 1.500
BELOW 1.400
%N
2.5
2.0
1.5
N content (mg N)
0.9
0.8
0.7
0.6
0.5
0.4
Grain weight (mg)
25
30
35
40
45
%N
1.5
2.0
2.5

The crop macro-processes involved in determining the nitrogen content of the grain at maturity are:

N uptake
N dilution as dry matter is produced
N partitioning

Nitrogen uptake

The crop is supplied with nitrogen from the soil and from fertiliser applications. The quantity of nitrogen which can be supplied by the soil depends on the nitrogen residue from the previous crop. Traditionally an indication of this has been provided by the ADAS N index. The organic matter of the soil will also have an influence, in that high organic matter (OM) soils are expected to provide more nitrogen. The availability of nitrogen from both crop residues and soil OM will vary during the growing season, being dependent on the processes of mineralisation, immobilisation and leaching. Generally speaking, over the winter months when soil temperatures are less than 7°C, there will be little mineralisation and thus little nitrogen supplied to the crop. In spring and summer as the soil warms up mineralisation will proceed and make available more nitrogen in the soil. If the soil is dry mineralisation will be curtailed, reducing the amount of nitrogen being made available to the crop. High rainfall during the winter months leading to elution of the soil will leach mineralised nitrogen and so reduce the mineralised nitrogen available to the crop.

Nitrogen is also supplied to crops as fertiliser and is applied on one or two occasions in spring. This nitrogen is readily available to the crop and, if it is in the nitrate form, it is readily leachable. Most of the fertiliser nitrogen is taken up by the crop soon after application.

The crop itself plays a role in determining uptake of nitrogen. Root growth will determine the extent to which the soil profile is scavenged for nitrogen. Clearly in the early stages of growth when there has been limited root extension, the crop will take up a smaller proportion of the available nitrogen. In spring and early summer when shoot growth is occurring at a high rate root growth and nitrogen uptake are also proceeding at a high rate. Root extension ends at about anthesis (Gregory, 1994) and after this stage there is reduced nitrogen uptake (Mary *et al.*, 1988). Therefore, most of the nitrogen in the crop at maturity is thought to be taken up before anthesis with nitrogen in the grain being remobilised from other organs (Sylvester-Bradley, 1993a)

In 19 of the 22 crops in this programme of experiments from which data are available, over 30% of the N content of the crop at harvest had been taken up by ZGS30/31 irrespective of N treatment (Table 3.36). Six of the crops had taken up over 50% of their final N content by this stage. Marshall and Ellis (1994) deduced that fast uptake of nitrogen was required early in the life cycle in order to obtain optimal growth.

At anthesis, the N status of the crops in this programme is intriguing for two reasons. Firstly, in many of the N0 crops less than 75% of the N content of the crop at harvest is present (Table 3.40). Therefore, it is possible for crops to continue taking up nitrogen into the grain filling period and indeed, up to 80kg/ha were taken up during this period (Table 3.44).

The extent and activity of the root system is of primary importance in considering the capacity of the crop to take up nitrogen during grain filling. As stated above, it is widely accepted that the root system largely ceases to develop and to function after anthesis. This cessation of growth at anthesis has been questioned following examination of root production in winter barley cv. Pastoral on 22 May and 24 June 1991 in an experiment being conducted at Crossnacreevy, Belfast. Over these 33 days, which extended well into grain filling, total root numbers per shoot increased by from 5.8 to 7.2, most of this increase being accounted for by the thick structural roots rather than the thin roots. These results suggest that rather than the root system going into decline after anthesis as is generally believed, it is still actively growing and, therefore, functioning.

Secondly, several of the NS crops and a few of the N0 crops had a higher N content at anthesis than at harvest. Nitrogen was, therefore, lost from the above-ground biomass. As reported in Results Section 3.7 above, losses of nitrogen during grain filling have been observed by other workers. The programme of experiments undertaken in this project did not provide any information on how these losses occurred. However, it is important that this phenomenon is recognised and taken into account in future work.

Nitrogen dilution

Once nitrogen has been taken up by the crop its primary influence on crop productivity is mediated via its effect on leaf size and longevity with consequent effects on tiller production and survival. Sylvester-Bradley, Scott and Stokes (1990) began to look at this effect more rigorously and to quantify the relationship between the amount of nitrogen in the crop and the green area which it produces. They argued that yield responses to nitrogen fertiliser are curvilinear because of the curvilinear relationship between light interception and green area which has a saturating value at a gai (green area index) of about 3.0. This was based on the assumptions that (i) dry matter production and intercepted light are linearly related (Monteith's coefficient - radiation use efficiency) and (ii) gai excluding the ear, shows a constant relation to nitrogen content. They calculated that in one wheat cultivar sown early and late at one location and receiving three rates of nitrogen, 0.33m^2 gai was produced per g N in the shoot (not including the ear). This ratio has evolved to become the amount of nitrogen in the crop per m^2 green area and was first termed 'Nitrogen: area ratio' (Scott, Foulkes and Sylvester-Bradley, 1994), but has now been renamed 'Canopy Nitrogen Requirement' (CNR), (Sylvester-Bradle and Scott, 1995). The CNR was initially considered to be constant throughout the life cycle of the crop but differences between wheat cultivars have been reported (Scott *et al*, 1994).

The CNR is the resultant of two processes which are simultaneously active, namely uptake of nitrogen and production of green area. If the CNR is constant both throughout the life cycle and irrespective of management and environment as suggested by Sylvester-Bradley *et al.* (1990), then the rates of these two processes must maintain a constant ratio and must have coincident durations. (See Note 1 at the end of this section).

It is clear from the results obtained in this programme that nitrogen taken up by crops is rapidly diluted as it is used to produce dry matter in the form of green area. Dilution will tend towards a maximum, i.e. nitrogen concentration will tend towards a minimum, because nitrogen is primarily used to promote growth, i.e. the size of all organs. However, there will be some variation in the extent to which dilution occurs because:

(1) growth is curtailed because of high temperatures hastening development and shortening its duration,

(2) water shortages curtail photosynthesis and therefore, growth.

These will result in nitrogen already taken up not being fully used in dry matter production.

Nitrogen is utilised in structural tissue and as functional protein in the leaves, the stem and the ear. There may be nitrogen in the shoot which is surplus to the plant's requirement for both structural tissue and functional protein. This might be more readily available for mobilisation to the grain during grain filling.

The nitrogen status of the plant is indicated by the CNR (gN/m^2 green area) and the nitrogen dry matter ratio, i.e. nitrogen concentration (gN/kg DM). The CNR and nitrogen dry matter ratio reflect the efficiency of the crop's use of nitrogen in producing green area and dry matter. Higher CNR's and nitrogen concentrations resulting from a lower apparent efficiency in use of nitrogen to produce green area and dry matter may indicate a greater availability of nitrogen within the plant for remobilisation leading to higher nitrogen in the grain. Lower CNR's and nitrogen concentrations indicate that there is little surplus nitrogen in the plant. Therefore, there will be less remobilisation of nitrogen to the grain leading to lower nitrogen concentrations.

Optimum CNR's and nitrogen concentrations may be conceived, where all the nitrogen in the shoot is used in structural tissue and as functional protein and there is none surplus to requirements. However, these optimum CNR's and nitrogen concentrations may vary from variety to variety and under different conditions. For example, in the N0 crops it would be expected that there would be no surplus nitrogen and that CNR's and nitrogen concentrations would be constant at all sites. However, crops deficient in nitrogen are yellowish in colour reflecting remobilisation within the plant and a decrease in CNR and nitrogen concentration to meet the demand from organs which 'must' develop. Determination of the optimum CNR's and nitrogen concentrations at anthesis, and consequently assessing the quantity of surplus N, will be difficult.

Data on green areas are available from some experiments in this programme. Examination of the CNR's during life cycles of individual crops would be very instructive but has not yet been undertaken.

N partitioning during grain filling

The nitrogen concentration of the crop at anthesis will be related to events earlier in the life cycle, in particular:

(a) the amount of nitrogen taken up, which is dependent on nitrogen supply, water availability, root growth of the crop and

(b) the amount of growth, i.e. carbohydrate production, which has taken place to dilute nitrogen, which is dependent on radiation intercepted, number of days growth, water availability.

Growth of all organs except for the grain has been completed by anthesis. The N status of the crop at this stage may have a strong bearing on the final nitrogen content of the grain. If maximum dilution has not occurred through utilisation of all the nitrogen taken up by the crop in the growth of organs, surplus nitrogen in the plants may be readily available for relocation to the grains during grain filling.

At anthesis the ear consists entirely of structural tissues which make up the parts of the florets namely the lemma and its awn and the palea. Glumes, sterile spikelets and the rachis are also present. Importation of nitrogen to the incumbent caryopsis has not yet begun. Briggs (1978) presented a graph showing the pattern of grain N content during the first 24 days after anthesis for barley growing in Idaho, USA. This showed that nitrogen content of the grain increased almost continuously throughout this period. This suggests that the final N content of the grain is very dependent on events during grain filling and their influence on both remobilisation of nitrogen to the grain and uptake of nitrogen by the crop. The grain requires nitrogen for structural and functional proteins but nitrogen is also found as storage proteins in the endosperm.

As with dry weight, nitrogen uptake and activity in the grains can be examined on an individual shoot basis taking into account their size. Grain number per shoot has been determined by anthesis. The nitrogen present in each shoot will be remobilised and distributed amongst the grains being filled by that shoot. Given a constant nitrogen content per shoot, where grain number is high, the contribution to grain nitrogen content from remobilised nitrogen may be lower than where grain number is low. Thus low grain numbers per ear and high N contents per shoot may lead to high grain N contents at harvest.

The concentration of nitrogen in the grain can be described in a few simple relationships and the influence of Nitrogen, Site and Year on these can be examined.

(1) %N in grain = Grain N offtake/grain yield

(2) Grain N offtake = Total N in crop at maturity x nitrogen harvest index (NHI)

(3) Increment in ear N content during grain filling, i.e. Grain N offtake
= N uptake during grain filling + remobilisation of N taken up before anthesis

The influence of the nitrogen status of the crop can be examined further using the relationship:

(4) N content per grain = N per shoot at anthesis/grain number per shoot (i.e. per ear).

(1) %N in grain = Grain N offtake/grain yield

Table 4.14 Summary of the effects of Nitrogen, Site and Year on %N in the grain, grain N offtake and grain yield

	%N in the grain	Grain N offtake (kg/ha)	Grain yield (t/ha)
N0	1.43	53	3.86
NS	1.69	98	6.50
Belfast	1.37	61	5.18
Blunham	1.53	78	5.54
Newcastle	1.51	85	6.88
Potton	1.45	70	4.31
Rothamsted	1.59	67	3.99
Sutton Bonington	1.91	91	5.17
1988	1.51	57	3.82
1989	1.62	87	5.76
1990	1.55	82	5.96

Application of nitrogen increased both grain yield and grain N offtake but its effect on grain N offtake was proportionately greater than its effect on yield (Table 4.14). Therefore, %N in the grain increased to a small degree when nitrogen was applied.

Grain yield and grain N offtake varied independently from site to site and both had an influence on %N in the grain. Belfast and Sutton Bonington had the same average yields but

Belfast, with the lowest grain N offtake, had the lowest %N in the grain and Sutton Bonington, with the highest grain N offtake, had the highest %N in the grain. On the other hand Newcastle also had a high grain N offtake but because it had the highest yield, its %N in the grain was intermediate.

Both grain yield and grain N offtake varied from year to year but in the same direction and to similar extents so that %N in the grain did not vary greatly.

- **Conclusion**

Since the magnitude and direction of the effects of Nitrogen, Site and Year on grain N offtake and grain yield were often similar, variation in %N in the grain was much less than variation in these two characteristics and was relatively conservative.

(2) Grain N offtake = Total N in crop at maturity x NHI

Table 4.15 Summary of the effects of Nitrogen, Site and Year on grain N offtake, total N offtake and nitrogen harvest index

	Grain N offtake (kg/ha)	Total N offtake (kg/ha)	NHI (%)
N0	53	78	79
NS	98	141	75
N0			
Belfast	45	-	-
Blunham	64	76	83
Newcastle	58	-	-
Potton	39	63	84
Rothamsted	43	65	83
Sutton Bonington	71	108	66
NS			
Belfast	77	-	-
Blunham	92	123	75
Newcastle	111	-	-
Potton	101	147	79
Rothamsted	92	122	82
Sutton Bonington	112	170	66
1988	57	76	74
1989	87	128	78
1990	82	123	80

Nitrogen application increased grain N offtake because of the large increases it produced in total N offtake and despite its small negative effect on nitrogen harvest index (Table 4.15).

Variation in grain N offtake from year to year and from site to site was largely attributable to differences in total N offtake. Nitrogen harvest index only played a significantly different role at Sutton Bonington where total N offtake was very high and NHI was lower than at other sites.

- **Conclusion**

The effects of Nitrogen, Site and Year on total N offtake largely accounted for variation in grain N offtake. The constancy of nitrogen harvest index in this programme is in agreement with Sylvester-Bradley (1993b).

(3) Increment in ear N content during grain filling, i.e. Grain N offtake

= N uptake during grain filling + remobilisation of N taken up before anthesis

Table 4.16 Summary of the effects of Nitrogen, Site and Year on the increment in ear N content, N uptake and the remobilisation of N reserves during grain filling

	Increment in ear N content during grain filling (g/m^2)	N uptake during grain filling (g/m^2)	Remobilisation of N reserves during grain filling (g/m^2)
N0	5.2	2.5	2.3
NS	8.5	1.9	6.9
N0			
Belfast	5.1	3.0	2.0
Blunham	6.6	4.9	1.7
Newcastle	-	1.1	-
Potton	-	2.6	-
Rothamsted	3.7	1.3	2.4
Sutton Bonington	5.6	2.2	3.4
Ns			
Belfast	7.2	1.1	6.6
Blunham	9.8	2.3	7.2
Newcastle	-	0.5	-
Potton	-	3.9	-
Rothamsted	8.1	0.9	7.2
Sutton Bonington	9.0	2.6	6.3
1988	4.4	0.4	4.4
1989	7.4	2.0	4.8
1990	8.9	4.2	4.6

In the NS crops, the increment in ear N content during grain filling was largely supplied by remobilisation of nitrogen from other parts of the plant (Table 4.16). In the N0 crops, the demand for nitrogen by the growing grains was not met by the crop and this led to higher uptake of nitrogen from the soil than in the NS crops.

Variation in the increment in ear N content amongst the sites and between years was attributable to variation in N uptake from the soil during grain filling, similar amounts of nitrogen being remobilised within each N treatment at the various sites and from year to year.

Application of nitrogen fertiliser had a very clear effect on the source of nitrogen utilised in increasing ear N content during grain filling, the N0 crops being reliant on N uptake fromthe soil during grain filling for a much higher proportion of their grain N offtake than the NS crops. However, in both the N0 and NS crops variation in the increment in ear N content which was largely attributable to variation in N uptake during grain filling from site to site and from year to year.

This relationship was also examined by conducting regression analyses, using results from all replicates, of the increment in ear N content during grain filling with (a) the increment in total N content, i.e. N uptake, during grain filling and (b) the contribution from pre-anthesis N uptake i.e. remobilised N reserves.

(a) Increment in ear N content during grain filling v N uptake during grain filling

When the **N0** crops were examined:

Ear N increment during grain filling =

2.90 (±0.413) + **0.85** (±0.103) x total N uptake during grain filling ($p<0.001$)

This relationship accounted for 66.7% of the variance in this dataset.

When the **NS** crops were examined:

Ear N increment during grain filling =

7.28 (±0.302) + **0.74** (±0.080) x total N total during grain filling ($p<0.001$)

This relationship accounted for 72.7% of the variance of the dataset.

In both the N0 and NS crops the increases in ear N content in response to increased uptake of nitrogen were similar, 0.85 (N0) and 0.74 (NS) g/m^2 per g/m^2, but the amount already present in the crops, i.e. the constant term in the regression, was much greater in the NS crops, 7.28 g/m^2, than in the N0 crops, 2.90 g/m^2.

(b) Increment in ear N content during grain filling v contribution from pre-anthesis N uptake

When the **N0** crops were examined:

Ear N increment during grain filling =

3.63 (±0.880) + **0.58** (±0.283) x contribution from pre-anthesis N uptake ($p<0.049$)

This relationship accounted for 8.8% of the variance of the dataset.

When the **NS** crops were examined:

Ear N increment during grain filling =

8.18 (±2.16) + **0.024** (±0.302) x contribution from pre-anthesis N uptake ($p = 0.936$)

This relationship did not account for any of the variance in the dataset.

In the NS crops there was little response in ear N content to an increase in the amount of remobilised nitrogen reserves, a high amount, 8.18 g/m^2, being remobilised in all crops. In the N0 crops, a much smaller amount, 3.63 g/m^2, was remobilised consistently in all crops and the response to increase in remobilised N reserves was quite large, 0.58 g/m^2 per g/m^2.

- **Conclusion**

In the NS crops a large amount of nitrogen was remobilised to the grain during grain filling and such variation in this as there was had little effect on ear N content. In the N0 crops, however, a smaller amount was remobilised and variation in this amount had some effect on ear N content. Both NS and N0 crops responded quite strongly to variation in the amount of nitrogen taken up during grain filling but in the NS crops this accounted for a much smaller proportion of the ear N content.

(4) N content per grain v N per shoot at anthesis and grain number per shoot

The regression relationships of N content per grain with N content per shoot at anthesis and grain number per shoot accounted for only 6.6 and 9.5% of the variance in N content per grain in the N0 crops and for none in the NS crops:

N0 crops

N per grain = **0.37** (±0.064) + **0.0086** (±0.00390) x grain number per shoot ($p = 0.031$)

N per grain = **0.43** (±0.030) + **0.0080** (±0.00381) x N per shoot at anthesis ($p = 0.045$)

NS crops

N per grain = **0.50** (±0.136) + **0.0069** (±0.00738) x grain number per shoot ($p = 0.357$)

N per grain = **0.61** (±0.052) - **0.0027** (±0.00366) x N per shoot at anthesis ($p = 0.464$)

- **Conclusion**

Neither the availability of nitrogen within the shoot at anthesis nor the competition between grains on individual shoots had an over-riding influence on the amount of nitrogen present in each grain at maturity.

Summary

The nitrogen content of the grain largely determined the variation in %N in the grain from crop to crop. Nitrogen fertiliser increased %N in the grain because of its effect on total N and grain N offtake. Variation in nitrogen content per grain from site to site and from year to year was related to total N offtake and in particular to N uptake during grain filling. The nitrogen status of the shoots at anthesis had little influence on the amounts of nitrogen remobilised to the grains. Within each nitrogen treatment similar amounts of nitrogen were remobilised from other parts of the plant in all crops.

Note 1.

Some work at Rothamsted by Lawlor, Kontturi and Young (1989) introduces another possible explanation of the curvilinear relationship between yield and nitrogen fertiliser. They found a curvilinear relationship between net photosynthesis per unit leaf area and total RuBPc-o activity in winter wheat. RuBPc-o comprised 50-70% of the total soluble protein and there were close correlations between the amounts of total soluble and RuBPc-o protein, chlorophyll and nitrogen content per unit leaf area. They suggested that above a content of 4g RuBPc-o per m^2 of leaf area there was a poor relationship between RuBPc-o and net photosynthesis per unit leaf area. Therefore nitrogen content of the leaves could increase without there being a corresponding increase in dry matter production and at higher nitrogen rates there would be a lower efficiency of dry matter production per unit nitrogen in the crop. Lawlor *et al.*'s results may also have implications for remobilisation of nitrogen to the grain, if nitrogen tied up in unutilised RuBPc-o is more readily mobilised than where it is fully utilised in photosynthesis.

In Lawlor *et al*'s experiment, net photosynthesis was determined on unshaded flag leaves so that light was not limiting to their activity. However, only two rates of nitrogen were used. Further work including several nitrogen rates is needed to confirm their findings. Cell volume increased in response to nitrogen, leading to a decrease in the cell wall to volume ratio. This might mean that the ratio of structural to functional protein would also decrease, although this would have to be determined on weight rather than a volume basis. If the structural and functional fractions were selectively remobilised then this would affect availability of nitrogen during grain filling. The effect of nitrogen on the proportionality of the various protein fractions also needs to be investigated further.

4.5 The influence of nitrogen, site and year

The results obtained in the programme of experiments conducted between 1988 and 1990 have been examined in two ways in this report. The first method has involved using the conventional categorisation of the influences on growth and yield into factors, namely Nitrogen, Site and Year. Analyses of Variance of the Sites x Years data matrices for all the characteristics have been used to compare the magnitudes and provide information on the consistency of Nitrogen and Site effects. The second method has involved ignoring Site and Year, and in some cases also Nitrogen and has involved examination of relationships between characteristics irrespective of crops or environment. Regressions amongst crop characteristics and between crop characteristics and meteorological variates have been carried out in order to identify non-factor specific relationships.

Role of nitrogen

Does nitrogen have the same effect at all sites and in all years? or

Does nitrogen have different effects from site to site which are consistent from year to year?

In statistical terms, is the N x site interaction more significant than the N x year and N x site x year interactions?

Application of the nitrogen fertiliser had, as expected, highly significant effects on all aspects of crop functioning. However, its effect on most characteristics varied from site to site and was inconsistent from year to year.

The following effects of nitrogen on the growth parameters were confirmed in this programme of experiments:

Timing of phases:	little effect
Duration ZGS30-65:	little effect
Duration ZGS65-87:	may be increased due to delayed senescence
Rate of dry matter production	
ZGS30-65:	markedly increased
ZGS65-87:	markedly increased
Total dry weight:	markedly increased
Dry weight at ZGS30:	little effect

Dry weight at ZGS65: markedly increased

Most tillers had been produced before nitrogen fertiliser was applied.

Nitrogen fertiliser enhanced the survival of tillers by 15% consistently across all sites and in all years.

Nitrogen taken up by the crop has, as expected, a significant effect on dry matter production and grain yield but this is modified significantly by factors which vary in their influence form site to site and from year to year.

The amount of nitrogen taken up before anthesis which is remobilised to the ear during grain filling was similar at all sites in all years.

Losses and uptake of nitrogen from the crop during grain filling occurred and these influenced the amount of nitrogen which was found in the ear at maturity.

Once nitrogen is in the crop it is used very efficiently in the production of green area to enhance the capture of light and production of dry matter. The nitrogen in the crop is also partitioned very efficiently, with 75-80% being harvested in the grain, leaving a relatively small amount in the straw and chaff.

Recovery of nitrogen applied as fertiliser has been found to be very variable. Bloom *et al.* (1988) calculated apparent recoveries of between 43 and 88% in winter wheat crops. Results are available from some experiments in this programme (Table 4.17)

Table 4.17 Apparent recovery of nitrogen applied as fertiliser (%)
i.e. (total N offtake in NS crop - total N offtake in N0 crop)/nitrogen applied

	1988	1989	1990
Blunham	55	42	20
Potton	79	-	-
Rothamsted	54	66	-
Sutton Bonington	54	45	56

Apparent recovery of the fertiliser nitrogen applied varied between 20 and 79%. These results support conclusions by Sylvester-Bradley (1993b) that a major source of variation in the influence of nitrogen on yield is associated with very large variation in the apparent recovery of the nitrogen applied to the crop. This may actually assist in management of nitrogen fertilisation. One of the factors taken into consideration in making decisions about the amount of nitrogen to apply is the expected yield. If, however, the crop is highly efficient at using whatever nitrogen it gets hold of and the major source of variation in the effect of nitrogen on yield is recovery of nitrogen, then once the crop has taken up the nitrogen, it should be possible to predict what the crop is going to do with it. The key objective then becomes identifying when to determine the amount of nitrogen taken up by the crop. A further objective is to understand what is governing variation in recovery of fertiliser nitrogen.

Influence of site and year

What are the effects of site and year?

How do they compare in magnitude and nature with those of nitrogen?

Year had highly significant effects on most characteristics. Crops grown in 1988 had contrasting behaviour to those grown in 1989 and 1990. By ZGS 30/31 there was much lower nitrogen uptake in 1988 than in 1989 and 1990. Dry matter production and grain yield were lower in 1988.

Behaviour of the crops frequently differed from site to site. Belfast was usually later sown and was therefore, later to devlop and slower to produce dry matter. However, the response of yield to nitrogen was large. Blunham tended to have very high total N content particularly early in the year. High ear numbers were produced but conversely grain weights were very low. Newcastle was usually early sown and was, therefore, early to develop. High yields were produced and the yield response to nitrogen was also large. Sutton Bonington had small dry weight and yield responses to nitrogen. There was a short phase of growth when dry matter was produced very rapidly. Higher proportions of the total N content were present earlier in the life cycle than at other sites. Consequently crops in 1988 and 1989 at Sutton Bonington had very high %N's in the grain.

In general applications of nitrogen resulted in increases in dry matter or yield or the N content of the crop with smaller effects on partitioning ratios. Site and year had effects on size characteristics but effects on partitioning ratios were much greater than those of nitrogen.

Conditions associated with Site and Year determine the supply of light, water and, to a lesser extent, nitrogen, through both the effects of synoptic weather on the supply of light and water and the juxtaposition of the crop's development with these as determined by its sowing date. The following effects on the growth parameters were confirmed in this programme of experiments:

Timing of phases: large variation.

Rates of dry matter production:

major effects because of variation in

(a) light availability, and

(b) water availability

- drought will result in reduced N uptake and curtailed photosynthesis,
- excess rainfall (by whatever method this is determined) will lead to leaching of nitrogen and reduced nitrogen availability for uptake by the crop.

Total dry weight: effects observed but not as marked as those of nitrogen

Dry weights at ZGS30 and ZGS65:

effects observed related to above effects

Information on previous cropping and residual nitrogen is lacking and this factor, along with variety, will also have influenced carbohydrate production and partitioning, nitrogen uptake and partitioning at each site.

How do we describe sites?

Can we group them according to their features?

Can we categorise the features, i.e. simplify their magnitudes, in a way which is physiologically meaningful?

Sites differ in measurable features of their soil and weather such as:

soil - N fertility, i.e. previous cropping
available water capacity, i.e.soil type and depth
weather - temperature
radiation
rainfall

Sites may also be described in terms of features which are related to development and growth of crops such as:

length of growing year
sowing date - (1) September (2) October (3) November
harvest date
date of N application - (1) pre-ZGS 30/31 (2) at ZGS 30/31
duration of elongation phase - (1) <40 (2) 40-50 (3) 50-60 (4) >60 days
or (1) <50 (2) >50 days

The consistency of each site feature in relation to the effect of year would have to be determined. Russell (1990) mapped variation in the dates of ear emergence and harvest for autumn and spring sown barley in the European Union, using intervals of ten days. Within the British Isles, ear emergence in autumn sown crops was found to ocur during a 30-day period between 10 May and 10 June. Thus there is considerable variation even in the small geographical area of the British Isles which may allow and even require further definition.

Given the number of features which can be used to describe each site, it can be seen that there are enormous numbers of permutations of combinations of these features. It might be possible to simplify our descriptions of the sites by (1) either identifying the most common combinations or (2) linking features which have consistent (a) similar but non-additive, (b) similar but additive or (c) opposing influences on the functioning of the crops. However, this may not be very helpful because such descriptions will always be summaries in scale over time and over space and the crop may be responding to events and variation in temperature and availability of inputs on a very small scale in time and space.

An attempt at more detailed definition of sites/environments is being made in the current HGCA-funded project on 'Exploitation of Varieties for UK Cereal Production' (Project 0037/1/91). Four features of sites, namely (1) length of growing season, (2) soil N availability, (3) water availability and (4) rotational position are being examined. Selected winter wheat varieties are being grown and various physiological characteristics are being measured in order to identify those conferring suitability for alternative scenarios for each feature.

Summary

The effects of factors associated with Site and Year on crop processes differ from those of Nitrogen, tending to be aspects of use of resources and partitioning rather than the size of the features involved in resource capture and supply.

The variation observed in these characteristics in the two N treatments suggests that they provide crops with flexibility which allows tham to perform much more consistently than would be the case otherwise.

4.6 Implications for management

(a) Application of nitrogen to the crop

Managing winter barley crops to produce grain for malting has two aspects in relation to application of nitrogen fertiliser:

(1) How much nitrogen to apply and when to apply it in the spring?

(2) How does the extant state of the crop and its projected growth and development modify these decisions on nitrogen fertilisation, for example:

  (i) If a crop is late sown, or is in a continuous cereal rotation, or has had a cold winter?

  (ii) If a crop is early sown, or follows a crop leaving high N residues, or has had a warm winter?

Effect of variation due to Site and Year

Traditionally agronomic experiments and advice have focused on the first of these aspects, the amount and timing of nitrogen applications. The value of addressing the second aspect has to be considered and will initially involve asking if the growth and development of crops can be predicted from their extant states in spring?

Clare and Spink (1994) have suggested that dry weight at ZGS 31 could be an indicator of final yield in winter wheat but provided no information on how well this has been tested either within or across experiments. The relationship found between total dry weight at harvest and dry weight at ZGS 30/31 using the data obtained in this programme, was poor:

Total dry weight at harvest = **802.1**(±74.8) + **1.55** (±0.339) x dry weight at ZGS 30/31 ($p<0.001$)

Although the regression was significant, only 17.5% of the variance was accounted for, suggesting that dry weight at ZGS 30/31 is of limited value in predicting total dry weight at harvest.

If crop growth and yield could be reliably predicted then it will be necessary to consider if crops with contrasting extant states and prognoses:

(a) respond in different ways to applied nitrogen?

(b) respond in consistent ways to applied nitrogen?

Does the site to site and year to year variation outweigh the effects of applied nitrogen?
Can variation due to site and year be predicted and taken into account in decision-making?

Recommendations concerning nitrogen fertilser applications already take into account previous cropping and estimates of the expected yield. Sylvester-Bradley (1993b) has reported on research aimed at clarifying how crop residues influence the availability of nitrogen to succeeding crops. He also points out the need to find criteria for characterising sites in order to reduce the 'unknown' nature of their effects.

To answer these questions, an experimental programme very different in nature from traditional agronomic or even crop physiological experiments would have to be set up. A much more complete model of crop growth and development would have to be used specifically oriented towards answering questions about the relationships between states of a crop during its life cycle.

Taking account of variation due to Site and Year will be difficult. Weather is unpredictable. Site, though, should be open to full and precise description by recording or measuring of a set of parameters such as soil AWC, soil mineral nitrogen, daylength. Some weather parameters may fall within a defined range for individual sites such as radiation receipts, temperature, rainfall totals, maximum soil moisture deficit (See Discussion Section 4.5). If Site is defined and then management strategies developed which are suited to different categories of sites, it may be possible to reduce the uncertainty of both decision making and the outcome of management. However, some noise will always remain in the outcome because of (a) the influence of weather and (b) the flexibility of the crop. If management towards a specified structure based on knowledge of site parameters is undertaken, allowance will still have to be made for weather conditions after the point when the decision has been made.

Crop flexibility

Biological variation should, in truth, be regarded as flexibility, i.e. adaptation of the crop to the variable weather conditions it experiences. The structure of cereal crops allows them to be very flexible in their development. Thus tillers in the axils of leaves may or may not grow and if they do begin to grow, they may or may not survive to produce ears. Which tillers begin to grow and which succeed in surviving will depend on events happening over short time spans both in the external environment of the crop and within the plants themselves. Primordia initiated at the apical meristem may or may not succeed in completing their development to become florets capable of being fertilised and producing grain. Carbohydrate produced by photosynthesis may be stored for later movement to the grains in response to their demand. Which florets survive, their potential size and therefore their demand for carbohydrate will also depend on events happening over short time spans both in the external environment of the crop and within the plants themselves.

This flexibility enables the crop to produce relatively stable yields in what are essentially very variable conditions. Thus short-term fluctuations in supply of the raw materials for photosynthesis and growth i.e. nitrogen, water and light, do not have irreversible or irrecoverable effects on development. However there is a limit to the buffering capacity provided by this flexibility. These limits are observed as large scale effects of major shortages of the factors limiting growth and also as the smaller scale unpredictable variation in yield.

The components of yield have been discounted as a useful model in explaining and predicting crop behaviour. However their use has introduced us to the concept of flexibility through observation of compensation amongst the components. More recent models of yield formation in cereal crops based on:

nitrogen uptake ➔green area ➔light interception ➔dry matter production ➔ grain yield

- have been expected to be less prone to variation and therefore more reliable for use in prediction of grain yield. However there are indications that the rate control variates in such models do show variation which will require further investigation and explanation. The model being used in current farm practice for making decisions on the quanitity of nitrogen to apply to crops based on knowledge of nitrogen uptake and grain productivity per kg N taken up also contains approximations which lead to a significant degree of variation in predicted yield.

The properties of the crop included in these models are the outcomes of flexibility in sub-processes of the crop. Thus even when we can determine how much nitrogen is available from the soil, uptake of nitrogen and utilisation of the nitrogen taken up will vary leading to variation in yield. Other properties of crops, which we have yet to identify, are determining their yield and thereby determining the magnitudes of these properties. Therefore, a major research objective must be to understand this flexibilty and learn how to manage it.

Effect of Nitrogen on crop processes

Decisions about how much nitrogen fertiliser to apply to cereal crops can be based on a model where assumptions are made about:

(1) the amount of nitrogen supplied by the soil
(2) the proportion of nitrogen fertiliser which will be taken up by the crop
(3) the productivity of nitrogen taken up in producing yield
(4) the potential yield of the crop and therefore its requirement for nitrogen

(1) The amount of nitrogen supplied by the soil

The amount of nitrogen supplied by the soil will depend on the residues left from the previous crop and the extent of losses due to leaching. In this programme, between 25 and 143 kg/ha nitrogen were available from the soil as indicated by total N offtake in the N0 crops. Whilst some confidence can be placed in measurement of soil mineral N to depths of 60 or 90cm on certain dates, consideration should be given to the pattern of soil N availability during the whole growing season and the extent to which such single point assessments are reliable indicators of whole season availability.

(2) The proportion of nitrogen fertiliser which will be taken up by the crop

In this programme the apparent recovery of nitrogen fertiliser varied between 20 and 79%. The reasons for variation in apparent recovery are not known.

(3) The productivity of nitrogen taken up in producing yield

Grain productivity varied between 36 and 64 kg grain/kg N in the N0 crops and between 30 and 68 kg grain/kg N in the NS crops. In some experiments grain productivity was better in the N0 than in the NS crops but in others, it was better in the NS than in the N0 crops (Table 4.18).

Table 4.18 Grain productivity (kg grain/kg N taken up)

	1988	1989	1990
N0 crops			
Blunham	56.4	58.2	52.3
Potton	64.1	-	-
Rothamsted	-	48.0	-
S. Bonington	52.7	36.3	47.1
NS crops			
Blunham	48.5	53.9	67.6
Potton	43.0	-	-
Rothamsted	-	51.3	-
S. Bonington	41.9	30.0	32.2

(4) The potential yield of the crop and therefore its requirement for nitrogen

Predicting the potential yield of the crop will be one of the most difficult and one of the most critical judgments involved in making decisions about nitrogen fertilser applications. We can take into account:

- previous yields in the field, which will incorporate knowledge of inherent fertility and extreme limiting factors,
- yield potential of the variety being grown,
- estimated or known sowing date.

Once this has been done, it will still be necessary to set a range for the predicted yield to allow for weather, the magnitude of this range being dependent on confidence in the model used and also some knowledge of the level of inherent variation.

Given the variation in both apparent recovery of nitrogen fertiliser and grain productivity per kg N taken up observed in this programme, much uncertainty about what levels of these sectors of the model would exist reducing confidence in the predictions produced.

Summary

Reasons for and processes involved in various aspects of the nitrogen economy of cereal crops have yet to be learned, before either control of te supply of nitrogen or prediction of the requirement for nitrogen can be confidently achieved.

Description and definition of Site features and prevailing weather patterns would aid in reducing the uncertainty relating to crop growth and performance.

(b) Prediction of %N in the grain

One of the objectives for obtaining knowledge of site/treatment effects on winter barley physiology is to enable an assessment of the possibility of predicting grain yield and %N in the grain prior to harvest. Obviously if this was possible at the stage in the growing season when the grower is applying the spring N top-dressing, management could be modified to achieve the desired %N in the grain. Prediction at such an early stage in crop development, i.e. at the beginning of stem elongation is going to be difficult to achieve. Prediction at a later stage, for example, at anthesis, whilst not giving the grower any opportunity to manipulate the crop through management, would enable an assessment of the likelihood of the crop producing grain with an acceptable %N in the grain for malting. In turn, maltsters would have a pre-harvest idea of the supply situation and could plan purchases accordingly. The possibility of being able to predict grain yield and %N in the grain at harvest can be examined using results from this programme.

Carreck and Christian (1991) considered whether %N in the grain may be associated with and therefore, predicted from %N in the ear at anthesis. In this programme %N in the grain varied between 1.12 and 2.94% and %N in the ear at anthesis between 0.51 and 2.73%. There was a positive relationship between %N in the grain at harvest and %N in the ear at anthesis:

$$\%\text{N in the grain} = \mathbf{0.81}\ (\pm 0.154) + \mathbf{0.49}\ (\pm 0.096) \times \%\text{N in the ear} \quad (p<0.001)$$

However, this relationship only accounted for only 18.5% of the variance. Thus %N in the ear at anthesis would have little value as an indicator of %N in the grain. This is in agreement with Carreck and Christian's conclusion and with Cranstoun (1992) who, in a review of HGCA-funded work on management of crops for malting, concluded that early N measurements could not be used to predict grain %N.

In crops of barley grown for malting the management objective is to produce grain with a low %N. It is generally accepted that this will involve reducing the amount of N fertilizer applied below the optimum required to produce maximum yields since high grain yields are more likely to have high nitrogen concentrations in the grain. The association between yield and %N in the grain was examined using the results for all replicates in this programme. Grain yield and %N in the grain were found to be positively but weakly associated, the relationship accounting for only 3.8% of the variance.

$$\text{grain yield} = \mathbf{2.74}\ (\pm 0.886) + \mathbf{1.29}\ (\pm 0.548) \times \%\text{N in the grain} \quad (p=0.021)$$

Grain with higher %N's tended to be associated with yields similar to or lower than the median yield of 4.84 t/ha at 0% moisture content (Figure 4.2). The highest yield in the programme was found to have a %N in the grain of less than 1.65%.

The high %N (>2.30%N) results were excluded from a further analysis because they were exerting a strong influence on the relationship:

$$\text{grain yield} = \mathbf{0.91}\ (\pm 1.11) + \mathbf{2.52}\ (\pm 0.712) \times \%\text{N in the grain} \quad (p<0.001)$$

This regression still only accounted for 9.6% of the variance, the scatter of points about the line being very large.

The conclusion from the examination of the results in this programme is that yield is highly responsive to weather, site-related factors and nitrogen application, while %N in the grain is much more stable. High %N's in the grain were not associated with either very high or very low yields.

In the experimental programme, 1988-1990, the intention was to apply nitrogen in the NS treatment at a rate and a time which would maximise yield and optimise %N in the grain. With six of the 17 samples from this treatment having greater than 1.75%N in the grain (Table 3.10), the difficulty of getting the nitrogen application right with respect to the grain nitrogen concentration is amply demonstrated. The remarkably low sensitivity of %N in the grain to nitrogen availability to the crop is apparent from the small effect of the applied nitrogen on %N relative to its large influence on grain yield (Table 3.4). This observation alone shows how the mechanisms by which nitrogen influences grain yield will be of fundamental importance in determining %N in the grain. However, since the rates of nitrogen in this programme were chosen to produce grain with acceptable, i.e. low %N's, this finding may have been somewhat self-fulfilling. At higher rates of nitrogen %N in the grain might be expected to be much more responsive to the amount of nitrogen applied.

Consistent site differences in %N were not detected. Significant differences between the sites and variation from year to year in characteristics associated with grain yield and with nitrogen uptake of the crops only rarely led to high %N's in the grain. For example, the crops at Sutton Bonington which were notable for having the highest %N's in the grain had low grain harvest indices and high nitrogen uptakes when compared with the remaining crops.

Summary

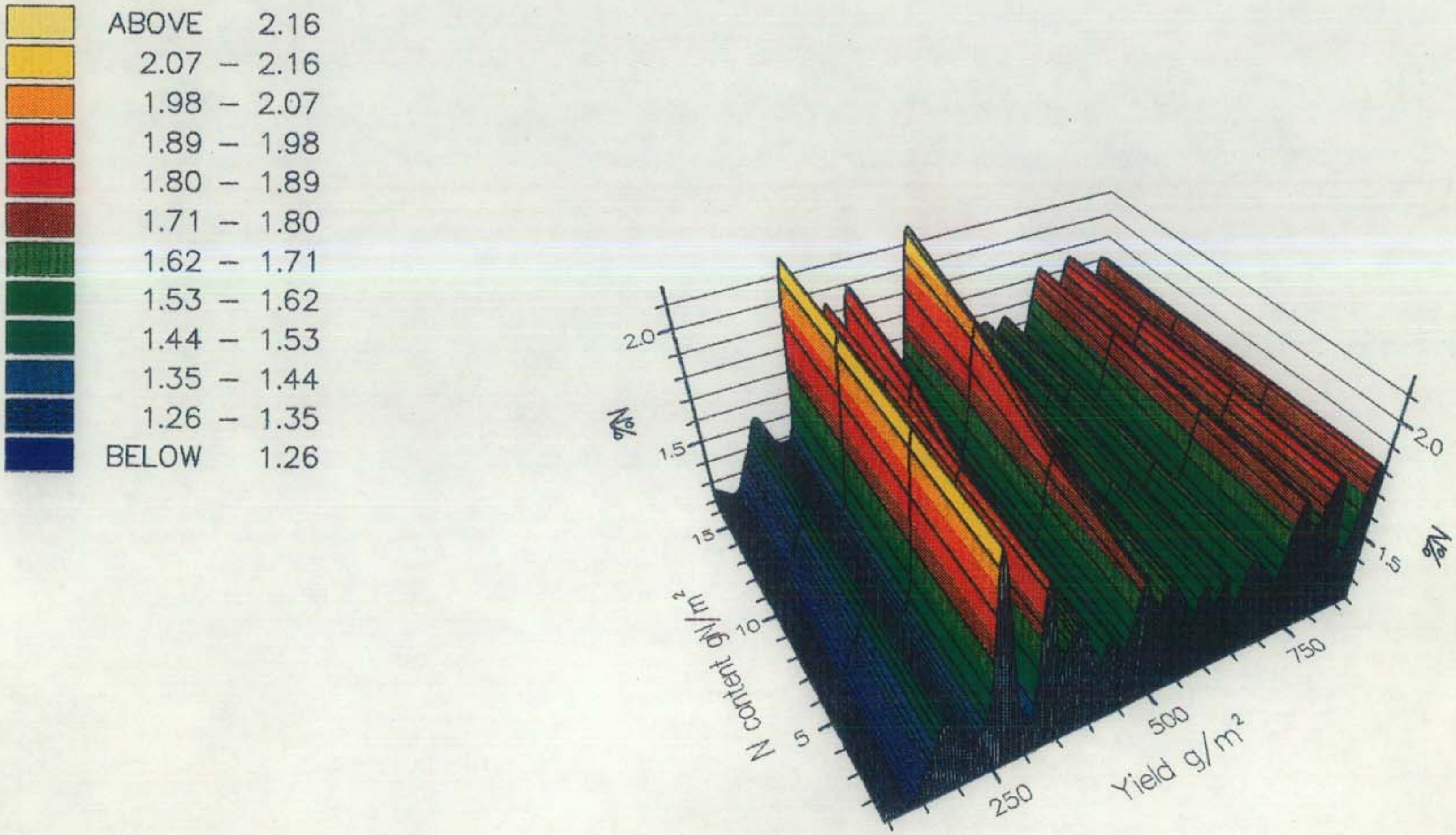
It seems that the crop's processes aim to utilise nitrogen fully in the production of carbohydrate on the one hand and on the other to stabilise the amount of nitrogen present in the grain. The optimal availability of nitrogen would be that which leads to maximum carbohydrate production and sufficient nitrogen in the grain. Considering the grain in relation to its function as a seed, provision of maximum energy supplies with the necessary, but not surplus, quantities of enzymes to begin growth of organs, would be sensible objectives for the seedling as it becomes established and heterotrophic. Greater concentrations of nitrogen in the grain might be expected to result from either failure of the crop to set up the carbohydrate-producing mechanisms to fully utilise the available supply of nitrogen, or failure of these mechanisms to deliver carbohydrate to the grain, or a supra-optimal supply of nitrogen to the crop which cannot be utilised in carbohydrate production and, therefore, is located in the grain and possibly other organs. However, the results obtained in this programme show that uptake of nitrogen during grain filling had a major effect on total N offtake by crops. Since (1) the nitrogen harvest index was relatively constant, grain N offtake was closely related to total N offtake and (2) the amount of nitrogen in the grain was the main determinant of %N in the grain, it appears that post-anthesis uptake of nitrogen is the major source of variation in %N. The extent and activity of the root system during the grain filling period as well as process in the soil governing the availability of nitrogen for uptake will be of major importance.

Figure 4.2

Relationship between %N in the grain

and

grain N content (mg) and grain yield (g/m^2)


ABOVE 2.16
2.07 – 2.16
1.98 – 2.07
1.89 – 1.98
1.80 – 1.89
1.71 – 1.80
1.62 – 1.71
1.53 – 1.62
1.44 – 1.53
1.35 – 1.44
1.26 – 1.35
BELOW 1.26
%N
2.0
1.5
N content gN/m²
15
10
5
Yield g/m²
250
500
750
1.5
2.0
%N

Conclusions

- **Summary of the effects of Nitrogen, Site and Year on characteristics associated with the production and partitioning of carbohydrate**

	Nitrogen	Site	Year
Grain yield	+++	+++	+++
Total dry weight	+++	++	++
Harvest index	-	+++	++
Rate of growth	+++	+++	++
Duration of growth	-	+++	++
At anthesis:			
Total dry weight	+++	+++	++
Shoot number	+++	+++	++
Dry weight per shoot	+	+++	++
During grain filling:			
Increment in ear dry weight	+++	+++	++
Increment in total dry weight	+++	+++	++
Contribution of stored reserves to ear dry weight	0	+++	++

Key: Each + or - represents an increase in the effect of the factor

0 represents a minimal effect

- **Summary of the relationships between the state of the crop at anthesis and characteristics associated with the production and partitioning of carbohydrate**

	Extent of correlation
Total dry weight at anthesis	
v Shoot number at anthesis	None
v Dry weight per shoot at anthesis	+ +
Grain population density	
v Total dry weight at anthesis	+
Grain number per shoot	
v Dry weight per shoot at anthesis	None
Grain mass	
v Dry weight per shoot at anthesis	None
Grain yield per shoot	
v Dry weight per shoot at anthesis	None
Utilisation of stored reserves	
v Dry weight per shoot at anthesis	None

- **Summary of the effects of Nitrogen, Site and Year on characteristics associated with the uptake and partitioning of nitrogen**

	Nitrogen	Site	Year
%N in the grain	+	+ +	+
Grain N offtake	+ + +	+ + +	+ + +
Grain yield	+ + +	+ + +	+ + +
Total N offtake	+ + +	+ +	+ +
Nitrogen harvest index	-	+	+
During grain filling:			
Increment in ear N content	+ + +	+ + +	+ + +
N uptake	-	+ + +	+ + +
Remobilisation of N reserves	+ + +	+	+

Key: Each + or - represents an increase in the effect of the factor

- **Summary of the relationships between the state of the crop at anthesis and characteristics associated with the partitioning of nitrogen to the grain**

	Extent of correlation
N content per grain	
v N per shoot at anthesis	None
v grain number per shoot	None

- Patterns of dry matter production were not determined by phenological development. There was very little association between key points at the beginning and end of the main phase of growth determined from the analyses of the time series of dry weights using the Gompertz function.

- Consistent effects of nitrogen from site to site on yield and growth characteristics were not observed in this programme of experiments. Differences in behaviour of the crops between the sites were not consistent from year to year for most characteristics. Frequently the magnitude of the unpredictable variation due to year was similar to the magnitudes of the effects of nitrogen and the differences between the sites.

- Yield and grain mass are primarily sink-limited, a consistent effect of nitrogen on ear dry weight being observed with variable utilisation of carbohydrate reserves. Exhaustion of reserves may have introduced source-limitation but the extent to which this occurred is not known.

- In the unfertilised crops, the more sensitive and more responsive relationships than in the fertilised crops between:
    - total dry weight at harvest and crop nitrogen content
    - total dry weight at anthesis and dry weight per shoot at anthesis
    - grain number per m^2 and total dry weight at anthesis
    - grain number per ear, grain mass and grain yield per shoot with dry weight per shoot at anthesis

\- suggests that where nitrogen is in limited supply, crop processes are highly coupled.

In the fertilised crops, crop processes were less inter-dependent, with only utilisation of carbohydrate reserves showing a relationship with dry weight per shoot at anthesis.

- Variation in the increment in ear N content amongst the sites and between years was attributable to variation in N uptake from the soil during grain filling, similar amounts of nitrogen being remobilised within the crop at the various sites and from year to year. Pre-anthesis uptake of nitrogen supplied 45% of the increment of 5.2 g/m^2 in ear N content during grain-filling in the unfertilised crops. In the fertilised crops the contribution from pre-anthesis uptake constituted a greater proportion, 80%, of the increment of 8.5 g/m^2.

- The uncertainty of crop performance is a fact farmers and researchers are aware of. The powerful effects of crop flexibility in buffering growth and yield formation have not always been acknowledged or valued. A respect for crop processes with their capacity to produce consistent performances in the face of erratic variation in supply and controlling factors is an important presupposition to adopt in future efforts to improve management and performance of crop production.

Implications for research:

- Multi-centre and in particular multi-organisation projects are fraught with all kinds of potential problems. Much has been learned in the course of this project about ensuring that:
    - management of experiments is consistent from site to site,
    - results are thoroughly checked after collection and prior to collation with other sites and are prepared or at least presented for collation in a standardised format,
    - a wide range of diverse sites are included in the programme.

Implications for management:

- Whilst considerable progress may be made in defining sites more fully and in predicting the progress of crop growth from measurements of its state at early stages in the life cycle, the time scale at which crop activity responds to variation in temperature and in the supply of nitrogen, water and radiation may be very short relative to that which it is possible to build into models. Simplifications on an inappropriate scale may introduce inaccuracies to the predictions so diminishing their value.

- Although nitrogen fertiliser has a major effect on the amount of nitrogen available for remobilisation within the crop, there will be difficulty in predicting %N in the grain because the nitrogen content of the crop at harvest appears to be related to nitrogen uptake during grain filling.

Future work

- Further analysis of green area, nitrogen concentration and CNR
- Further analysis of the relationships between dry matter production and meteorological variates.
- Development of concepts and experimental techniques for understanding flexibility of cereal crops.
- Methods of definition of sites using weather and soil data and including an investigation of the implications of the scale of definition on modelling of crop behaviour.
- The nitrogen economy of crops during grain filling - an investigation of processes influencing uptake and loss of nitrogen by crops and internal factors governing the remobilisation of nitrogen to the grain.

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References

Austin, R.B., Morgan, C.L., Ford, M.A. and Blackwell, R.D. (1980) Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. Annals of Botany, 45, 309-319.

Bloom, T.M., Sylvester-Bradley, R., Vaidyanathan, L.V. and Murray, A.W.A. (1988) Apparent recovery of fertiliser nitrogen by winter wheat in 'Nitrogen Efficiency in Agricultural Soils' ed. Jenkinson, D.S. and Smith, K.A., Commission of the European Communities, pp. 27-37.

Bradbury, N.J., Tuck, G., Whitmore, A.P. and Jenkinson, D.S. (1993) Development and testing of a computer model for predicting the amount and timing of nitrogen release from soil. Project Report No. 74, Home-Grown Cereals Authority, London, 90pp.

Briggs, D.E. (1978) Barley. Chapman and Hall, London, 612pp.

Carreck, N.L. and Christian, D.G. (1991) Studies in the patterns of nitrogen uptake and translocation to the grain of winter barley intended for malting. Annals of Applied Biology, 119, 549-559.

Clare, R. and Spink, J. (1994) The challenge of CAP reform and beyond - Decision support models in crop management with particular reference to disease control. HGCA 1994 Conference on Cereals R & D, 11.1-11.33, Home-Grown Cereals Authority, London.

Cranstoun, D. (1992) Crop management for malting. HGCA 1992 Conference on Cereals R & D, 73-89, Home-Grown Cereals Authority, London.

Cranstoun, D. and Wiseman, J. (1994) Theme Review: Barley quality. Home-Grown Cereals Authority, London. 12pp.

Dyson, P.W. (1977) An investigation into the relations between some growth parameters and yield of barley. Annals of Applied Biology, 87, 471-483.

Gallagher, J.N., Biscoe, P.V. and Scott, R.K. (1975) Barley and its environment V. Stability of grain weight. Journal of Applied Ecology, 12, 319-336.

Garstang, J.R., Vaughan, Jill and Dyer, C.J. (1993) Effects of soil type and nitrogen on the quality of autumn-sown malting barley. Project Report No. 70, Home-Grown Cereals Authority, London. 68pp.

Greenwood, D.J. and Draycott, A. (1988) Recovery of fertiliser-N by diverse vegetable crops: processes and models in 'Nitrogen Efficiency in Agricultural Soils' ed. Jenkinson, D.S. Smith, K.A., Commission of the European Communities, pp. 46-61.

Gregory, P.J. (1994) Resource capture by root networks in 'Resource Capture by Crops' ed. Monteith, J.L., Scott, R.K. and Unsworth, M.H., Nottingham University Press, pp. 77-97.

Hay, R.K.M. and Walker, A.J. (1989) An Introduction to the Physiology of Crop Yield. Longman Scientific and Technical, Harlow, Essex, 292pp.

Kirby, E.J.M. and Appleyard, Margaret (1984) Cereal Development Guide, 2nd Edition. NAC Arable Unit, Stoneleigh, Kenilworth, Warwicks CV8 2LZ 96pp.

Lawlor, D.W., Konturri, M. and Young, A.T. (1989) Photosynthesis by flag leaves of wheat in relation to protein, ribulose bisphosphate carboxylase activity and nitrogen supply. Journal of Experimental Botany, 40 (210), 43-52.

Leigh, R.A. (1992) Interpretation of site/treatment effects on growth and N uptake of winter barley in relation to quality criteria, particularly %N in barley for malting. HGCA Project Report No. 48, 33pp.

Marshall, B. and Ellis, R.P. (1994) Analysis and modelling of the effects of nitrogen on the growth, partitioning and quality of malting barley. Project Report No. 94, Home-Grown Cereals Authority, London. 202pp.

Mary, B., Recous, S. and Machet, J.-M. (1988) A comprehensive approach to the fertiliser part of plant nitrogen uptake in 'Nitrogen Efficiency in Agricultural Soils' ed. Jenkinson, D.S. and Smith, K.A., Commission of the European Communities, pp. 85-94.

Monteith, J.L. (1977) Climate and the efficiency of crop production in Britain. Philosophical Transactions of the Royal Society of London, B281, 277-294.

Murphy, D. (1993) Crop structure and crop productivity in winter barley, *Hordeum sativum*. Ph.D Thesis, University of Newcastle upon Tyne.

Nielsen, N.E., Schjorring, J.K. and Jensen, H.E.(1988) Efficiency of fertiliser nitrogen uptake by spring barley in 'Nitrogen Efficiency in Agricultural Soils' ed. Jenkinson, D.S. and Smith, K.A., Commission of the European Communities, pp. 62-72.

Russell, G. (1990) Barley Knowledge Base. Commission of the European Communities, Joint Research Centre, Luxembourg, 135pp.

Scott, R.K., Foulkes, J. and Sylvester-Bradley, R. (1994) Exploitation of varieties for UK cereal production. Annual Interim Report for Project No. 0037/1/91, Home-Grown Cereals Authority, London. 48pp.

Scott, R.K., Jaggard, K.W. and Sylvester-Bradley, R. (1994) Resource capture by arable crops in 'Resource Capture by Crops' ed. Monteith, J.L., Scott, R.K. and Unsworth, M.H., Nottingham University Press, pp. 279-302.

Sylvester-Bradley, R., Scott, R.K. and Stokes, D.T. (1990) A physiological analysis of the diminishing responses of winter wheat to applied nitrogen. 1. Theory. Aspects of Applied Biology 25, Cereal Quality II, 277-287.

Sylvester-Bradley, R. (1993a) Opportunities for lower nitrogen inputs without loss of yield or quality: an agronomic and economic appraisal. Proceedings of the HGCA Cereals R&D Conference, Cambridge, pp. 198-217. Home-Grown Cereals Authority, London

Sylvester-Bradley, R. (1993b) Nitrogen prediction I. Review of current advice on cereal crop requirements. II. Effects of previous cropping on responses of winter wheat to applied nitrogen. Project Report No. 73, Home-Grown Cereals Authority, London. 111pp.

Sylvester-Bradley, R., Scott, R.K. and Wright, C.E. (1990) Physiology in the production and improvement of cereals. Research Review No. 18, Home-Grown Cereals Authority, London. 156pp.

Sylvester-Bradley, R. and Scott, R.K. (1995) Personal communication.

Appendix 2.1

Time series of data from each site for the N0 and NS treatments in 1988, 1989 and 1990

N applied :- 0 kg/ha

1988 N0

Site	Julian Day	Total Dry Weight (g/m2) mean	Total Dry Weight (g/m2) s.d.	Ear Dry Weight (g/m2) mean	Ear Dry Weight (g/m2) s.d.	Total N Uptake (g/m2) mean	Total N Uptake (g/m2) s.d.	N Uptake in Ears (g/m2) mean	N Uptake in Ears (g/m2) s.d.	Total Number of Shoots (m2) mean	Total Number of Shoots (m2) s.d.
Belfast	88	12.1	3.00	•	•	0.49	0.185	•	•	534	195.1
	102	28.1	9.03	•	•	0.73	0.278	•	•	671	177.1
	116	44.9	14.57	•	•	1.11	0.474	•	•	645	135.7
	130	67.9	14.18	•	•	1.24	0.311	•	•	636	131.0
	145	127.6	22.90	•	•	1.53	0.306	•	•	603	98.2
	158	269.8	122.34	•	•	2.07	1.215	•	•	626	201.1
	165	304.7	85.64	•	•	1.61	1.105	•	•	482	111.7
	172	380.3	78.15	•	•	2.24	1.210	•	•	480	87.1
	179	429.6	56.16	•	•	2.36	0.688	•	•	503	94.5
	186	369.3	93.59	•	•	2.38	0.368	•	•	473	71.1
	193	399.2	54.23	•	•	2.96	0.483	•	•	452	47.4
	200	316.7	42.70	•	•	2.10	0.521	•	•	318	52.8
	207	396.0	111.45	•	•	2.91	0.903	•	•	467	62.5
	214	349.9	97.23	•	•	2.78	0.736	•	•	366	108.9:
ADAS (Blunham)	55	95.3	10.00	•	•	2.80	0.265	•	•	1158	106.1
	69	94.9	27.82	•	•	3.10	1.235	•	•	1231	191.5
	83	136.9	22.60	•	•	3.16	0.882	•	•	1147	119.2
	97	164.8	13.77	•	•	3.24	0.464	•	•	1091	124.7
	111	266.8	47.89	•	•	•	•	•	•	1154	44.5
	125	321.8	67.48	•	•	4.25	0.891	•	•	764	151.9
	139	432.1	91.54	70.5	4.42	4.26	0.943	1.04	0.087	520	47.6
	146	436.5	55.80	89.5	7.30	3.75	0.513	1.26	0.116	522	8.4
	153	500.4	76.74	129.9	14.18	4.08	0.489	1.68	0.148	559	47.8
	160	562.5	38.33	186.9	9.20	4.19	0.143	2.07	0.098	526	10.6
	174	642.2	183.66	325.6	102.30	5.18	1.334	3.54	0.763	553	66.0
	181	648.1	49.85	359.6	30.59	5.59	0.530	4.27	0.349	525	26.0
	188	618.2	108.89	363.7	39.96	5.83	1.205	4.73	0.800	543	82.0
	195	667.5	100.02	393.1	35.84	6.64	0.999	5.46	0.738	534	41.5
	203	602.5	46.48	369.2	29.76	6.09	0.562	5.06	0.405	552	15.5:
Newcastle	77	54.4	9.72	•	•	2.08	0.400	•	•	761	203.0
	97	98.3	11.65	•	•	2.47	0.190	•	•	929	98.9
	111	139.9	32.84	•	•	3.64	1.241	•	•	665	222.1
	126	251.2	43.23	•	•	3.06	2.760	•	•	699	170.9
	138	293.2	37.12	•	•	4.31	0.690	•	•	699	79.1
	152	404.4	180.31	•	•	4.60	0.299	•	•	408	103.8
	166	582.8	118.21	130.4	26.64	1.07	0.572	0.88	0.380	553	63.7
	169	402.2	84.22	•	•	3.93	1.082	•	•	463	60.7
	172	639.6	93.12	177.6	32.43	4.23	1.967	2.66	0.881	781	229.2
	176	543.7	193.91	179.6	21.08	4.82	1.698	8.57	11.281	495	89.6
	179	736.2	111.40	309.2	32.75	5.95	0.216	4.60	0.932	576	20.2
	183	826.1	215.77	404.9	131.46	•	•	•	•	710	100.2
	190	749.3	102.77	434.6	65.29	9.21	2.095	5.99	1.924	641	46.1
	193	586.0	66.46	370.5	17.91	8.96	3.757	5.15	0.940	507	26.3
	197	828.5	223.28	497.1	136.04	6.93	1.987	6.03	1.986	618	144.6
	200	897.2	141.55	620.2	83.54	8.39	2.901	8.62	2.854	736	90.7
	204	652.3	167.21	459.5	117.09	7.20	0.872	6.56	1.207	492	50.0
	207	789.1	93.69	562.8	47.32	6.00	0.439	6.06	0.788	601	77.1:
ADAS (Potton)	55	27.9	13.90	•	•	0.74	0.318	•	•	907	312.2
	69	29.1	10.05	•	•	0.73	0.251	•	•	990	183.1
	83	41.9	13.37	•	•	0.97	0.358	•	•	1032	159.1
	97	54.9	9.53	•	•	1.05	0.088	•	•	918	77.3
	111	85.4	22.59	•	•	•	•	•	•	987	204.1
	125	117.3	23.33	•	•	1.56	0.256	•	•	665	58.6
	139	184.7	11.66	•	•	1.74	0.055	•	•	639	65.8
	146	260.5	57.07	44.2	6.01	2.12	0.376	0.66	0.153	494	26.2
	153	309.5	75.43	66.8	16.32	2.27	0.453	0.83	0.207	532	117.6
	160	327.0	59.15	97.5	21.90	2.23	0.378	1.16	0.247	461	47.0
	167	350.3	47.97	141.4	19.96	2.42	0.273	1.59	0.203	587	59.0
	174	802.5	752.54	414.7	399.47	5.61	5.116	4.10	3.812	532	43.4
	181	353.2	82.51	203.1	54.00	3.12	0.981	2.48	0.879	506	77.3
	188	279.8	29.02	177.0	18.58	2.47	0.197	2.10	0.204	415	60.2
	195	289.2	18.62	167.7	17.53	2.49	0.082	2.08	0.155	433	22.0:
Rothamsted	74	•	•	•	•	•	•	•	•	533	152.0
	89	80.4	18.71	•	•	2.17	0.523	•	•	900	184.1
	103	98.2	18.25	•	•	2.28	0.426	•	•	825	78.4
	116	128.8	25.00	•	•	3.60	2.496	•	•	813	130.9
	131	162.3	42.30	•	•	2.66	0.604	•	•	496	111.7
	146	223.0	21.66	42.8	4.46	3.15	0.299	0.38	0.048	409	24.0
	173	279.0	118.82	65.0	23.91	2.16	1.010	0.81	0.348	399	53.1
	180	254.7	111.55	71.0	35.62	1.79	0.699	0.83	0.404	318	162.3
	183	312.0	10.54	117.7	15.01	•	•	•	•	303	20.0
	187	280.0	100.14	130.0	37.24	2.17	0.811	1.51	0.476	318	84.3
	189	500.0	133.23	289.0	79.81	•	•	•	•	437	78.4
	194	383.7	174.65	233.0	125.05	3.54	1.892	2.96	1.658	399	159.4
	196	330.3	19.76	202.3	16.92	•	•	•	•	337	66.9:
Sutton Bonington	91	95.0	0.00	•	•	•	•	•	•	•	•
	109	119.3	24.44	•	•	2.89	0.165	•	•	•	•
	124	214.3	18.18	•	•	•	•	•	•	•	•
	137	306.7	73.68	•	•	3.37	0.285	•	•	•	•
	144	400.7	67.56	52.4	12.08	•	•	•	•	•	•
	152	509.2	73.31	82.3	19.39	4.64	0.781	1.20	1.195	•	•
	156	610.2	66.80	119.3	8.74	•	•	•	•	•	•
	165	672.2	147.56	129.0	44.62	5.84	2.162	1.96	1.355	•	•
	180	663.2	124.34	286[illegible]	71.63	•	•	•	•	•	•
	[illegible]	453.7	49.34	187.5	17.25	•	•	•	•	•	•:

H-GCA Barley Project 0080/2/87

1988 Ns

N applied :- standard application

Site	Julian Day	Total Dry Weight (g/m2)		Ear Dry Weight (g/m2)		Total N Uptake (g/m2)		N Uptake in Ears (g/m2)		Total Number of Shoots (m2)	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Belfast	88	14.8	4.45	*	*	0.58	0.212	*	*	582	274.4
	102	26.9	8.70	*	*	0.94	0.417	*	*	611	127.3
	116	75.9	16.86	*	*	3.86	0.922	*	*	842	180.3
	130	200.2	17.57	*	*	7.53	1.357	*	*	1002	64.4
	145	491.9	26.76	*	*	7.38	2.434	*	*	1064	125.5
	158	953.5	35.09	*	*	9.30	1.818	*	*	1158	105.6
	165	1066.5	199.08	*	*	7.18	4.897	*	*	1027	221.9
	172	1151.1	54.39	*	*	5.73	3.944	*	*	911	202.1
	179	1414.7	103.10	*	*	9.23	2.342	*	*	1020	22.0
	186	1326.7	158.02	*	*	9.20	3.470	*	*	979	131.8
	193	1284.4	111.20	*	*	9.78	5.960	*	*	862	51.8
	200	1488.5	169.11	*	*	10.87	3.018	*	*	1139	91.1
	207	1251.9	88.42	*	*	8.82	3.237	*	*	932	93.5
	214	1152.3	111.62	*	*	7.84	3.956	*	*	589	214.0:
ADAS (Blunham)	55	98.7	11.40	*	*	3.29	0.826	*	*	1490	0.0
	69	113.1	21.48	*	*	4.19	1.348	*	*	1300	141.2
	83	154.8	25.19	*	*	6.37	1.319	*	*	1201	119.3
	97	253.4	16.34	*	*	11.80	0.911	*	*	1292	43.6
	111	431.7	12.59	*	*	*	*	*	*	1298	160.6
	125	626.5	46.13	*	*	14.24	0.906	*	*	1046	36.9
	139	976.2	107.57	140.0	16.11	14.83	2.872	2.38	0.274	952	126.6
	146	1061.2	41.19	161.2	5.83	13.61	1.944	2.66	0.248	955	38.9
	153	1028.0	84.89	200.9	17.90	10.82	1.360	2.89	0.276	893	81.4
	160	1210.6	91.91	309.2	13.84	11.09	1.339	3.90	0.422	880	25.5
	174	1398.0	87.12	606.2	44.58	12.09	1.830	7.14	0.788	945	25.2
	181	1403.7	177.25	707.9	96.36	13.55	3.220	9.54	2.438	935	101.8
	188	1366.1	123.26	742.0	61.61	14.01	3.060	10.35	2.061	1000	24.3
	195	1238.5	155.65	657.4	139.09	12.77	3.408	9.46	2.755	878	247.6
	203	1140.8	56.39	641.9	30.47	12.59	1.077	9.36	0.706	809	66.7:
Newcastle	77	54.4	9.72	*	*	*	*	*	*	761	203.0
	97	98.3	11.65	*	*	*	*	*	*	929	98.9
	111	190.5	36.55	*	*	8.92	2.181	*	*	743	150.6
	126	298.0	25.18	*	*	3.93	0.512	*	*	724	86.6
	138	599.8	117.16	*	*	9.49	2.553	*	*	995	147.9
	152	831.9	158.06	*	*	10.47	2.261	*	*	672	36.3
	166	1058.4	97.66	207.4	34.02	6.83	2.349	1.92	0.909	679	77.5
	169	795.8	297.73	*	*	8.82	5.152	*	*	547	171.3
	172	1033.9	220.48	292.9	68.06	11.23	5.176	3.73	1.731	830	251.5
	176	1036.0	258.35	381.5	51.16	7.35	2.978	4.53	1.277	783	484.2
	179	1340.1	82.32	534.1	47.02	14.13	1.832	8.73	0.712	893	60.4
	183	1432.7	91.83	643.4	62.29	*	*	*	*	798	123.6
	190	1301.7	19.07	671.7	48.90	14.06	1.551	9.48	0.779	699	98.1
	193	1002.2	102.91	641.3	90.08	7.97	6.509	8.64	1.881	820	199.2
	197	950.0	371.32	533.1	181.56	8.44	3.593	6.82	2.633	547	195.0
	200	1510.2	126.60	868.6	60.76	11.66	0.459	9.14	1.721	852	87.3
	204	1141.7	127.99	732.1	72.00	13.07	0.452	11.01	0.903	638	55.0
	207	1340.5	241.36	912.0	162.69	9.94	1.371	11.11	4.167	919	97.4:
ADAS (Potton)	55	29.6	2.33	*	*	0.85	0.109	*	*	941	79.5
	69	37.6	3.52	*	*	0.97	0.061	*	*	1116	32.7
	83	49.5	10.14	*	*	2.13	0.396	*	*	1192	176.6
	97	95.9	19.29	*	*	5.20	0.969	*	*	1470	134.4
	111	207.3	27.74	*	*	*	*	*	*	1569	121.2
	125	405.8	59.67	*	*	9.60	0.936	*	*	1092	177.4
	139	707.0	48.63	*	*	10.19	1.517	*	*	1055	31.8
	146	840.4	44.25	113.7	10.87	10.34	0.796	1.74	0.341	963	15.7
	153	1013.9	131.36	157.8	19.62	10.06	0.903	2.49	0.310	978	145.4
	160	1187.5	28.00	240.1	5.86	9.70	1.706	2.69	1.985	963	56.0
	167	1344.8	211.56	424.8	50.06	11.27	2.335	6.20	1.289	1233	101.2
	174	1323.6	69.77	543.3	42.62	11.02	1.062	7.12	0.604	1020	57.0
	181	1263.4	279.27	593.8	134.52	12.22	3.083	8.76	2.097	1005	140.5
	188	1101.8	52.61	581.6	34.76	11.55	0.690	9.07	0.543	958	40.8
	195	1146.4	32.71	604.9	24.43	12.56	0.744	10.09	0.526	918	46.3:
Rothamsted	74	*	*	*	*	*	*	*	*	*	*
	89	85.1	1.76	*	*	3.96	0.281	*	*	1013	235.6
	103	178.2	39.68	*	*	7.26	2.969	*	*	1420	284.7
	116	253.7	37.73	*	*	8.32	2.958	*	*	1104	217.4
	131	470.6	71.52	*	*	10.67	2.721	*	*	811	201.3
	146	719.0	164.33	102.3	26.28	13.42	1.482	1.36	0.135	674	47.9
	173	817.7	87.64	155.7	1.80	7.18	1.623	2.23	0.115	687	72.0
	180	886.0	136.92	201.6	18.39	5.76	0.670	2.50	0.235	659	73.9
	183	840.7	137.00	239.7	51.94	*	*	*	*	638	77.3
	187	971.3	76.49	395.3	14.05	8.21	1.670	5.54	0.935	600	26.0
	189	1147.0	249.10	600.5	140.15	*	*	*	*	737	131.2
	194	1119.3	261.26	636.7	175.22	11.51	4.688	9.58	4.018	812	450.3
	196	1013.7	316.07	586.3	181.09	*	*	*	*	537	110.9:
Sutton Bonington	91	95.0	0.00	*	*	*	*	*	*	*	*
	109	151.3	7.93	*	*	6.95	0.490	*	*	*	*
	124	287.7	51.43	*	*	*	*	*	*	*	*
	137	486.7	27.10	*	*	2.83	4.736	*	*	*	*
	144	628.5	129.80	72.9	24.26	*	*	*	*	*	*
	152	702.0	108.53	110.0	5.29	2.79	2.848	1.83	1.825	*	*
	156	846.7	134.11	153.3	[illegible]9.27	*	*	*	*	*	*
	165	1296.5	181.98	257.0	60.51	7.13	3.066	4.84	4.840	*	*
	180	1243.5	188.80	476.5	122.33	*	*	*	*	*	*
	210	806.5	78.39	370.0	37.94	*	*	*	*	*	*:

1989 N0

H-GCA Barley Project 0080/2/87

N applied :- 0 kg/ha

Site	Julian Day	Total Dry Weight (g/m2)		Ear Dry Weight (g/m2)		Total N Uptake (g/m2)		N Uptake in Ears (g/m2)		Total Number of Shoots (m2)	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Belfast	87	57.5	7.25	*	*	1.79	0.708	*	*	1306	137.4
	102	65.9	9.91	*	*	2.10	0.915	*	*	869	57.0
	116	127.3	24.01	*	*	2.77	0.744	*	*	881	123.3
	130	235.3	37.75	*	*	3.68	0.447	*	*	998	261.5
	144	402.3	110.14	*	*	4.74	1.224	*	*	942	146.6
	152	444.7	102.65	49.2	7.62	3.85	0.803	0.67	0.102	573	86.2
	158	618.7	146.29	73.0	12.12	5.00	1.076	0.95	0.174	562	69.3
	165	578.3	112.90	97.2	15.01	3.48	0.930	1.48	0.179	544	57.6
	172	821.3	95.24	242.0	23.52	4.33	0.609	3.22	0.216	689	142.7
	179	769.3	24.03	295.3	11.06	3.85	0.345	3.92	0.319	555	59.2
	186	871.0	175.31	420.0	82.82	3.40	0.890	5.60	1.241	605	62.6
	192	901.7	125.08	483.3	57.77	3.17	0.724	6.64	1.165	642	49.5
	200	878.3	231.37	506.0	133.30	2.44	0.745	7.04	1.931	577	72.2:
ADAS (Blunham)	53	23.6	*	*	*	1.32	*	*	*	440	*
	67	49.2	*	*	*	2.01	*	*	*	675	*
	81	62.7	*	*	*	2.11	*	*	*	723	*
	95	74.9	*	*	*	1.86	*	*	*	681	*
	109	104.8	*	*	*	2.16	*	*	*	601	*
	123	314.6	97.15	*	*	5.17	1.463	*	*	1229	229.4
	137	412.0	73.41	*	*	4.53	0.581	*	*	823	67.1
	151	726.5	76.73	147.3x	15.09	11.86	1.402	2.10	0.221	961	183.8
	159	932.5	52.06	239.3x	30.65	9.51	0.055	3.19	0.462	1126	73.4
	165	1117.5	53.15	377.8x	40.33	11.95	0.996	4.65	0.496	1087	79.0
	172	1085.8	105.01	541.0x	77.05	*	*	*	*	926	167.5
	179	909.7	176.75	553.0x	88.81	*	*	*	*	857	140.3
	186	999.5	85.45	630.1x	43.21	*	*	*	*	978	110.3
	193	1009.2	91.30	641.2x	64.04	*	*	*	*	1005	104.6:
Newcastle	80	138.4	10.89	*	*	*	*	*	*	1002	49.7
	94	206.5	38.31	*	*	5.39	2.306	*	*	1170	141.7
	109	226.5	54.48	*	*	4.34	1.017	*	*	997	228.1
	124	388.8	158.02	*	*	*	*	*	*	1037	244.0
	136	428.7	50.56	*	*	3.91	0.972	*	*	805	137.4
	152	781.7	120.40	135.6	26.07	5.51	1.300	1.56	0.076	943	16.5
	163	746.7	249.72	191.8	60.88	5.80	1.379	2.62	1.100	860	156.5
	174	887.5	94.11	420.3	32.21	5.30	1.143	4.48	0.939	747	98.2
	180	1089.0	189.77	597.5	91.27	6.54	3.159	6.33	1.471	836	132.7
	188	960.7	226.88	598.1	134.74	16.65	13.889	7.34	0.952	788	203.3
	195	691.8	107.20	473.0	68.77	6.66	0.467	5.62	1.259	629	89.1:
ADAS (Potton)	53	29.9	*	*	*	1.04	*	*	*	702	*
	67	40.0	*	*	*	1.12	*	*	*	728	*
	81	45.2	*	*	*	1.34	*	*	*	571	*
	95	52.9	*	*	*	1.29	*	*	*	642	*
	109	85.1	*	*	*	1.41	*	*	*	614	*
	123	145.2	*	*	*	1.99	*	*	*	718	*
	137	374.4	99.84	*	*	3.47	1.107	*	*	963	98.0
	151	600.4	162.77	159.0	48.60	6.50	1.506	2.24	0.646	944	142.5
	158	668.5	183.97	221.0	76.64	6.99	1.794	3.34	0.558	994	201.0
	165	734.8	157.09	340.8	95.91	6.13	1.454	3.39	0.764	1008	102.1
	172	756.8	158.04	447.9	96.11	*	*	*	*	962	220.8
	179	648.8	155.13	423.9	102.97	*	*	*	*	865	141.1
	186	694.7	185.20	459.3	119.28	*	*	*	*	920	268.0
	193	786.0	77.38	510.8	55.34	*	*	*	*	1041	89.4:
Rothamsted	94	182.0	46.86	*	*	3.54	1.052	*	*	1486	196.1
	107	251.1	72.86	*	*	4.49	1.771	*	*	1123	287.6
	122	323.2	19.50	*	*	5.21	0.166	*	*	1068	61.7
	135	324.9	83.29	54.1	15.83	4.70	0.654	0.94	0.378	569	96.1
	142	395.6	87.49	95.7	18.74	4.36	1.224	1.37	0.460	581	76.5
	151	471.2	35.67	156.5	13.89	4.36	1.190	2.06	0.267	557	46.5
	156	479.4	77.99	176.2	25.37	5.26	1.077	2.53	0.245	501	66.1
	163	572.9	252.58	269.8	113.16	5.29	2.265	3.24	1.428	533	183.4
	170	573.4	96.60	346.8	51.65	4.95	0.675	3.97	0.514	511	74.3
	177	628.8	129.11	425.0	87.68	6.10	1.055	5.38	0.911	573	61.2
	186	640.8	224.39	432.8	137.46	6.53	1.787	5.81	1.507	564	140.5:
Sutton Bonington	117	420.0	41.93	*	*	9.18	1.299	*	*	*	*
	128	572.2	58.80	*	*	9.82	1.663	*	*	*	*
	136	644.2	164.16	*	*	9.44	1.914	*	*	*	*
	142	752.2	133.28	*	*	10.14	2.750	*	*	*	*
	150	847.0	82.51	192.3	40.51	9.06	1.994	3.09	3.085	*	*
	156	988.2	51.31	259.5	12.26	10.66	0.458	4.00	3.995	*	*
	163	1055.3	131.20	348.7	7.04	12.17	1.854	5.30	5.295	*	*
	170	1135.5	67.28	453.7	48.04	11.90	0.784	6.72	6.723	*	*
	177	1103.0	181.79	581.0	95.52	11.60	1.694	8.86	8.858	*	*
	184	981.5	93.15	547.7	26.73	11.88	2.032	7.58	7.578	*	*
	198	976.2	140.61	516.7	69.11	*	*	*	*	*	*:

1989 Ns

H-GCA Barley Project 0080/2/87

N applied :- standard application

Site	Julian Day	Total Dry Weight (g/m2)		Ear Dry Weight (g/m2)		Total N Uptake (g/m2)		N Uptake in Ears (g/m2)		Total Number of Shoots (m2)	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Belfast	87	73.1	18.92	*	*	2.50	0.481	*	*	1606	395.3
	102	77.5	12.08	*	*	3.96	0.655	*	*	993	69.9
	116	200.0	22.34	*	*	8.92	0.645	*	*	1198	93.1
	130	464.0	66.09	*	*	12.94	1.672	*	*	1219	186.1
	144	791.0	53.36	*	*	12.09	0.775	*	*	1136	194.9
	152	757.7	154.77	74.7	16.69	7.50	1.602	1.12	0.262	646	216.4
	158	1036.7	137.61	103.7	16.14	11.02	1.801	1.42	0.209	703	103.8
	165	1206.7	53.26	148.3	40.13	9.93	0.018	2.38	0.687	751	123.2
	172	1282.7	67.41	350.0	22.00	9.24	1.001	5.43	0.145	789	118.8
	179	1477.0	125.37	540.7	78.05	8.82	0.876	8.22	0.905	806	227.2
	186	1408.3	9.02	623.3	37.54	7.03	1.180	9.54	0.611	744	90.7
	192	1610.3	92.79	838.7	58.02	7.96	0.798	12.77	0.900	912	213.2
	200	1427.0	144.82	763.0	15.59	5.90	1.214	11.55	0.434	825	64.5:
ADAS (Blunham)	53	23.7	*	*	*	1.24	*	*	*	445	*
	67	42.3	*	*	*	1.62	*	*	*	597	*
	81	54.3	*	*	*	2.27	*	*	*	701	*
	95	101.2	*	*	*	4.04	*	*	*	694	*
	109	161.6	*	*	*	5.93	*	*	*	683	*
	123	391.6	50.32	*	*	11.63	1.673	*	*	1458	301.7
	137	583.6	43.56	*	*	10.86	0.656	*	*	1104	55.1
	151	1085.8	218.06	185.1	29.29	18.27	3.575	3.11	0.475	1301	246.9
	159	1287.1	127.84	272.5	29.90	13.87	1.743	4.60	0.542	1336	100.2
	165	1065.5	390.83	308.9	116.29	11.26	3.821	5.28	1.661	997	345.7
	172	1296.2	41.69	606.7	54.49	*	*	*	*	1134	91.3
	179	1339.6	222.26	726.3	147.67	*	*	*	*	1177	292.2
	186	1330.6	99.34	731.4	76.83	*	*	*	*	1198	55.1
	193	1383.6	80.96	790.7	58.83	*	*	*	*	1278	109.5:
Newcastle	80	142.3	44.85	*	*	*	*	*	*	1061	352.8
	94	231.8	60.00	*	*	11.50	1.356	*	*	1236	310.9
	109	315.4	90.35	*	*	9.92	3.057	*	*	1151	286.9
	124	530.5	90.65	*	*	*	*	*	*	1202	255.9
	136	682.9	35.79	*	*	10.53	3.564	*	*	1118	85.3
	152	1128.6	238.00	197.1	31.10	10.27	3.914	2.79	0.858	1120	147.6
	163	1305.9	242.08	311.3	74.83	10.29	1.768	4.50	0.760	1156	109.1
	174	1382.7	145.83	617.3	68.07	8.11	1.813	7.59	1.079	910	93.7
	180	1592.8	75.41	831.4	34.43	16.68	8.454	7.94	1.153	1020	31.3
	188	1619.3	112.68	932.5	69.48	14.31	1.788	12.08	0.389	1051	82.6
	195	1417.2	220.36	891.6	120.75	14.18	5.188	11.52	1.972	996	158.8:
ADAS (Potton)	53	26.9	*	*	*	0.93	*	*	*	732	*
	67	33.0	*	*	*	0.88	*	*	*	735	*
	81	31.2	*	*	*	1.16	*	*	*	648	*
	95	49.2	*	*	*	2.15	*	*	*	571	*
	109	112.7	*	*	*	3.66	*	*	*	707	*
	123	221.1	*	*	*	5.09	*	*	*	770	*
	137	568.9	41.25	*	*	8.90	0.675	*	*	1151	75.0
	151	1011.0	136.22	214.5	15.04	11.72	1.747	3.93	0.296	1436	55.9
	158	1047.1	144.91	271.2	33.53	10.90	1.260	4.76	0.222	1264	61.6
	165	1182.9	179.96	459.2	10.39	11.76	1.995	6.77	0.600	1276	153.6
	172	1190.0	185.81	576.4	66.24	*	*	*	*	1235	112.9
	179	1096.9	178.99	587.8	85.05	*	*	*	*	1100	66.7
	186	1175.7	207.26	662.2	102.49	*	*	*	*	1329	156.1
	193	1208.0	168.73	692.0	111.72	*	*	*	*	1239	17.8:
Rothamsted	94	285.0	37.99	*	*	11.69	2.598	*	*	1625	199.6
	107	364.4	7.77	*	*	10.76	1.048	*	*	1457	191.0
	122	582.4	65.25	*	*	12.47	1.299	*	*	1290	100.0
	135	834.0	131.46	94.9	19.05	17.63	5.177	1.78	0.369	1048	120.0
	142	858.5	107.05	172.4	6.39	10.89	2.401	3.04	0.400	909	36.1
	151	883.8	29.46	214.7	14.78	8.67	0.592	3.16	0.601	791	19.5
	156	1000.4	39.45	293.9	37.46	10.67	1.345	4.74	0.869	879	174.9
	163	1132.1	77.55	448.4	11.72	13.52	1.543	6.10	0.043	836	89.2
	170	1164.1	197.78	637.6	82.84	11.39	1.865	8.43	1.038	834	141.4
	177	1410.0	148.16	860.2	88.28	15.78	1.617	13.24	1.478	1105	98.0
	186	1321.2	130.97	844.0	85.45	14.35	1.161	12.67	1.109	968	128.7:
Sutton Bonington	117	393.7	14.41	*	*	8.33	0.897	*	*	*	*
	128	633.2	39.89	*	*	11.62	0.839	*	*	*	*
	136	739.7	76.73	*	*	13.99	2.064	*	*	*	*
	142	735.7	130.42	*	*	11.76	3.251	*	*	*	*
	150	964.2	41.57	171.5	13.77	15.08	0.572	3.12	3.120	*	*
	156	1022.0	52.10	283.7	42.29	15.60	1.308	5.57	5.573	*	*
	163	1125.8	105.91	360.2	42.02	17.61	2.225	6.98	6.978	*	-
	170	1069.0	47.91	425.2	37.67	16.08	0.444	8.65	8.648	*	*
	177	967.2	134.74	475.0	74.68	15.09	2.347	9.91	9.910	*	*
	184	992.5	102.44	554.2	49.11	14.69	1.882	11.87	11.873	*	*
	198	988.7	156.72	533.5	79.58	*	*	*	*	*	*:

1990 N0 H-GCA Barley Project 0080/2/87

N applied :- 0 kg/ha

Site	Julian Day	Total Dry Weight (g/m2) mean	Total Dry Weight (g/m2) s.d.	Ear Dry Weight (g/m2) mean	Ear Dry Weight (g/m2) s.d.	Total N Uptake (g/m2) mean	Total N Uptake (g/m2) s.d.	N Uptake in Ears (g/m2) mean	N Uptake in Ears (g/m2) s.d.	Total Number of Shoots (m2) mean	Total Number of Shoots (m2) s.d.
Belfast	86	116.8	11.88	*	*	4.13	0.539	*	*	1230	246.8
	100	137.6	17.76	*	*	3.76	0.674	*	*	1255	173.8
	113	234.6	32.71	*	*	4.35	0.624	*	*	1278	164.6
	128	481.6	185.78	*	*	5.73	2.016	*	*	1162	168.3
	141	431.7	105.88	44.4	8.70	4.12	1.283	0.55	0.131	805	158.0
	148	564.6	123.03	76.4	7.29	7.20	3.008	1.05	0.051	842	239.7
	155	594.9	126.99	97.8	25.49	4.99	1.036	1.33	0.305	793	131.1
	162	635.6	89.06	159.1	26.41	5.23	1.030	2.02	0.526	794	238.5
	169	764.9	115.73	280.4	50.14	6.66	1.736	3.51	0.927	887	150.5
	176	782.0	122.64	355.6	56.20	6.60	1.425	4.03	0.742	878	170.2
	183	730.2	170.70	367.1	141.81	6.58	2.349	4.32	1.873	893	180.8
	190	758.8	267.38	415.4	155.70	7.18	3.441	5.05	2.416	833	154.2
	197	817.7	189.35	483.4	115.56	8.49	2.384	6.54	1.768	828	171.8
	204	864.9	107.33	519.9	79.56	9.61	2.232	7.48	1.614	948	81.4:
ADAS (Blunham)	59	136.8	6.01	*	*	*	*	*	*	1695	46.1
	73	199.5	8.77	*	*	*	*	*	*	1710	152.0
	86	250.0	33.51	*	*	4.74	0.499	*	*	1686	185.2
	100	305.4	17.39	*	*	3.89	0.206	*	*	1512	108.0
	115	352.3	7.90	*	*	4.06	0.059	*	*	1346	146.1
	129	405.0	78.80	56.5	9.11	3.00	0.361	*	*	*	*
	143	709.5	79.82	155.2	18.01	4.90	0.677	2.36	0.428	*	*
	150	761.4	42.21	222.4	24.22	4.94	0.390	2.53	0.243	*	*
	158	776.5	51.04	368.9	32.28	4.82	0.223	3.33	0.223	*	*
	164	765.5	32.34	368.8	18.09	4.80	0.000	3.27	0.000	*	*
	171	1012.8	68.94	538.8	13.44	6.18	0.559	*	*	*	*
	178	1176.1	120.28	666.7	64.56	16.25	1.992	7.48	0.912	*	*
	190	1126.0	46.33	394.4	2.25	6.99	0.499	4.65	0.480	*	*
	198	1296.6	61.55	441.6	29.99	10.14	1.501	7.69	1.470	*	*:
Newcastle	85	228.8	28.91	*	*	11.27	1.711	*	*	1452	53.7
	100	344.6	144.55	*	*	5.20	2.799	*	*	1471	404.7
	113	397.2	50.49	*	*	10.75	2.917	*	*	1201	140.7
	124	509.6	19.48	*	*	0.95	0.849	*	*	1024	71.5
	141	511.6	70.35	*	*	5.87	0.644	*	*	645	132.8
	155	721.2	81.35	*	*	6.94	3.741	*	*	604	160.4
	170	854.7	63.81	*	*	9.02	0.395	*	*	808	20.7
	183	813.1	153.92	*	*	*	*	*	*	720	188.8:
Rothamsted	93	83.2	37.57	*	*	*	*	*	*	935	397.6
	108	126.3	34.85	*	*	*	*	*	*	1144	333.3
	120	99.1	57.80	*	*	*	*	*	*	681	130.2
	134	248.0	89.70	*	*	*	*	*	*	557	168.2
	150	291.2	96.09	66.3	24.19	*	*	*	*	390	76.0
	155	336.7	123.08	95.9	41.96	*	*	*	*	406	130.2
	163	409.0	155.11	157.1	85.37	*	*	*	*	480	153.8
	171	395.6	100.02	201.8	64.82	*	*	*	*	415	83.2
	176	458.4	39.31	261.2	29.96	*	*	*	*	429	7.9
	184	389.0	54.45	254.6	39.21	*	*	*	*	394	32.9
	190	420.0	58.14	284.1	42.56	*	*	*	*	417	52.8
	197	410.3	120.81	280.2	87.90	*	*	*	*	362	69.2
	207	426.2	107.90	297.5	77.24	*	*	*	*	420	70.6:
Sutton Bonington	93	284.6	47.08	*	*	7.53	0.874	*	*	*	*
	100	337.2	51.82	*	*	*	*	*	*	*	*
	108	386.4	64.15	*	*	8.35	1.087	*	*	*	*
	113	451.8	63.26	*	*	*	*	*	*	*	*
	120	602.8	69.28	*	*	*	*	*	*	*	*
	128	735.6	122.23	20.4	15.65	7.79	2.312	0.33	0.330	*	*
	134	829.8	71.81	86.8	27.15	*	*	*	*	*	*
	141	990.8	102.39	145.8	25.33	10.97	2.511	2.40	2.402	*	*
	149	1152.0	121.01	251.0	36.83	10.25	1.452	3.94	3.936	*	*
	155	1291.4	158.62	369.4	32.64	11.23	1.571	5.59	5.590	*	*
	162	1278.2	143.41	478.4	103.99	11.07	2.723	6.18	6.180	*	*
	170	1354.6	129.25	790.0	119.39	13.22	2.332	9.92	9.916	*	*
	176	1385.4	136.61	767.4	91.41	12.98	2.361	9.07	9.070	*	*
	183	1425.0	68.96	891.2	156.76	14.72	3.079	11.00	11.002	*	*
	191	1599.8	197.97	1016.2	57.09	18.05	2.792	14.63	14.630	*	*:

1990 Ns

H-GCA Barley Project 0080/2/87

N applied :- standard application

Site	Julian Day	Total Dry Weight (g/m2)		Ear Dry Weight (g/m2)		Total N Uptake (g/m2)		N Uptake in Ears (g/m2)		Total Number of Shoots (m2)	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Belfast	86	106.3	9.12	*	*	5.53	0.555	*	*	1079	113.5
	100	185.3	16.52	*	*	8.88	0.758	*	*	1267	113.6
	113	314.7	64.17	*	*	10.48	2.724	*	*	1143	279.1
	128	784.6	134.18	*	*	14.43	2.065	*	*	1176	174.9
	141	937.3	88.95	77.1	24.91	10.99	1.658	1.04	0.332	1128	116.2
	148	1082.9	115.08	117.4	13.21	14.75	2.100	1.75	0.104	1025	151.1
	155	1132.9	157.72	176.3	9.09	11.70	1.413	2.74	0.260	1036	94.1
	162	1054.8	94.60	207.4	33.96	10.22	1.150	3.02	0.551	867	74.7
	169	1096.7	165.48	322.9	81.62	10.69	1.969	4.51	0.751	857	160.7
	176	1129.2	137.86	434.9	23.76	9.96	1.384	5.17	0.457	922	25.5
	183	1129.5	85.05	545.8	39.58	10.42	1.182	6.55	0.675	885	37.8
	190	1088.3	91.58	568.1	122.83	10.83	2.262	7.46	1.906	927	145.9
	197	1193.2	35.55	617.4	81.19	12.17	1.176	8.67	1.100	930	72.5
	204	1110.2	318.19	563.2	178.10	11.77	2.935	8.50	2.550	911	56.2:
ADAS (Blunham)	59	122.9	2.56	*	*	3.91 ✓	0.078	*	*	1587	152.3
	73	193.9	29.91	*	*	4.57 ✓	0.768	*	*	1780	178.5
	86	248.2	11.62	*	*	9.45 ✓	0.164	*	*	1668	36.3
	100	379.2	33.58	*	*	11.18 ✓	0.584	*	*	1750	60.9
	115	520.9	18.18	*	*	11.56 ✓	1.148	*	*	1655	109.2
	129	701.6	195.09	107.8	23.92	8.94 ✗	4.443	*	*	*	*
	143	973.6	96.01	207.1	16.81	12.07	1.150	4.13	0.090	*	*
	150	1167.0	88.80	368.6	27.88	12.83	0.286	6.06	0.569	*	*
	158	1335.5	77.96	618.8	29.34	13.98	0.653	8.87	0.473	*	*
	164	1477.5	110.25	719.8	73.38	15.41	2.368	10.32	1.640	*	*
	171	1581.7	101.89	861.3	22.43	15.42	1.667	*	*	*	*
	178	2039.6	246.43	1090.4	102.66	38.88	2.907	14.78	3.225	*	*
	190	1988.7	133.23	668.2	63.64	18.50	2.418	12.19	1.210	*	*
	198	1730.7	203.61	562.7	53.57	13.70	2.416	8.35	2.338	*	*:
Newcastle	85	258.9	22.92	*	*	17.62	3.999	*	*	1528	71.9
	100	384.9	40.00	*	*	11.31	1.295	*	*	1424	174.5
	113	455.7	78.60	*	*	9.31	1.592	*	*	1059	264.9
	124	569.3	34.31	*	*	4.41	1.187	*	*	1002	59.1
	141	683.1	86.56	*	*	9.67	3.030	*	*	858	115.9
	155	1002.0	68.56	*	*	16.09	10.570	*	*	852	103.5
	170	1348.0	45.44	*	*	18.66	2.152	*	*	1032	81.2
	183	1484.5	242.26	*	*	*	*	*	*	1007	70.7:
Rothamsted	93	115.5	19.54	*	*	*	*	*	*	1127	104.6
	108	149.7	68.70	*	*	*	*	*	*	922	161.1
	120	213.5	43.14	*	*	*	*	*	*	941	196.2
	134	583.1	29.74	*	*	*	*	*	*	841	72.1
	150	736.2	114.31	123.0	31.14	*	*	*	*	654	43.9
	155	1046.0	169.08	206.8	27.21	*	*	*	*	678	112.3
	163	1028.0	161.48	272.7	42.92	*	*	*	*	698	151.2
	171	1033.9	34.37	362.6	31.89	*	*	*	*	630	42.5
	176	1109.7	236.82	491.9	103.55	*	*	*	*	645	107.7
	184	1082.7	64.26	591.8	48.70	*	*	*	*	641	53.6
	190	1082.1	50.20	640.5	12.45	*	*	*	*	696	72.2
	197	1071.2	88.49	647.5	36.79	*	*	*	*	704	59.0
	207	901.5	99.75	554.7	69.10	*	*	*	*	615	89.7:
Sutton Bonington	93	292.8	42.54	*	*	11.53	1.312	*	*	*	*
	100	337.6	41.02	*	*	*	*	*	*	*	*
	108	453.2	62.76	*	*	14.39	1.222	*	*	*	*
	113	523.4	67.46	*	*	*	*	*	*	*	*
	120	663.2	62.45	*	*	*	*	*	*	*	*
	128	858.6	36.83	5.8	6.98	15.76	1.217	0.05	0.050	*	*
	134	912.8	84.20	56.0	11.55	*	*	*	*	*	*
	141	1115.6	42.24	195.2	12.83	15.01	2.038	3.93	3.934	*	*
	149	1315.0	116.53	284.0	47.94	16.95	2.120	5.26	5.260	*	*
	155	1456.6	46.85	393.4	64.17	18.04	1.826	7.34	7.342	*	*
	162	1451.0	139.40	585.2	100.63	17.32	2.043	9.19	9.186	*	*
	170	1561.4	182.38	746.2	31.74	18.56	3.002	11.09	11.094	*	*
	176	1439.0	157.93	923.2	213.25	16.22	2.208	12.19	12.194	*	*
	183	1507.3	140.66	915.0	102.28	20.53	2.537	16.32	16.318	*	*
	191	1797.3	81.83	1156.5	97.91	23.70	2.281	19.42	19.415	*	*:

Appendix 2.2

Database Construction - Verification

Genstat programmes to read, analyse, tabulate and graph database files to facilitate examinination of outliers and residuals.

(a) Serial Data

```
JOB[OUTP=*] 'BLUNHAM89_2'
TEXT GENTITLE;VALUE=!T ('EXAMINATION OF RESIDUALS')
TEXT [VALUE='STRAW DRY WT'] H[1]
TEXT [VALUE='SHOOT NO'] H[2]
VARI Y[1...2];EXTRA=H[1,2]
VARI [N=9] A [1...12], B
OPEN 'BLUNHAM89_2.DAT'; CH=2; WIDTH=132
READ [CH=2] B,A[1...12]
VARI [N=54] Y[1,2]
VARI [VAL=1...6] C
FOR I=1...2
 EQUA OLD=!P{A[#C]}; NEW=Y[I]
 CALC C=C+6
ENDFOR
VARI [N=54] V[10]
EQUA OLD=B ; NEW=V[10]
SORT [INDEX=V[10]; GROUP=DAY; LEV=LF]
VARI [VAL=(1...9)3,(10...18)3] COUNTER
UNIT [54]
FACTOR[LEVELS=3] BLOCK
FACTOR[LEVELS=!V (0, 120)] NITROGEN
GENERATE NITROGEN,BLOCK,DAY
BLOCKS BLOCK
TREATMENTS DAY*POL (NITROGEN;2)
FOR YY=Y[1,2]; RR=R[1,2]
 ANOVA [SE=M; FPROB=Y;CO=] YY; RES=RR
ENDFOR
ENDJOB
STOP
```

(b) Parallel Data

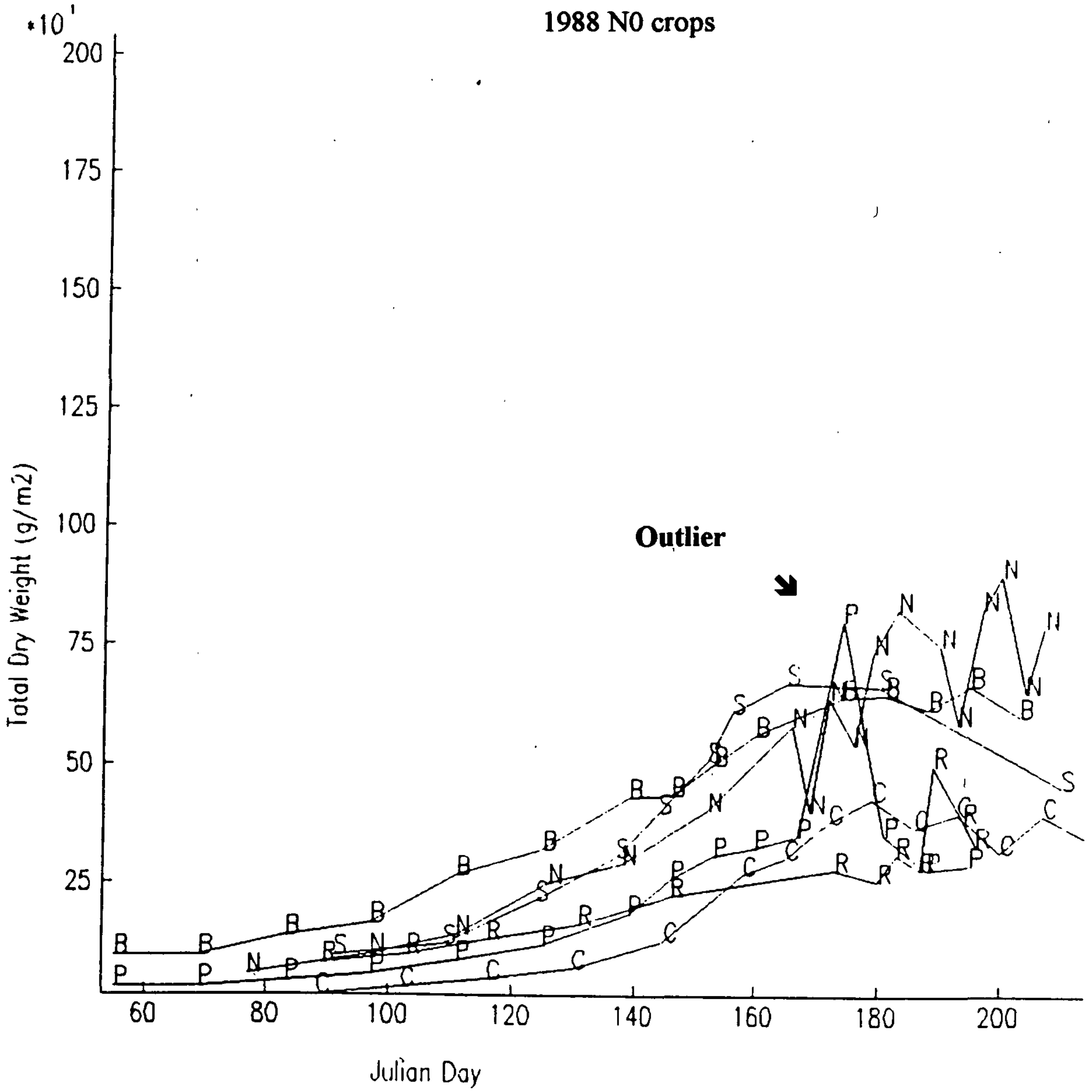
```
JOB[OUTP=*] ‘NCSTLE88’
UNITS[108]
TEXT GENTITLE;VALUE=!T(‘NEWCASTLE88’)
TEXT SUBTITLE[1];VALUE=!T(‘  ’)
SCAL ISUB[1...6];VALUE=1,1,1,1,1,1
TEXT ITEMNAME[1];VALUE=!T(‘DAY’)
TEXT ITEMNAME[2];VALUE=!T(‘BL’)
TEXT ITEMNAME[3];VALUE=!T(‘N’)
TEXT ITEMNAME[4];VALUE=!T(‘NOSH’)
TEXT ITEMNAME[5];VALUE=!T(‘TDW’)
TEXT ITEMNAME[6];VALUE=!T(‘PGA’)
FOR _ITEMNAM=ITEMNAME[];_ISUB=ISUB[]
 IF _ISUB.GT.0
  CONCATENATE _ITEMNAM,SUBTITLE[ _ISUB]
 ENDIF
ENDFOR
VARIATE V[1...6;EXTRA=ITEMNAME[]
OPEN CHANNEL=2;NAME=‘NCSTLESS.DAT’;FILETYPE=INPUT;WIDTH=132
SKIP[CHANNEL=2;FILETYPE=INPUT]  1
READ[CHANNEL=2;END=‘:’;SKIP=*] V[1,2,4,5,6];SKIP=0,0,1,0,0
SORT[INDEX=V[1];GROUP=DAY;LEVELS=LABELS[1]]
SORT[INDEX=V[2];GROUP=BL;LEVELS=LABELS[2]]
DELETE[REDERFINE=Y] V[3] : TEXT V[3] : READ V[3]
‘N0’etc
‘N120’ etc
SORT[INDEX=V[3];GROUP=N;LABELS=LABELS[3]]
BLOCKS BL
TREATMENTS POL(DAY;2) *N
FOR YY=V[4...6]; RR=R[4...6]
 ANOVA [SE=M; FPROB=Y;CO=] YY; RES=RR
ENDFOR
ENDJOB
STOP
```

Appendix 2.3

Database Verification

Example of input/sampling error

(a) Graphical Examination



(b) Data Examination

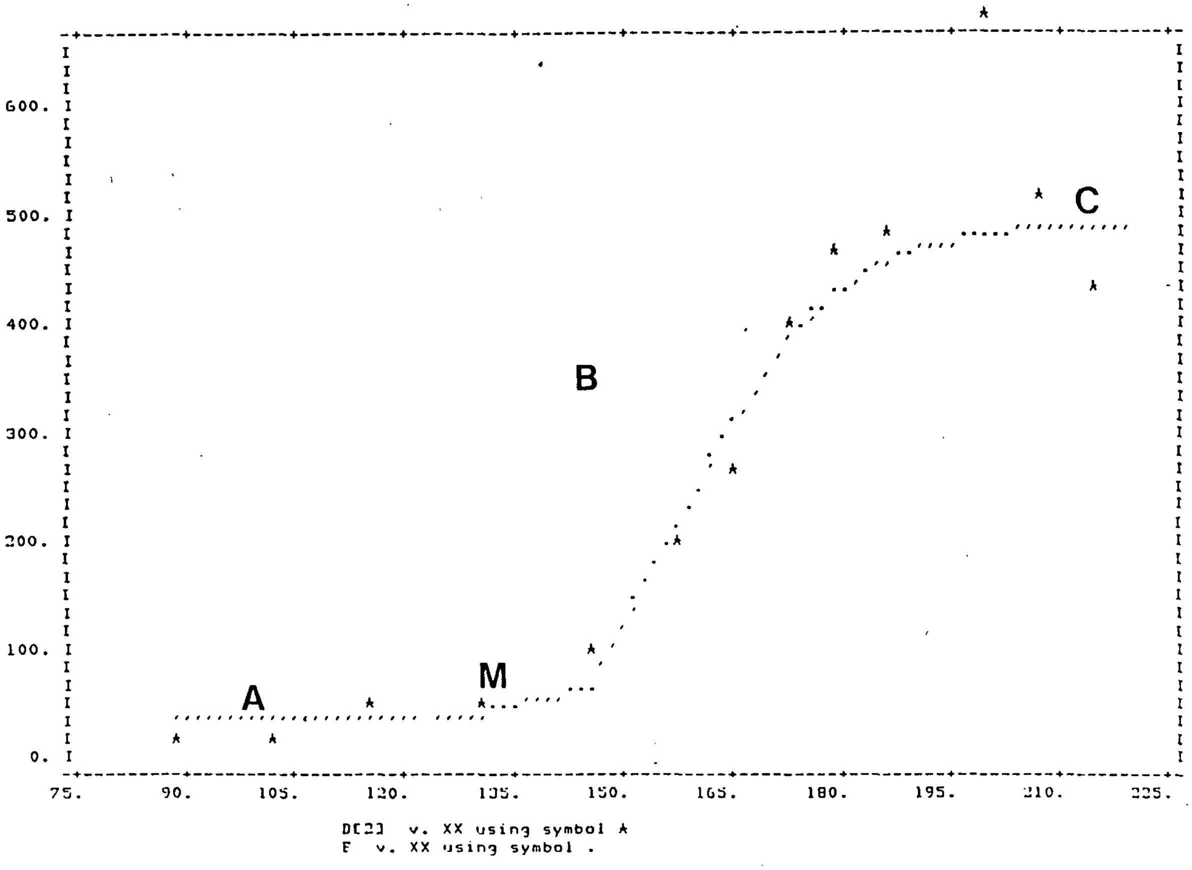
Julian Day	Treatment Applied	Rep.	Total Dry Wt.	Number of Shoots	Dry Wt. of Ear
55	0	1	22.28	784	*
69	0	1	25.92	909	*
83	0	1	44.74	1002	*
97	0	1	48.38	890	*
111	0	1	64.93	818	*
125	0	1	99.95	685	*
139	0	1	186.02	664	*
146	0	1	207.86	466	38.19
153	0	1	230.38	435	51.82
160	0	1	270.55	439	81.44
167	0	1	295.89	540	121.38
174	0	1	1670.60 ←	495	875.30 ←
181	0	1	282.83	462	162.24
188	0	1	246.36	373	157.42
195	0	1	284.19	455	181.79
55	0	2	17.70	675	*
69	0	2	21.05	862	*
83	0	2	27.37	890	*
97	0	2	50.41	858	*
111	0	2	81.58	930	*
125	0	2	109.33	899	*
139	0	2	172.48	564	*
146	0	2	252.48	518	44.28
153	0	2	317.60	499	64.45

Appendix 2.4

Curve fitting procedure - Genstat program for fitting the Gompertz function

```
Nonlinear regression analysis

Response variate:   V[5]TDW
Explanatory:        XX
Fitted Curve:       A + C*EXP(-EXP(-B*(X-M)))
Constraints:        B > 0


*** Summary of analysis ***

                    d.f.        s.s.        m.s.      v.r.

Regression            3     3354026.    1118009.    34.71
Residual             13      418783.      32214.
Total                16     3772809.     235801.

Percentage variance accounted for 86.3


MESSAGE: The following units have high leverage:

                    80          0.565


*** Estimates of parameters ***

            estimate      s.e.

B           0.0512        0.233
M           133.37        6.81
C           1202.         179.
A           91.           122.
```

Sample data fitted with GOMP curve (Gompertz function)



Appendix 3

Tables of results

Table 3.2 Crop development

Site	Year	Sown (1 = Jan 1st)	N Application	ZGS 30/31	Anthesis	Harvest	* ZGS 30 >Anthesis	** Grain Filling Period	*** Date of maximum Shoot N0.	***
		(Days)		(Days)			(Days)	(Days)	N0 Crops	NS Crops
Belfast	1988	-59	98	115	153	214	38	61	107	154
Blunham	1988	-92	77	77	131	203	64	72	74	74
Newcastle	1988	-95	96	95	152	217	57	65	90	102
Potton	1988	-71	76	76	128	195	no data	67	74	102
Rothamsted	1988	-98	74	89	153	207	64	54	93	106
S.Bonington	1988	-97	91	91	156	200	34	44	no data	no data
Belfast	1989	-38	90	116	161	206	45	45	87	120
Blunham	1989	-74	74	95	141	194	46	53	76	90
Newcastle	1989	-105	74	74	145	200	43	55	99	118
Potton	1989	-75	73	95	136	194	41	58	58	114
Rothamsted	1989	-103	73	94	138	191	44	53	94	94
S. Bonington	1989	no data	117	93	157	198	64	41	no data	no data
Belfast	1990	-76	75	113	144	204	30	60	195	148
Blunham	1990	-104	74	100	129	198	29	69	77	100
Newcastle	1990	-108	71	71	141	204	70	63	85	85
Potton	1990	no data	no data	no data	no data	no data	no data	no data	no data	no data
Rothamsted	1990	-102	73	92	141	207	49	66	98	98
S. Bonington	1990	-91	78	71	141	207	73	66	no data	no data

* Defined as the number of days between growth stage 30 and anthesis

** Defined as the number of days between anthesis and harvest

*** The maximum shoot number is defined as the earliest maximum in each data set

\+ Dates for these sites refer to ZGS 23

Table 3.3 Harvest results - Variance ratios

	Grain yield (t/ha at 15% mc)	Ear number per m^2	Grain number per ear	Grain mass (mg)	Total dry weight at harvest (t/ha at 0% mc)	Harvest Index (%)	% N in the grain	Grain N offtake (kg/ha)	Total N offtake (kg/ha)	NHI (%)
Site	5.6 *	5.4 *	1.1 NS	2.4 NS	0.8 NS	3.2 NS	5.6 *	1.4 NS	1.3 NS	4.8 NS (*
Year	191.1 ***	221.6 ***	5.0 *	4.6 *	102.4 ***	22.1 ***	7.1 *	96.4 ***	137.0 ***	41.0 ***
Site x Year	12.8 ***	12.8 ***	14.8 ***	42.8 ***	24.5 ***	9.1 ***	7.0 ***	16.6 ***	26.6 ***	37.0 ***
										2.1 NS
N	55.3 *	21.2 *	27.8 *	0.9 NS	39.6 *	123.4 ***	33.4 *	95.2 *(**)	116.7 **	6.1 *
Site x N	4.8 *	1.3 NS	2.5 NS	4.3 *	4.4 *	0.4 NS	5.9 *	5.7 *	3.8 *	19.5 ***
Year x N	21.8 ***	11.6 ***	1.9 NS	17.9 ***	14.0 ***	0.1 NS	4.1 *	3.7 *	3.3 *	1.2 NS
Site x year x N	4.3 ***	4.9 ***	1.2 NS	2.9 *	2.2 *	4.7 ***	3.2 **	0.9 NS	1.1 NS	

Table 3.4 Grain yield (t/ha at 15% moisture content)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	1.76	5.02	4.40	8.58	4.71	6.62	**3.62**	**6.74**	**5.18**
Blunham	3.07	5.82	5.36	7.69	4.26	7.08	**4.23**	**6.87**	**5.55**
Newcastle	3.82	7.81	4.95	8.08	6.89	9.74	**5.22**	**8.54**	**6.88**
Potton	1.61	5.18	3.33	5.59	-	-	**3.01**	**5.62**	**4.31**
Rothamsted	-	-	3.45	6.57	3.03	5.61	**2.40**	**5.57**	**3.99**
S. Bonington	2.14	4.41	5.21	5.94	6.63	6.70	**4.66**	**5.69**	**5.17**
Means									
N x years	**2.19**	**5.46**	**4.45**	**7.08**	**4.94**	**6.98**			
Years	**3.82**		**5.76**		**5.96**				
N0	**3.86**								
Ns	**6.50**								

Standard errors

N	0.334
Site	0.557
Year	0.110
N x site	0.354
N x year	0.121
N x site x year	0.295

Table 3.5 Ear number/m^2

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	333.2	855.0	602.3	803.7	748.3	979.7	**561.3**	**879.5**	**720.4**
Blunham	526.2	772.0	1005.6	1277.8	1347.3	1186.3	**959.7**	**1078.7**	**1019.2**
Newcastle	462.4	689.4	724.3	960.0	832.3	1074.3	**673.0**	**907.9**	**790.4**
Potton	420.0	917.7	1041.2	1239.1	-	-	**812.1**	**1126.5**	**969.3**
Rothamsted	307.9	611.1	641.9	828.6	419.7	615.0	**456.5**	**684.9**	**570.7**
S. Bonington	431.5	543.3	919.5	1001.3	853.2	1037.2	**734.7**	**860.8**	**797.6**
Means									
N x years	413.5	731.4	822.5	1018.4	862.7	1019.2			
Years	**572.5**		**920.4**		**940.9**				
N0	**699.6**								
Ns	**923.0**								

Standard errors

N	45.63
Site	90.92
Year	17.96
N x site	70.58
N x year	22.59
N x site x year	55.33

Table 3.6 Grain number per ear

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	14.0	14.5	15.3	17.3	15.5	17.9	**14.9**	**16.6**	**15.7**
Blunham	17.3	21.3	16.3	18.8	10.1	16.5	**14.6**	**18.9**	**16.7**
Newcastle	15.7	18.0	18.0	20.0	16.1	18.1	**16.6**	**18.7**	**17.6**
Potton	12.5	18.5	15.0	15.7	-	-	**13.4**	**17.0**	**15.2**
Rothamsted	18.6	20.3	19.3	21.8	15.2	18.0	**17.7**	**20.0**	**18.9**
S. Bonington	14.5	16.3	16.2	15.5	20.0	19.9	**16.9**	**17.2**	**17.1**
Means									
N x years	15.4	18.1	16.7	18.2	14.9	17.9			
Years	**16.8**		**17.4**		**16.4**				
N0	**15.7**								
Ns	**18.1**								

Standard errors

N	0.43
Site	1.63
Year	0.30
N x site	0.81
N x year	0.53
N x site x year	1.29

Table 3.7 Grain mass (mg)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	31.2	33.3	44.2	45.6	34.6	34.0	**36.7**	**37.6**	**37.1**
Blunham	33.1	34.9	34.3	29.1	29.3	26.3	**32.2**	**30.1**	**31.2**
Newcastle	40.7	43.8	37.7	41.9	42.9	42.8	**40.4**	**42.8**	**41.6**
Potton	31.2	33.3	30.1	31.3	-	-	**31.3**	**32.2**	**31.7**
Rothamsted	36.7	42.3	33.0	35.6	38.1	42.0	**35.9**	**40.0**	**37.9**
S. Bonington	27.6	30.5	33.7	33.2	40.8	37.5	**43.0**	**33.7**	**33.9**
Means									
N x years	33.4	36.4	35.5	36.1	36.4	35.7			
Years	**34.9**		**35.8**		**36.1**				
N0	**35.1**								
Ns	**36.1**								

Standard errors

N	0.98
Site	3.39
Year	0.37
N x site	0.94
N x year	0.39
N x site x year	0.96

Table 3.8 Total dry matter production (t/ha at 0% moisture content)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	2.97	11.07	9.21	15.75	7.68	10.83	**6.61**	**12.55**	**9.58**
Blunham	6.02	11.41	10.09	13.84	8.08	11.44	**8.06**	**12.23**	**10.15**
Newcastle	6.06	11.94	7.46	13.13	8.55	12.63	**7.34**	**12.57**	**9.96**
Potton	2.89	11.46	7.86	12.08	-	-	**5.93**	**11.85**	**8.89**
Rothamsted	-	-	6.86	11.61	4.26	9.02	**5.25**	**10.23**	**7.74**
S. Bonington	4.54	8.07	9.76	9.88	13.60	15.62	**9.30**	**11.19**	**10.25**
Means									
N x years	**4.52**	**10.67**	**8.54**	**12.72**	**8.20**	**11.93**			
Years	**7.59**		**10.63**		**10.07**				
N0	**7.09**								
Ns	**11.77**								

Standard errors

N	0.721
Site	1.442
Year	0.206
N x site	0.658
N x year	0.315
N x site x year	0.771

Table 3.9 Harvest index (%)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	N0	Ns	Site
Belfast	50.0	36.5	44.9	43.1	52.0	53.6	**49.0**	**44.4**	**46.7**
Blunham	49.8	49.8	56.4	51.0	49.3	44.8	**51.8**	**48.5**	**50.2**
Newcastle	57.2	52.5	54.9	52.8	57.8	57.1	**56.6**	**54.1**	**55.4**
Potton	56.0	49.1	51.2	51.0	-	-	**54.7**	**51.1**	**52.9**
Rothamsted	-	-	58.6	55.7	57.4	51.1	**54.1**	**52.9**	**53.5**
S. Bonington	37.3	40.2	47.3	47.8	51.2	49.6	**45.2**	**45.9**	**45.5**
Means									
N x years	**49.4**	**46.7**	**52.2**	**50.2**	**54.1**	**51.6**			
Years	**48.1**		**51.2**		**52.8**				
N0	**51.9**								
Ns	**49.5**								

Standard errors

N	0.21
Site	2.83
Year	0.66
N x site	2.82
N x year	0.92
N x site x year	2.26

Table 3.10 % N in the grain

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	1.24	1.21	1.45	1.54	1.44	1.37	**1.37**	**1.37**	**1.37**
Blunham	1.37	1.46	1.45	1.68	1.74	1.48	**1.51**	**1.54**	**1.53**
Newcastle	1.40	1.81	1.44	1.52	1.34	1.58	**1.39**	**1.64**	**1.51**
Potton	1.24	1.67	1.17	1.73	-	-	**1.22**	**1.67**	**1.45**
Rothamsted	1.37	1.60	1.52	1.64	1.53	1.87	**1.47**	**1.70**	**1.59**
S. Bonington	1.58	2.18	1.77	2.54	1.49	1.88	**1.62**	**2.20**	**1.91**
Means									
N x years	**1.37**	**1.66**	**1.47**	**1.77**	**1.47**	**1.63**			
Years	**1.51**		**1.62**		**1.55**				
N0	**1.43**								
Ns	**1.69**								

Standard errors

N	0.041
Site	0.101
Year	0.027
N x site	0.087
N x year	0.034
N x site x year	0.084

Table 3.11 Grain N offtake (kg/ha)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	18.1	48.8	60.4	103.4	57.7	78.9	**45.4**	**77.1**	**61.2**
Blunham	41.0	83.0	81.3	118.4	69.4	75.6	**63.9**	**92.3**	**78.1**
Newcastle	48.3	114.7	59.6	105.3	66.2	113.6	**58.0**	**111.2**	**84.6**
Potton	20.1	94.0	47.1	105.1	-	-	**39.0**	**101.0**	**70.0**
Rothamsted	29.9	85.4	61.0	105.9	37.0	85.4	**42.6**	**92.2**	**67.4**
S. Bonington	26.6	70.4	81.3	119.7	104.8	145.5	**70.9**	**111.9**	**91.4**
Means									
N x years	**30.7**	**82.7**	**65.1**	**109.7**	**64.2**	**100.5**			
Years	**56.7**		**87.4**		**82.3**				
N0	**53.3**								
Ns	**97.6**								

Standard errors

N	4.26
Site	12.46
Year	2.16
N x site	4.99
N x year	3.72
N x site x year	9.11

Table 3.12 Total N offtake (kg/ha)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	-	-	-	-	-	-	-
Blunham	54.4	120.0	92.1	142.7	81.4	104.8	**76.0**	**122.5**	**99.2**
Newcastle	-	-	-	-	-	-	-	-	-
Potton	25.1	120.4	-	-	-	-	**62.9**	**147.4**	**105.2**
Rothamsted	38.6	106.2	71.9	128.0	-	-	**64.5**	**121.9**	**93.2**
S. Bonington	40.6	105.3	143.4	197.9	140.7	208.0	**108.2**	**170.4**	**170.4**
Means									
N x years	**39.6**	**113.0**	**97.4**	**158.3**	**96.7**	**150.2**			
Years	**76.3**		**127.8**		**123.4**				
N0	**77.9**								
Ns	**140.5**								

Standard errors

N	7.48
Site	22.98
Year	3.15
N x site	7.49
N x year	5.08
N x site x year	12.45

Table 3.13 Nitrogen Harvest Index (%)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	-	-	-	-	-	-	-
Blunham	75.5	69.2	88.1	83.1	85.0	71.3	**82.9**	**74.5**	**78.7**
Newcastle	-	-	-	-	-	-	-	-	-
Potton	80.2	78.0	-	-	-	-	**84.5**	**79.4**	**81.9**
Rothamsted	76.4	80.5	84.9	82.9	-	-	**83.3**	**81.8**	**82.5**
S. Bonington	65.4	66.8	56.9	60.5	74.4	69.9	**65.6**	**65.8**	**65.7**
Means									
N x years	**74.4**	**73.6**	**78.3**	**76.7**	**84.3**	**75.6**			
Years	**74.0**		**77.5**		**79.9**				
N0	**79.0**								
Ns	**75.3**								

Standard errors

N	3.24
Site	5.22
Year	0.61
N x site	1.41
N x year	0.90
N x site x year	2.20

Table 3.14 Total dry weight: % variance accounted for by the fitted Gompertz functions

Site	Year	N0 1	N0 2	N0 3	N0 4	NS 1	NS 2	NS 3	NS4
Belfast	88	97.4	89.9	88.7	-	92.6	95.7	94.5	-
Belfast	89	97.3	94.0	93.6	-	96.1	96.8	95.4	-
Belfast	90	91.3	97.8	78.7	-	96.1	94.2	95.5	-
Blunham	88	94.4	94.9	93.6	-	94.5	96.4	96.5	-
Blunham	89	93.4	86.9	97.3	-	94.0	97.8	97.4	-
Blunham	90	-	-	-	-	-	-	-	-
Newcastle	88	84.1	78.4	69.6	-	88.6	86.3	87.8	-
Newcastle	89	94.0	81.5	81.5	-	95.8	94.4	95.1	-
Newcastle	90	90.8	97.9	70.3	-	93.8	95.5	96.1	-
Potton	88	97.4	94.9	84.5	-	94.5	96.3	92.1	-
Potton	89	91.6	94.4	96.6	-	97.8	98.3	96.9	-
Rothamsted	88	79.4	35.5	66.9	56.6	85.5	89.6	94.9	87.0
Rothamsted	89	71.0	83.2	87.2	92.0	91.6	96.1	97.1	83.6
Rothamsted	90	89.7	88.1	82.3		95.1	84.5	91.8	
S. Bonington	88	95.0	73.2	76.3	86.5	72.0	72.7	84.1	80.3
S. Bonington	89	66.5	81.3	89.6	75.4	64.5	79.1	73.0	94.1
S. Bonington	90	95.9	98.4	96.5	96.2	95.0	95.0	97.6	97.1

Table 3.15 Production of total dry weight - Variance ratios

	Phase of Rapid Growth				
	Dry weight at beginning of phase i.e. A	Beginning of phase - Day	End of phase - Day	Duration (days)	Rate of growth $g/m^2/day$
Site	5.29 *	0.31 NS	1.94 NS	0.92 NS	2.58 NS
Year	31.61 ***	20.65 ***	0.58 NS	7.00 **	4.58 *
Site x Year	7.01 ***	11.65 ***	5.12 ***	9.98 ***	4.95 ***
N	0.45 NS	0.42 NS	0.65 NS	0.03 NS	2.13 NS
Site x N	4.07 *	8.38 **	0.70 NS	0.68 NS	4.68 *
Year x N	10.50 *	7.69 **	6.49 **	8.95 ***	10.77 ***
Site x Year x N	0.81 NS	0.59 NS	6.70 ***	4.59 ***	2.30 *

	Proportion of total dry wt. present at beginning of phase of rapid growth	Total dry wt. at anthesis	Proportion of total dry wt. present at anthesis	Dry weight increment during grain-filling
Site	4.23 *	5.92 *	5.34 *	1.42 NS
Year	12.30 ***	24.70 ***	3.31 *	3.25 *
Site x Year	12.20 ***	2.59 ***	1.82 NS	4.29 ***
N	6.71 NS	188.72 **	0.04 NS	9.89 NS
Site x N	3.46 NS	1.79 NS	0.47 NS	0.39 NS
Year x N	6.33 **	1.47 NS	5.91 **	7.02 **
Site x Year x N	1.42 NS	7.58 ***	5.17 ***	4.16 **

Table 3.16 Beginning of phase of rapid growth (Julian day)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	142	136	124	120	95	108	**120**	**121**	**121**
Blunham	110	102	130	118	-	-	**115**	**109**	**112**
Newcastle	115	121	120	117	100	116	**112**	**118**	**115**
Potton	121	117	110	111	-	-	**110**	**113**	**112**
Rothamsted	128	103	115	98	128	121	**124**	**107**	**116**
S. Bonington	131	128	122	115	110	108	**121**	**117**	**119**
Means									
N x years	**124**	**118**	**120**	**113**	**107**	**112**			
Years	**121**		**117**		**109**				
N0	117								
Ns	114								

Standard errors

N	3.4
Site	8.0
Year	1.5
N x site	2.6
N x year	2.1
N x site x year	5.1

Table 3.18 End of phase of rapid growth (Julian day)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	177	169	182	198	197	151	**185**	**173**	**179**
Blunham	155	162	153	178	-	-	**156**	**169**	**163**
Newcastle	221	183	162	186	208	215	**197**	**195**	**196**
Potton	157	162	186	173	-	-	**173**	**167**	**170**
Rothamsted	206	169	199	188	165	157	**190**	**172**	**181**
S. Bonington	150	162	159	156	179	173	**163**	**164**	**163**
Means									
N x years	**178**	**168**	**173**	**180**	**180**	**172**			
Years	**173**		**177**		**176**				
N0	177								
Ns	173								

Standard errors

N	6.5
Site	15.0
Year	3.2
N x site	12.2
N x year	2.9
N x site x year	7.2

Table 3.20 Duration of the phase of rapid growth (days)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	35	35	58	78	102	43	**65**	**52**	**58**
Blunham	46	60	22	59	-	-	**41**	**60**	**51**
Newcastle	106	62	42	68	108	100	**86**	**77**	**81**
Potton	36	45	76	62	-	-	**63**	**54**	**59**
Rothamsted	78	66	84	91	37	36	**66**	**64**	**65**
S. Bonington	20	33	37	41	69	66	**42**	**47**	**44**
Means									
N x years	**53**	**50**	**53**	**67**	**75**	**60**			
Years	**52**		**60**		**67**				
N0	60								
Ns	59								

Standard errors

N	9.3
Site	18.6
Year	3.4
N x site	12.7
N x year	3.8
N x site x year	9.4

Table 3.21 Rate of growth during the rapid phase ($g\ m^{-2}\ day^{-1}$)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	5.2	23.6	10.7	12.7	5.3	20.7	**7.1**	**19.0**	**13.0**
Blunham	10.0	13.4	36.1	15.3	-	-	**22.2**	**14.8**	**18.5**
Newcastle	5.3	12.9	15.3	19.5	5.9	11.4	**8.8**	**14.6**	**11.7**
Potton	6.0	16.1	7.1	12.3	-	-	**5.7**	**14.6**	**10.1**
Rothamsted	5.8	8.7	6.5	10.7	8.2	18.8	**6.8**	**12.8**	**9.8**
S. Bonington	19.3	20.3	21.9	17.9	15.1	17.3	**18.8**	**18.5**	**18.6**
Means									
N x years	**8.6**	**15.8**	**16.3**	**14.7**	**9.8**	**16.5**			
Years	**12.2**		**15.5**		**13.2**				
N0	11.6								
Ns	15.7								

Standard errors

N	2.98
Site	3.81
Year	0.90
N x site	2.90
N x year	1.43
N x site x year	8.97

Table 3.22 Dry weight at beginning of phase of rapid growth (A)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	28.5	86.7	81.9	76.3	22.5	125.1	**44.3**	**96.0**	**70.2**
Blunham	137.5	137.3	148.9	139.3	-	-	**143.3**	**161.8**	**152.6**
Newcastle	69.4	99.6	192.7	210.6	192.1	303.4	**151.4**	**204.5**	**178.0**
Potton	55.2	74.0	86.3	77.5	-	-	**70.9**	**99.3**	**85.1**
Rothamsted	112.8	49.2	213.3	173.3	102.3	134.2	**142.8**	**118.9**	**130.9**
S. Bonington	130.0	151.3	396.8	301.8	296.8	294.4	**274.5**	**249.2**	**261.9**
Means									
N x years	**88.9**	**99.7**	**186.7**	**163.1**	**138.0**	**202.1**			
Years	**94.3**		**174.9**		**170.1**				
N0	137.9								
Ns	155.0								

Standard errors

N	20.23
Site	38.97
Year	10.24
N x site	17.85
N x year	12.43
N x site x year	30.45

Table 3.23 % dry weight present at beginning of the rapid phase of growth

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast		6.7	9.4	4.5	1.5	10.9	**6.6**	**7.4**	**7.0**
Blunham	19.7	10.5	14.5	9.6	-	-	**16.0**	**11.0**	**13.4**
Newcastle	7.3	7.5	22.6	12.7	19.4	18.0	**16.4**	**12.7**	**14.6**
Potton	15.7	5.9	10.6	6.1	-	-	**12.0**	**6.9**	**9.5**
Rothamsted	20.9	6.7	26.4	14.3	24.7	12.6	**24.0**	**11.2**	**17.6**
S. Bonington	23.5	15.3	37.5	29.6	19.1	17.9	**26.7**	**20.9**	**23.8**
Means									
N x years	**16.0**	**8.8**	**20.2**	**12.8**	**14.7**	**13.5**			
Years	**12.4**		**16.5**		**14.1**				
N0	17.0								
Ns	11.7								

Standard errors

N	1.75
Site	3.55
Year	0.75
N x site	2.08
N x year	1.28
N x site x year	9.79

Table 3.24 Total dry weight at anthesis (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	155.8	815.4	653.4	1101.8	529.2	1004.3	**446.1**	**973.8**	**710.0**
Blunham	465.5	825.0	663.6	778.4	-	-	**591.3**	**847.8**	**719.6**
Newcastle	434.0	857.5	651.0	982.9	642.4	834.6	**575.8**	**891.7**	**733.8**
Potton	125.0	469.0	426.6	685.5	-	-	**301.0**	**621.8**	**416.4**
Rothamsted	501.8	349.8	412.6	789.8	255.3	736.1	**389.9**	**625.2**	**507.6**
S. Bonington	535.1	570.3	967.4	950.6	1019.2	1156.5	**840.6**	**892.5**	**866.5**
Means									
N x years	**369.5**	**647.9**	**629.1**	**881.5**	**573.8**	**897.1**			
Years	**508.7**		**755.3**		**735.4**				
N0	524.1								
Ns	808.8								

Standard errors

N	17.94
Site	72.41
Year	31.83
N x site	94.14
N x year	24.17
N x site x year	59.21

Table 3.25 Proportion of total dry weight present at anthesis

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	46.8	62.6	75.9	65.3	59.2	86.0	**60.6**	**71.3**	**66.0**
Blunham	66.0	63.6	64.6	53.6	-	-	**62.3**	**60.7**	**61.5**
Newcastle	49.3	64.4	75.9	59.6	63.1	49.2	**62.8**	**57.7**	**60.3**
Potton	38.7	37.6	52.1	54.8	-	-	**42.3**	**48.2**	**45.2**
Rothamsted	77.2	43.5	54.7	63.0	57.4	69.9	**63.1**	**58.8**	**61.0**
S. Bonington	96.5	56.1	92.3	93.2	65.0	69.5	**84.6**	**72.9**	**78.8**
Means									
N x years	**62.4**	**54.6**	**69.3**	**64.9**	**56.2**	**65.2**			
Years	**58.5**		**67.1**		**60.7**				
N0	62.6								
Ns	61.6								

Standard errors

N	4.44
Site	5.39
Year	2.83
N x site	9.59
N x year	2.98
N x site x year	7.31

Table 3.26 Dry weight increment during grain filling (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	186	494	238	590	375	184	**266**	**423**	**344**
Blunham	216	472	364	674	-	-	**350**	**564**	**457**
Newcastle	454	474	210	686	429	865	**364**	**675**	**520**
Potton	199	778	387	579	-	-	**353**	**670**	**512**
Rothamsted	1	629	377	569	169	318	**182**	**505**	**344**
Sutton	19	422	82	70	565	529	**222**	**341**	**281**
Bonington									
Means									
N x years	**179**	**545**	**277**	**528**	**413**	**516**			
Years	**362**		**402**		**464**				
N0	290								
Ns	530								

Standard errors

N	66.1
Site	96.8
Year	33.0
N x site	117.4
N x year	40.7
N x site x year	99.7

Table 3.27 **Ear dry weight: % variance accounted for by the fitted Gompertz functions**

Site	Year	N01	N0 2	N0 3	N04	NS 1	NS 2	NS 3	NS4
Belfast	88	-	-	-	-	-	-	-	-
Belfast	89	98.3	94.4	96.1	-	96.8	95.4	94.3	-
Belfast	90	92.6	99.4	90.8	-	97.5	97.7	94.3	-
Blunham	88	95.7	96.8	96.5	-	89.1	90.0	95.8	-
Blunham	89	98.2	98.4	99.0	-	95.9	99.5	97.9	-
Blunham	90	-	-	-	-	-	-	-	-
Newcastle	88	77.6	92.6	79.1	-	92.3	81.9	88.4	-
Newcastle	89	93.8	92.4	85.0	-	94.9	95.3	94.2	-
Newcastle	90	90.8	97.9	70.3	-	93.8	95.5	96.1	-
Potton	88	98.0	92.5	82.2	-	92.8	96.8	93.6	-
Potton	89	94.1	96.4	99.5	-	97.7	98.9	98.9	-
Rothamsted	88	75.8	44.8	58.0	56.3	93.2	94.3	93.4	88.6
Rothamsted	89	91.3	95.8	91.8	96.8	96.7	99.0	96.0	95.6
Rothamsted	90	94.9	93.1	91.1		95.5	92.7	88.8	
Sutton Bonington	88	64.4	80.3	98.7	88.5	72.2	95.9	98.3	92.0
Sutton Bonington	89	92.7	94.2	99.2	88.1	98.3	92.9	98.4	94.1
Sutton Bonington	90	94.3	98.6	98.6	97.8	97.9	96.8	98.8	90.1

Table 3.28 Production of ear dry weight - Variance ratios

	Ear dry wt at anthesis (g/m^2)	Final ear dry wt. (g/m^2)	Ear dry wt. increment during grain filling (g/m^2)	Contribution of stored reserves to ear dry weight increment (g/m^2)
Site	6.29 *	6.91 *	15.99 **	2.05 NS
Year	8.99 ***	46.95 ***	33.96 ***	4.94 *
Site x Year	16.94 ***	2.65 *	3.10 *	1.74 NS
N	2.67 NS	36.44 *	66.22 *	0.006 NS
Site x N	5.27 *	1.06 NS	0.73 NS	0.31 NS
Year x N	13.40 ***	26.38 ***	14.83 **	14.02 ***
Site x Year x N	0.41 NS	21.20 ***	32.84 ***	1.13 NS

Table 3.29 Ear dry weight at anthesis (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	72.3	93.5	71.2	108.7	**55.0**	**102.4**	**78.7**
Blunham	21.8	101.6	9.6	5.4	-	-	**19.8**	**51.5**	**35.7**
Newcastle	0	75.2	42.1	65.3	-	-	**13.7**	**68.3**	**41.0**
Potton	4.6	47.1	9.0	11.7	-	-	**10.8**	**27.3**	**19.1**
Rothamsted	0	46.7	63.5	68.4	21.3	29.3	**23.8**	**48.1**	**36.0**
S. Bonington	120.1	155.8	294.1	284.6	-	-	**29.6**	**216.6**	**213.1**
Means									
N x years	**21. 9**	**88.5**	**81.8**	**88.2**	**62.7**	**80.4**			
Years	**55.2**		**85.0**		**71.5**				
N0	55.4								
Ns	85.7								

Standard errors

N	19.72
Site	35.42
Year	5.52
N x site	7.26
N x year	6.46
N x site x year	15.81

Table 3.30 Final ear dry weight (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	520.3	862.5	518.1	633.7	**461.2**	**724.8**	**593.0**
Blunham	410.6	666.0	650.7	844.6	-	-	**528.5**	**722.6**	**625.6**
Newcastle	523.0	757.5	529.9	923.8	-	-	**524.6**	**808.3**	**666.4**
Potton	189.1	626.0	601.1	740.0	-	-	**392.3**	**649.6**	**521.0**
Rothamsted	350.7	724.1	584.9	793.9	310.1	639.8	**415.2**	**719.3**	**567.2**
S. Bonington	200.6	358.0	539.4	585.3	-	-	**369.5**	**440.6**	**405.0**
Means									
N x years	**336.6**	**635.0**	**571.0**	**791.7**	**438.1**	**605.9**			
Years	**485.8**		**681.4**		**522.0**				
N0	448.4								
Ns	677.5								

Standard errors

N	32.32
Site	211.89
Year	20.66
N x site	64.11
N x year	24.24
N x site x year	59.39

Table 3.31 Increment in ear dry weight during grain filling (g/m^2)

	1988		1989		1990		Means		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	448.0	769.0	446.9	525.1	**406.5**	**622.3**	**514.4**
Blunham	388.9	564.4	641.1	839.1	-	-	**508.5**	**671.3**	**589.9**
Newcastle	546.1	682.3	487.8	858.5	-	-	**510.7**	**740.2**	**625.4**
Potton	184.6	578.9	592.1	728.2	-	-	**381.3**	**622.5**	**501.9**
Rothamsted	365.5	677.4	521.4	725.5	288.8	610.4	**391.9**	**671.1**	**531.5**
S. Bonington	80.6	202.2	245.4	300.7	-	-	**159.7**	**224.3**	**191.9**
Means									
N x years	**315.0**	**546.4**	**489.3**	**703.5**	**374.9**	**525.9**			
Years	**430.7**		**596.4**		**450.4**				
N0	393.1								
Ns	591.9								

Standard errors

N	23.47
Site	44.64
Year	17.93
N x site	72.72
N x year	8.97
N x site x year	21.98

Table 3.32 Contribution of stored reserves to ear dry weight (g/m^2)

	1988		1989		1990		Means		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	161	179	59	341	**113**	**189**	**151**
Blunham	173	92	248	166	-	-	**184**	**186**	**185**
Newcastle	315	208	278	172	-	-	**270**	**247**	**259**
Potton	-15	-199	168	149	-	-	**49**	**31**	**40**
Rothamsted	227	77	144	157	163	292	**178**	**175**	**177**
S. Bonington	88	-166	163	266	-	-	**100**	**108**	**104**
Means									
N x years	**151**	**10**	**194**	**181**	**102**	**277**			
Years	**81**		**187**		**190**				
N0	149								
Ns	156								

Standard errors

N	88.2
Site	60.4
Year	32.4
N x site	52.1
N x year	34.7
N x site x year	84.9

Table 3.33 Nitrogen content: Variance ratios

	Total N content (g/m²)				% Final total N content in the crop at:		
	Harvest	ZGS 31	N Application	Anthesis	ZGS 31	N Application	Anthesis
Site	1.78 NS	0.89 NS	11.72 NS	3.43 NS	1.12 NS	4.49 NS	3.95 *
Year	129.45 ***	68.19 ***	26.12 ***	43.24 ***	4.80 *	1.83 NS	11.16 ***
Site x Year	18.34 ***	17.27 ***	15.52 ***	14.30 ***	4.26 **	11.40 **	2.44 *
N	1024.29 ***	8.28 NS	0.003 NS	160.49 **	0.37 NS	67.71 *	59.32 *
Site x N	0.64 NS	1.44 NS	0.19 NS	1.29 NS	1.23 NS	0.53 NS	2.08 NS
Year x N	0.48 NS	90.19 ***	13.54 ***	4.82 *	60.44 ***	2.23 NS	0.62 NS
Site x Year x N	5.05 ***	20.21 ***	17.52 ***	3.71 **	10.89 ***	5.39 *	2.09 NS

	Increment in total N content ZGS31-anthesis	% total N taken up ZGS31 - anthesis	Increment in total N content N application - anthesis	Increment in total N during grain filling	% total N taken up or lost during grain filling
Site	1.28 NS	0.92 NS	0.52 NS	0.94 NS	3.21 NS
Year	26.58 ***	35.36 ***	0.81 NS	30.63 ***	11.16 ***
Site x Year	3.96 *	4.41 **	8.96 **	5.78 ***	2.44 *
N	4.76 NS	1.78 NS	22.91 *	7.49 NS	59.32 *
Site x N	10.00 *	1.29 NS	14.63 NS	1.27 NS	2.08 NS
Year x N	54.94 ***	31.45 ***	55.78 ***	0.37 NS	0.62 NS
Site x Year x N	0.93 NS	2.02 NS	0.57 NS	1.92 NS	2.09 NS

Table 3.34 Total N content at harvest (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	2.78	7.77	8.08	14.30	9.60	11.77	**6.82**	**11.28**	**9.05**
Blunham	6.07	12.60	10.07	15.53	-	-	**9.29**	**15.12**	**12.20**
Newcastle	6.00	9.93	8.23	18.37	-	-	**8.34**	**15.20**	**11.77**
Potton	2.49	12.55	6.00	11.73	-	-	**5.46**	**13.19**	**9.32**
Rothamsted	3.44	8.92	8.36	13.77	4.23	10.10	**5.35**	**10.93**	**8.14**
S. Bonington	3.99	10.53	11.88	14.69	18.05	23.76	**11.09**	**16.27**	**13.68**
Means									
N x years	**4.13**	**10.38**	**8.77**	**14.73**	**10.27**	**15.88**			
Years	**7.26**		**11.75**		**13.08**				
N0	7.72								
Ns	13.67								

Standard errors

N	0.166
Site	1.875
Year	0.310
N x Site	1.204
N x Year	0.379
N x Site x Year	0.929

Table 3.35 Total N content at ZGS 30/31 (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	1.11	3.93	2.77	8.92	4.35	10.48	**2.74**	**7.78**	**5.26**
Blunham	3.13	5.30	3.73	7.43	-	-	**3.57**	**6.56**	**5.07**
Newcastle	2.47	2.47	-	-	-	-	**3.16**	**4.90**	**4.08**
Potton	0.85	1.55	2.57	4.63	-	-	**1.83**	**3.27**	**2.55**
Rothamsted	2.01	1.91	4.07	11.94	1.58	4.23	**2.55**	**6.03**	**4.29**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**1.95**	**3.06**	**3.33**	**7.99**	**3.02**	**6.10**			
Years	**2.51**		**5.66**		**4.56**				
N0	2.76								
Ns	5.72								

Standard errors

N	1.072
Site	1.315
Year	0.245
N x Site	0.972
N x Year	0.167
N x Site x Year	0.374

Table 3.36 Proportion of final total N content in the crop at ZGS 30/31 (%)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	40.7	51.4	37.1	62.7	48.1	94.8	**42.0**	**69.6**	**55.8**
Blunham	51.1	41.7	37.1	48.3	-	-	**43.0**	**49.5**	**46.2**
Newcastle	41.1	25.4	-	-	-	-	**37.7**	**44.3**	**41.0**
Potton	34.3	12.4	42.5	39.4	-	-	**37.2**	**30.3**	**33.7**
Rothamsted	63.3	21.5	49.2	87.6	38.2	41.9	**50.2**	**50.3**	**50.3**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**46.3**	**30.6**	40.4	**58.4**	**39.4**	**57.4**			
Years	**38.5**		**49.4**		**48.4**				
N0	42.0								
Ns	48.8								

Standard errors

N	11.72
Site	9.27
Year	3.48
N x Site	9.53
N x Year	2.24
N x Site x Year	5.00

Table 3.37 Total N content at N application (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	0.73	0.84	1.79	2.50	-	-	**1.03**	**1.43**	**1.23**
Blunham	3.13	5.30	4.17	3.30	-	-	**3.42**	**4.07**	**3.75**
Newcastle	2.47	2.47	-	-	-	-	**3.26**	**2.60**	**2.92**
Potton	0.85	1.55	2.53	1.73	-	-	**1.46**	**1.41**	**1.43**
Rothamsted	-	-	-	-	1.68	1.68	**2.17**	**2.18**	**2.18**
S. Bonington	-	-	9.18	8.33	-	-	**7.73**	**7.52**	**7.62**
Means									
N x years	**2.62**	**3.30**	**4.22**	**3.60**	**2.69**	**2.70**			
Years	**2.96**		**3.91**		**2.70**				
N0	3.18								
Ns	3.20								

Standard errors

N	0.436
Site	0.801
Year	0.144
N x Site	0.860
N x Year	0.145
N x Site x Year	0.356

Table 3.38 Proportion of final total N present in the crop at N application (%)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	27.2	3.6	24.4	17.4	-	-	**23.6**	**10.5**	**17.0**
Blunham	51.1	41.7	41.4	21.2	-	-	**44.1**	**31.5**	**37.8**
Newcastle	41.1	25.4	-	-	-	-	**41.0**	**27.3**	**34.2**
Potton	34.3	12.4	42.4	14.8	-	-	**36.1**	**13.6**	**24.8**
Rothamsted	-	-	-	-	39.6	16.6	**44.0**	**16.6**	**30.3**
S. Bonington	-	-	78.9	57.3	-	-	**72.9**	**53.6**	**63.2**
Means									
N x years	**45.3**	**25.0**	**46.4**	**26.1**	**39.0**	**25.3**			
Years	**35.2**		**36.3**		**32.2**				
N0	43.6								
Ns	25.5								

Standard errors

N	2.54
Site	8.63
Year	1.81
N x Site	6.84
N x Year	2.08
N x Site x Year	5.10

Table 3.39 Total N content at anthesis (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	1.80	8.80	5.29	11.32	4.45	11.02	**3.85**	**10.38**	**7.11**
Blunham	3.57	14.57	4.43	10.87	-	-	**4.43**	**12.65**	**8.54**
Newcastle	4.60	10.50	9.07	19.36	-	-	**7.28**	**14.88**	**11.08**
Potton	1.56	9.60	3.43	8.90	-	-	**2.91**	**9.16**	**6.03**
Rothamsted	2.88	9.42	5.03	12.65	3.20	8.00	**3.70**	**10.03**	**6.87**
S. Bonington	4.64	10.29	10.66	15.60	10.97	15.01	**8.90**	**13.45**	**11.17**
Means									
N x years	**3.17**	**10.53**	**6.32**	**13.12**	**6.03**	**11.63**			
Years	**6.85**		**9.72**		**8.83**				
N0	5.18								
Ns	11.76								

Standard errors

N	0.465
Site	1.378
Year	0.258
N x Site	0.912
N x Year	0.335
N x Site x Year	0.820

Table 3.40 Proportion of final total N content present in the crop at anthesis (%)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	64.6	115.3	71.0	79.4	46.8	100.1	**60.8**	**98.3**	**79.5**
Blunham	59.6	115.3	44.5	70.6	-	-	**46.5**	**87.8**	**67.1**
Newcastle	76.9	104.9	114.6	112.5	-	-	**90.4**	**103.7**	**97.1**
Potton	62.9	76.5	57.7	75.9	-	-	**54.7**	**71.0**	**62.8**
Rothamsted	96.4	111.2	68.1	91.8	76.9	79.2	**80.5**	**94.1**	**87.3**
S. Bonington	117.1	97.3	92.2	108.0	63.7	65.7	**92.6**	**89.4**	**91.0**
Means									
N x years	**79.6**	**103.4**	**74.7**	**89.7**	**58.5**	**79.0**			
Years	**91.5**		**82.2**		**68.7**				
N0	70.9								
Ns	90.7								

Standard errors

N	2.31
Site	8.75
Year	3.96
N x Site	9.45
N x Year	4.62
N x Site x Year	11.32

Table 3.41 Increment in total N content from ZGS 31 to anthesis (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	0.69	4.87	2.53	2.40	0.10	0.54	**1.10**	**2.60**	**1.85**
Blunham	0.43	9.27	0.70	3.43	-	-	**0.49**	**5.83**	**3.16**
Newcastle	2.13	8.03	-	-	-	-	**2.33**	**5.12**	**3.72**
Potton	0.71	8.04	0.87	4.27	-	-	**0.71**	**5.63**	**3.17**
Rothamsted	0.88	7.52	0.97	0.72	1.62	3.77	**1.15**	**4.00**	**2.58**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**0.95**	**7.52**	**1.57**	**2.83**	**0.97**	**3.57**			
Years	**4.23**		**2.20**		**2.27**				
N0	1.16								
Ns	4.64								

Standard errors

N	1.665
Site	0.727
Year	0.283
N x Site	0.415
N x Year	0.333
N x Site x Year	0.745

Table 3.42 Proportion of total N taken up ZGS 30/31 to anthesis (%)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	23.9	64.0	33.9	16.6	-1.3	5.3	**18.8**	**28.6**	**23.7**
Blunham	8.5	73.6	7.4	22.3	-	-	**6.7**	**42.2**	**24.5**
Newcastle	35.8	79.5	-	-	-	-	**33.0**	**48.1**	**40.6**
Potton	28.6	64.1	15.2	36.6	-	-	**20.7**	**144.7**	**32.7**
Rothamsted	33.1	89.8	18.9	4.2	38.7	37.3	**30.2**	**43.7**	**37.0**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**25.7**	**74.0**	**21.9**	**21.9**	**18.5**	**29.0**			
Years	**49.8**		**21.9**		**23.8**				
N0	22.0								
Ns	41.6								

Standard errors

N	15.33
Site	9.01
Year	3.32
N x Site	21.98
N x Year	4.06
N x Site x Year	9.07

Table 3.43 Increment in total N content between N application and anthesis (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	1.07	8.47	3.51	8.82	-	-	**2.77**	**8.01**	**5.39**
Blunham	0.43	9.27	0.27	7.57	-	-	**0.82**	**7.77**	**4.30**
Newcastle	2.13	8.03	-	-	-	-	**2.91**	**6.93**	**4.92**
Potton	0.71	8.04	0.90	7.17	-	-	**1.28**	**6.96**	**4.12**
Rothamsted	-	-	-	-	1.52	6.32	**0.63**	**7.65**	**4.14**
S. Bonington	-	-	1.48	7.28	-	-	**1.65**	**7.11**	**4.38**
Means									
N x years	**0.83**	**8.45**	**1.58**	**7.64**	**2.61**	**6.13**			
Years	**4.64**		**4.61**		**4.37**				
N0	1.68								
Ns	7.41								

Standard errors

N	1.382
Site	0.813
Year	0.192
N x Site	0.242
N x Year	0.214
N x Site x Year	0.555

Table 3.44 Increment in total N content during grain filling (g/m^2)

	1988		1989		1990		**Means**		
	NO	Ns	NO	Ns	NO	Ns	**NO**	**Ns**	**Site**
Belfast	0.98	-0.70	2.78	2.98	5.16	0.75	**2.97**	**1.01**	**1.99**
Blunham	2.50	-1.97	5.63	4.67	-	-	**4.91**	**2.38**	**3.64**
Newcastle	1.40	-0.57	-0.83	-0.43	-	-	**1.12**	**0.52**	**0.82**
Potton	0.93	2.96	2.57	2.83	-	-	**2.59**	**3.92**	**3.26**
Rothamsted	0.56	-0.51	2.37	1.12	1.03	2.10	**1.32**	**0.90**	**1.11**
S. Bonington	-0.64	0.24	1.22	-0.91	7.07	8.03	**2.19**	**2.61**	**2.40**
Means									
N x years	**0.95**	**-0.09**	**2.29**	**1.71**	**4.31**	**4.06**			
Years	**0.43**		**2.00**		**4.18**				
NO	2.52								
Ns	1.89								

Standard errors

N	0.205
Site	1.737
Year	0.393
N x Site	1.043
N x Year	0.532
N x Site x Year	1.303

Table 3.45 Proportion of the total N content taken up or lost during grain filling (g/m^2)

	1988		1989		1990		**Means**		
	NO	Ns	NO	Ns	NO	Ns	**NO**	**Ns**	**Site**
Belfast	35.4	-15.3	29.0	20.6	53.2	-0.1	**39.2**	**1.7**	**20.5**
Blunham	40.4	-15.3	55.5	29.4	-	-	**53.5**	**12.2**	**32.9**
Newcastle	23.1	-4.9	-14.6	-12.5	-	-	**19.6**	**-3.7**	**2.9**
Potton	37.1	23.5	42.3	24.1	-	-	**45.3**	**29.0**	**37.2**
Rothamsted	3.6	-11.2	31.9	8.2	23.1	20.8	**19.5**	**5.9**	**12.7**
S. Bonington	-17.1	2.7	7.8	-8.0	31.6	37.0	**7.4**	**10.6**	**9.0**
Means									
N x years	**20.4**	**-3.4**	**25.3**	**10.3**	**41.5**	**21.0**			
Years		**8.5**			**17.8**		**31.3**		
NO	29.1								
Ns	9.3								

Standard errors

N	2.31
Site	8.75
Year	3.96
N x Site	9.45
N x Year	4.62
N x Site x Year	11.32

Table 3.46 Ear N content (g/m^2): Variance ratios

	Final	Anthesis	Increment in ear N content during grain filling	Contribution from pre-anthesis N uptake to ear N content
Site	0.68 NS	6.07 NS	0.36 NS	0.16 NS
Year	96.80 ***	92.39 ***	112.86 ***	1.05 NS
Site x Year	29.19 ***	10.66 ***	32.49 ***	5.12 **
N	2819.80 ***	126.09 **	976.4 ** (nearly ***)	117.32 **
Site x N	2.35 NS	5.26 *	1.16 NS	1.28 NS
Year x N	0.15 NS	3.59 **	0.20 NS	1.84 NS
Site x Year x N	2.48 **	4.01 **	2.31 NS	1.66 NS

Table 3.47 Ear N content at harvest (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	7.04	11.55	7.48	8.50	**6.01**	**8.86**	**7.43**
Blunham	5.07	9.37	9.17	13.27	-	-	**7.81**	**11.97**	**9.89**
Newcastle	6.06	9.39	-	-	5.87	9.67	**6.52**	**10.04**	**8.28**
Potton	2.08	10.09	5.32	10.41	-	-	**4.38**	**10.89**	**7.64**
Rothamsted	2.89	7.17	7.46	12.11	3.62	9.85	**4.66**	**9.71**	**7.18**
S. Bonington	2.70	7.40	7.58	11.87	14.63	19.27	**8.13**	**12.68**	**10.41**
Means									
N x years	**3.72**	**8.33**	**7.37**	**11.71**	**7.67**	**12.04**			
Years	**6.02**		**9.54**		**9.85**				
N0	6.25								
Ns	10.69								

Standard errors

N	0.078
Site	1.908
Year	0.250
N x Site	0.680
N x Year	0.305
N x Site x Year	0.748

Table 3.48 N content of ears at anthesis (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	1.21	1.90	0.81	1.40	**0.64**	**1.20**	**0.93**
Blunham	1.03	2.40	2.07	2.82	-	-	**1.52**	**2.58**	**2.05**
Newcastle	-	-	2.60	4.83	-	-	**1.83**	**3.89**	**2.86**
Potton	-	-	-	-	-	-	-	-	-
Rothamsted	0.36	0.79	1.31	2.46	0.92	1.46	**0.87**	**1.57**	**1.22**
S. Bonington	1.20	1.83	4.00	5.57	2.49	3.82	**2.56**	**3.74**	**3.15**
Means									
N x years	**0.74**	**1.68**	**2.23**	**3.51**	**1.50**	**2.61**			
Years	**1.21**		**2.87**		**2.06**				
N0	1.49								
Ns	2.60								

Standard errors

N	0.103
Site	0.459
Year	0.109
N x Site	0.210
N x Year	0.081
N x Site x Year	0.033

Table 3.49 Increment in ear N content during grain filling (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	5.83	9.64	6.66	7.10	**5.06**	**7.16**	**6.11**
Blunham	4.03	6.97	7.10	10.85	6.67	4.19	**6.56**	**9.83**	**8.20**
Newcastle	-	-	-	-	-	-	-	-	-
Potton	-	-	-	-	-	-	-	-	-
Rothamsted	2.53	6.38	5.96	9.65	2.70	8.39	**3.73**	**8.14**	**5.93**
S. Bonington	1.50	5.58	3.58	6.30	11.64	14.96	**5.58**	**8.95**	**7.26**
Means									
N x years	**2.74**	**5.96**	**5.62**	**9.11**	**7.35**	**10.49**			
Years	**4.35**		**7.37**		**8.91**				
N0	5.23								
Ns	8.52								

Standard errors

N	0.111
Site	2.037
Year	0.309
N x Site	0.715
N x Year	0.407
N x Site x Year	0.814

Table 3.50 Contribution from pre-anthesis N uptake to ear N content (g/m^2)

	1988		1989		1990		**Means**		
	N0	Ns	N0	Ns	N0	Ns	**N0**	**Ns**	**Site**
Belfast	-	-	3.05	6.66	1.51	6.35	**1.97**	**6.56**	**4.26**
Blunham	1.53	8.93	1.46	5.82	-	-	**1.68**	**7.21**	**4.44**
Newcastle	-	-	-	-	-	-	-	-	-
Potton	-	-	-	-	-	-	-	-	-
Rothamsted	1.97	6.89	3.60	8.53	1.66	6.29	**2.41**	**7.24**	**4.82**
S. Bonington	2.15	5.34	2.36	7.21	5.64	6.46	**3.38**	**6.34**	**4.86**
Means									
N x years	**1.77**	**6.98**	**2.63**	**7.06**	**2.72**	**6.50**			
Years	**4.38**		**4.84**		**4.61**				
N0	2.37								
Ns	6.85								

Standard errors

N	0.453
Site	0.844
Year	0.323
N x Site	0.785
N x Year	0.528
N x Site x Year	1.056

Table 3.51 Shoot Number - Variance ratios

	Shoot number at: N application	Anthesis	Maximum shoot number	Date of maximum shoot number	Final shoot number	Shoot productivity	Shoot survival
Site	1.58 NS	4.04 *	3.36 NS	3.76 *	7.34 **	0.24 NS	1.29 NS
Year	58.50 ***	21.79 ***	38.20 ***	16.85 ***	125.63 ***	31.28 ***	1.34 NS
Site x Year	8.50 ***	8.44 ***	6.78 ***	22.05 ***	15.40 ***	9.86 ***	18.89 ***
N	0.09 NS	43.06 *	6.24 NS	3.38 NS	63.10 *	70.45 *	138.95 **
Site x N	4.59 *	0.30 NS	2.43 NS	0.60 NS	0.33 NS	2.17 NS	1.80 NS
Year x N	5.29 **	4.23 *	8.24 ***	18.97 ***	10.95 ***	0.39 NS	1.07 NS
Site x Year x N	1.25 NS	2.55 *	2.19 NS	13.39 ***	9.08 ***	7.67 ***	0.96 NS

	Dry wt. per shoot at anthesis	N content per shoot at anthesis
Site	10.02 **	2.46 NS
Year	3.25 NS	3.24 NS
Site x Year	3.65 *	26.42 ***
N	0.40 NS	647.58 **
Site x N	1.49 NS	0.16 NS
Year x N	26.53 ***	0.50 NS
Site x Year x N	19.19 ***	17.62 ***

Table 3.52 Shoot number per m^2 at N application

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	671	626	1306	1238	-	-	**1085**	**981**	**1033**
Blunham	1147	1201	1350	1240	1782	1673	**1427**	**1371**	**1399**
Newcastle	929	929	1012	958	1452	1528	**1131**	**1138**	**1135**
Potton	1032	1192	-	-	-	-	**1364**	**1398**	**1381**
Rothamsted	509	885	1474	1646	1104	1127	**1029**	**1219**	**1124**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**858**	**967**	**1320**	**1302**	**1443**	**1396**			
Years	**912**		**1311**		**1419**				
No	**1207**								
Ns	**1222**								

Standard errors

N	43.9
Site	151.7
Year	40.3
N x site	42.8
N x year	29.6
N x site x year	66.1

Table 3.53 Shoot number per m^2 at anthesis

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	482	1072	573	646	487	858	**514**	**844**	**679**
Blunham	764	1046	809	1104	-	-	**776**	**1071**	**923**
Newcastle	408	672	943	1120	645	858	**665**	**883**	**774**
Potton	665	1092	1259	1415	-	-	**952**	**1251**	**1101**
Rothamsted	390	631	631	947	557	841	**526**	**806**	**666**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**542**	**893**	**843**	**1047**	**675**	**973**			
Years	**718**		**945**		**824**				
No	**687**								
Ns	**971**								

Standard errors

N	38.0
Site	105.5
Year	28.1
N x site	61.4
N x year	29.8
N x site x year	66.6

Table 3.54 Maximum shoot number per m^2

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	715	1156	1306	1383	885	1081	**968**	**1207**	**1088**
Blunham	1256	1336	1553	1565	1782	1750	**1531**	**1550**	**1540**
Newcastle	936	962	1200	1262	1452	1528	**1196**	**1251**	**1223**
Potton	1051	1526	1536	1596	-	-	**1340**	**1584**	**1462**
Rothamsted	887	1156	1474	1646	1104	1148	**1155**	**1316**	**1235**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**969**	**1227**	**1414**	**1490**	**1331**	**1427**			
Years	**1098**		**1452**		**1379**				
No	**1238**								
Ns	**1382**								

Standard errors

N	
N	48.6
Site	117.3
Year	34.9
N x site	54.1
N x year	28.3
N x site x year	63.3

Table 3.55 Date of maximum shoot number (Julian day)

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	107	154	87	120	195	148	**129**	**141**	**135**
Blunham	74	74	76	90	77	100	**76**	**88**	**82**
Newcastle	90	102	99	118	85	85	**91**	**102**	**97**
Potton	74	102	58	114	-	-	**74**	**108**	**91**
Rothamsted	93	106	94	94	98	98	**95**	**99**	**97**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**87**	**107**	**83**	**107**	**109**	**108**			
Years	**97**		**95**		**108**				
No	**93**								
Ns	**107**								

Standard errors

N	6.6
Site	12.2
Year	2.0
N x site	12.1
N x year	2.6
N x site x year	5.7

Table 3.56 Final shoot number per m^2 (mean shoot number during grain filling)

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	443	932	594	772	666	881	**567**	**862**	**715**
Blunham	560	923	1008	1253	809	1076	**793**	**1084**	**938**
Newcastle	582	730	801	1042	695	937	**693**	**903**	**798**
Potton	526	1018	1084	1256	-	-	**814**	**1134**	**974**
Rothamsted	372	621	564	899	427	680	**454**	**733**	**594**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**497**	**845**	**810**	**1044**	**685**	**940**			
Years	**671**		**927**		**813**				
No	**664**								
Ns	**943**								

Standard errors

N	29.7
Site	67.1
Year	12.1
N x site	58.4
N x year	13.7
N x site x year	33.6

Table 3.57 Shoot productivity (%)

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	7.9	87.2	0.0	14.4	-	-	**-7.3**	**34.2**	**13.4**
Blunham	9.6	11.2	16.8	28.1	0.0	4.7	**8.8**	**14.6**	**11.7**
Newcastle	0.7	4.0	18.6	34.9	0.0	0.0	**6.4**	**13.0**	**9.7**
Potton	1.6	30.0	-	-	-	-	**-4.2**	**12.5**	**4.1**
Rothamsted	78.2	36.4	0.0	0.0	0.0	1.9	**26.1**	**12.8**	**19.4**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**19.6**	**33.7**	**8.2**	**17.8**	**-10.0**	**0.7**			
Years	**26.7**		**13.0**		**-4.7**				
No	**5.9**								
Ns	**17.4**								

Standard errors

N	1.25
Site	13.17
Year	3.25
N x site	11.10
N x year	3.11
N x site x year	6.95

Table 3.58 Shoot survival (%)

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	63.3	81.0	46.0	55.7	75.3	82.3	**61.6**	**73.0**	**67.3**
Blunham	45.0	69.3	65.3	80.3	55.4	74.6	**55.3**	**74.8**	**65.0**
Newcastle	62.7	75.6	67.0	82.7	47.7	61.7	**59.1**	**73.3**	**66.2**
Potton	50.7	66.7	72.0	79.0	-	-	**61.4**	**72.8**	**67.1**
Rothamsted	42.5	56.5	39.0	55.3	39.0	59.7	**40.2**	**57.1**	**48.7**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**52.8**	**69.8**	**57.9**	**70.6**	**55.8**	**70.2**			
Years	**61.3**		**64.2**		**63.0**				
No	**55.5**								
Ns	**70.2**								

Standard errors

N	1.05
Site	8.12
Year	1.45
N x site	2.16
N x year	1.70
N x site x year	3.81

Table 3.59 Dry weight per shoot (g) at anthesis

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	0.314	1.218	0.700	0.990	0.825	1.177	**0.613**	**1.128**	**0.871**
Blunham	1.000	1.225	1.160	0.857	-	-	**1.157**	**1.013**	**1.085**
Newcastle	1.063	0.856	1.143	1.602	1.238	0.978	**1.148**	**1.145**	**1.147**
Potton	0.169	0.449	0.524	0.621	-	-	**0.423**	**0.507**	**0.465**
Rothamsted	0.764	0.478	0.335	0.591	0.780	0.450	**0.626**	**0.506**	**0.566**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**0.662**	**0.846**	**0.773**	**0.932**	**0.946**	**0.803**			
Years	**0.754**		**0.852**		**0.874**				
No	**0.794**								
Ns	**0.860**								

Standard errors

N	0.0972
Site	0.1109
Year	0.0449
N x site	0.1786
N x year	0.0316
N x site x year	0.0706

Table 3.60 N content per shoot (mg) at anthesis

	1988		1989		1990		**Means**		
	No	Ns	No	Ns	No	Ns	**No**	**Ns**	**Site**
Belfast	5.00	13.05	5.60	10.16	6.89	12.97	**5.83**	**12.06**	**8.94**
Blunham	8.77	21.57	7.78	11.97	-	-	**8.51**	**16.71**	**12.61**
Newcastle	10.06	10.46	16.01	31.30	13.84	20.79	**13.31**	**20.85**	**17.08**
Potton	2.13	9.20	4.21	8.08	-	-	**3.36**	**8.53**	**5.95**
Rothamsted	4.79	9.81	4.02	9.22	5.01	9.22	**4.61**	**9.42**	**7.01**
S. Bonington	-	-	-	-	-	-	-	-	-
Means									
N x years	**6.15**	**12.81**	**7.51**	**14.12**	**7.67**	**13.55**			
Years	**9.48**		**10.82**		**10.61**				
No	**7.11**								
Ns	**13.49**								

Standard errors

N	0.233
Site	0.652
Year	0.505
N x site	2.977
N x year	0.549
N x site x year	1.229