HGCA

PROJECT REPORT No. 94

ANALYSIS AND MODELLING OF THE EFFECTS OF NITROGEN ON THE GROWTH, PARTITIONING AND QUALITY OF MALTING BARLEY

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ANALYSIS AND MODELLING OF THE EFFECTS OF NITROGEN ON THE GROWTH, PARTITIONING AND QUALITY OF MALTING BARLEY

by

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The work was also supported by the Scottish Office Agriculture and Fisheries Department.

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All numbered tables in Appendix A2 are numbered by the Results Section they relate to.

ABBREVIATIONS

cv.	Cultivar.
df	Degrees of freedom used in statistical analyses to assess significance tests.
DW	Dry weight.
ha	Hectare.
High N	High nitrogen treatment.
HWE	Hot Water Extract units are litre degrees per kilogram of malt (previously Imperial Units were Brewer's lbs per quarter).
kg	Kilogram.
LAI	Leaf area index – the total area of leaf lamina per unit area of ground. LAI = 3 implies a fully closed canopy in cereal crop.
Low N	Low nitrogen treatment.
m	Metre.
MS	Mean Square derived during the analysis of variance and used in the assessment of variability of an experimental factor.
MS	Main stem.
N	Nitrogen.
NRB	Plant dry weight after removal of the roots and ear.
PTX	Polythene tunnel experiment.
VNT	Variety by nitrogen trial.
NS	In statistical analyses – not significant.
RGR	Relative growth rate – the instantaneous growth rate of a plant divided by the weight of the plant organ etc.
se	Standard error of the mean.

SOLX	Solution culture experiment.
SR	Sowing rate experiment.
TCW	Thousand Corn Weight.
Tc, T1–T4	Tillers, coleoptile and tillers 1–4.

SUMMARY

A considerable amount of effort, thought and synthesis of ideas has gone into preparing this final report. In light of the failure of simulation models to provide an adequate explanation of the effect of sub–optimal supplies of nitrogen on crop growth extra time was taken, in agreement with HGCA, to develop a new approach. Funding in this particular phase of the work was supplied completely from cognate research objectives funded by the Scottish Office Agriculture and Fisheries Department.

Crop modelling aims to examine the complex processes that occur in growing crops. A successful model promotes understanding and can lead to the development of a basic set of rules that aid the farmer and agronomist in the management of crops. By the same argument a model can also indicate how breeders might manipulate genetic control of growth rate and duration to maximise partioning of dry matter to useful yield and quality.

The grower of malting barley faces the most critical crop management situation of UK cereal growers. The maltster wishes to use plump grain with low nitrogen content as these samples give the best extracts. In barley, as in wheat, the growing plant responds to application of nitrogen top–dressings by the proliferation of lateral stems or tillers. It is possible to demonstrate that any reasonable increase in top–dressing levels will produce an economic return for the wheat farmer. The situation for the malting barley grower is not so clear cut. If perceived environmental problems related to nitrogen contamination of ground water and the routine use of fungicides and herbicides are ignored then two main considerations arise. Firstly simple physical constraints ensure that higher yield is coupled with smaller grain size for any particular cultivar. Secondly, nitrogen application effectively prolongs the period over which the crop actively grows. This can lead to higher nitrogen content and dormancy levels in the harvested grain. Successful crop management depends on an understanding of how the processes that occur in plant development and growth are integrated over the crop's history.

Choice of cultivar is one of the main management tools for growers and maltsters. It has been well understood that erectoid cultivars such as cv. Golden Promise, the choice where early maturity is critical, can suffer from greater stress when droughted. By comparison more modern, large grained cultivars are more widely adapted to natural conditions. Higher yield will still be associated with increases in the level of grain nitrogen but, because they were bred under modern farming conditions, modern cultivars such as cvs Triumph and Prisma show more rapid breakdown of grain protein during malting. While higher enzyme activity may compensate to an extent for higher grain nitrogen and allow the maltster to produce good quality lager or whisky malt, high starch content still equates with extract and profitability.

In this project we have studied the interaction of nitrogen uptake and carbon assimilation in relation to its effects on partitioning, development and variations in yield and characteristics of grain quality. Experiments were carried out using controlled nutrient environments. These experiments have been compared with specially grown field trials to ensure general validity. If a crop is grown without water stress or diseases it is possible to measure the parameters of growth and manipulate growth without complicating factors. Soil is a very complex system which is still not well understood. It is possible to detect, particularly in breeders' small plot trials – but also in farmers' fields where precise measurements are made, large variation in crop growth and yield over very short distances.

While the design of field trials and analysis of trial data has been developed to a sophisticated state, allowing estimates of yield to be made even of cultivars which are not grown in all years, it is still desirable to use a controlled environment to derive the basic parameters of a crop model.

The initial phase of work in the project consisted of growing field trials and experimenting with possible controlled nutrient systems. After a year of experimentation, a perlite bed system, protected by a polythene tunnel and with trickle irrigation, was adopted (PTX). A spring barley variety (cultivar) by nitrogen trial (VNT) indicated that while the lowest level of top dressing resulted in lower yield it also

resulted in the harvest of more nitrogen than applied to the crop. The impact of restricted nitrogen uptake on nitrogen productivity was explored in the PTX. Sieving fractions of the grain from the VNT lead to an hypothesis that nitrogen content of grain was dependent on grain position of the ear and ear position in the developmental hierarchy. This hypothesis was tested and elaborated with novel effects found on germination rate in the PTX. At the whole plant level differences between cultivars were found in the magnitude of changes of nitrogen concentration of the grain (or ear) in response to reductions in nitrogen supply. Within the plant, nitrogen concentration of grains was found to change with position on the ear, highest concentrations being found near the top of the ear. This effect was most pronounced in the main-stem, present in tiller T1 and not detectable in T3. Grain size, as in previous studies, varied with stem type, grain position and nitrogen uptake. Greatest variation was experienced in later tillers that experience most competition for resources. In contrast, grain borne on main-stem ears showed little variation in response to nitrogen uptake. Grain size is known to affect germination rate. However, an equally important and previously unknown effect is the variation in germination rate with grain position on the ear. This was present in all stem types and nitrogen treatments. A systematic increase in the time to germinate as one moves from the base of the ear to the top was found in all ears. The scale of this change differed between the two cultivars tested.

The development and growth of crops in the PTX was carefully followed. The major effect of nitrogen was on total dry matter production which was manifest in the total amount of dry weight present in the tillers. Once inside either tiller or main-stem the proportions partitioned to tissue types (leaves, stems and ears) was unaffected by nitrogen. Tiller development lagged that on the main-stem (partitioning to the ears was later and nitrogen concentration in leaf and stem tissues on tillers greater). Effects on partitioning of nitrogen were similar. The main contrast being the much greater proportions of nitrogen residing in the leaves. Hence, during grain growth the leaves were the main tissue source for nitrogen and stems the main source for carbon. These data allowed the development of a mechanistic model for nitrogen limited growth in barley.

Attempts were made to base the interpretation of nitrogen uptake and carbon assimilation interactions on the use of existing simulation models of cereal growth and one under development specifically for barley. The CERES model for wheat, produced in the USA under the IBSNAT programme, was first explored in a parallel project. It was found to be unsatisfactory for our purposes. We then developed a simulation model based on the models of Keulen & Seligman (1987) for spring wheat and the AFRC winter wheat model. Sensitivities to empirical functions of partitioning and critical nitrogen concentrations at the whole plant level convinced us that an entirely new approach was required based on mechanisms operating at the cellular level. The mechanism chosen was that nitrogen concentration of the photosynthetic system is proportional to the light intensity incident on the tissue. The nitrogen content of the non-reproductive biomass (leaf plus stem tissue) was shown to be the main driving force for carbon assimilation. Early uptake of nitrogen is critical for attaining high growth rates. The history of nitrogen uptake determines the nitrogen productivity of a crop.

1.0 OBJECTIVES

The aim of the project is to develop a mathematical model to describe the interactions between dry matter production and nitrogen uptake in barley. This can then be used to examine grain yield and quality in a quantitative way and to predict the effects of solar radiation, temperature and nitrogen uptake on malting quality.

The barley model simulates the distribution of carbon and nitrogen in the plant, under the assumption that water is not limiting and the uptake of nitrogen is prescribed. Particular emphasis is placed on the processes of tillering, tiller survival and grain development to complement the experimental observations of potential differences in malting quality between grain born on main-stems and tillers.

The main thrust of this project was to concentrate on the interaction between the patterns of nitrogen supply and carbon assimilation. Nitrogen can influence malting quality in three ways; a simple dilution effect (more protein and less starch), grain size (variation in germination rate), and variation in maturity of grains within plant (tiller hierarchy). The objectives of the model are to predict the effects of nitrogen on tiller and spikelet survival, production of grains and grain nitrogen.

2.0 INTRODUCTION

In many farming situations there is a conflict between the aim of growing barley crops to meet the requirements of maltsters and of achieving the highest gross margin if the standard for grain nitrogen content is not met. Maximum yield is obtained by the application of nitrogen fertilizer at the higher end of current recommendations. Before anthesis low nitrogen supply limits the survival of tiller buds and apical primordia and decreases the size of individual leaves. After anthesis no more effective grain sites can be formed so nitrogen tends to be deposited in the grain. In the extreme case many grains are formed and grain size is limited by the available carbohydrate. As high grain nitrogen concentration and low thousand corn weight are undesirable for malting, crops aimed for this market are often grown on lighter land with small amounts of top-dressing.

HGCA surveys of barley quality (1983-87) show, that in farm practice, autumn sown crops always have higher grain nitrogen concentrations than those that are spring sown. In autumn sown crops the concentrations are similar in feed and malting cultivars (about 2.0%). In contrast spring sown cultivars with good malting quality (mean 1.78%) showed 0.10% less grain nitrogen than feed types. There was a similar range of nitrogen concentrations over seasons in spring and winter types (0.14 and 0.18% respectively) but the difference between the types varied from 0.11% in 1987 to 0.18% in 1986. The end result is that cv. Golden Promise (spring) showed the lowest nitrogen concentration (1.76%) while cv. Triumph (spring) was similar to cv. Maris Otter (1.82%, winter). The feed cultivars cv. Atem (1.92%) and cv. Igri (2.02%) (spring and winter types respectively) were markedly higher in nitrogen concentration than the limits normally accepted for malting.

High nitrogen concentration and small grain size reduce the potential hot water extract (HWE) that can be produced from a grain sample. The empirical relation between hot Hough & Stevens, 1971),

$$HWE = A - 11.0\ N + 0.22\ G$$

where

HWE = Hot Water Extract (Brewers' pounds per quarter)
A = varietal constant (Brewers' pounds per quarter)
N = grain nitrogen content (%DM)
G = thousand corn weight (g).

This relation implies that about 1.0% reduction in HWE is caused by an increase in nitrogen concentration of 0.1% DM or by a 5 g decrease in thousand corn weight. Grain size also affects the rate of germination as small grains imbibe water faster per unit of corn weight than larger grains. It is also possible that the enzymes controlling starch break–down and protein synthesis take less time to diffuse from the aleurone to the starchy endosperm.

Field trial methodology has been greatly refined so the breeders and agronomists can rely on routine trials to identify the yield potential of new genotypes. However, uncontrolled environments can often obscure the understanding of processes that take place during crop development and growth. Simultaneous variation in multiple factors such as radiation, water availability and disease epidemics can have greater or lesser effects which may be additive, in conflict or interactive depending on a particular season. In cultivar development this problem is addressed by growing trials over a series of sites and seasons i.e. selection of new genotypes implies the necessary phenotypic plasticity to yield well over many environments. Only in retrospective analysis can the particular traits which influence good yield performance be identified. Cultivar characteristics, while being essential for the current crops, for example drought avoidance by early maturity, can result in developmental dead ends. We have sought to explore the relationship between nitrogen uptake, yield and grain quality in a series

of protected experiments to extend knowledge gathered from field trials. Treatments were imposed to examine the maximum phenotypic response and differences between and within cultivars. In particular, we desired to explore the variation due to differences between stems on a plant. Controlled nutrient flow gave the necessary regulation of nutrient uptake without complication by differences in rates of root growth and function. In addition this system allows the effect of water and nutrients to be separated which is difficult in soils.

The major difficulty in studying the interaction between growth and nitrogen uptake is the uncertainty of soil nitrogen supply with time. An essential part in determining the partitioning functions of nitrogen and carbon is a system for controlling the supply of nutrients to the plant. We used an inexpensive perlite culture system with recirculating nutrient solution. A range of repeatable nitrogen experiments was then imposed under the same climatic conditions. Nitrogen uptake and water use was monitored non–destructively. Measurements of plant development and distribution of carbon and nitrogen within the plant were made (roots, tillers and grain but excluding roots).

3.0 MATERIALS AND METHODS

3.1 *Description of Cultivars*

A range of spring barley genotypes was chosen for study in a variety by nitrogen trial (VNT) (see 3.2). Good malting quality was found in cvs Doublet, Natasha and Heriot, medium quality in cvs Tyne and SCRI240 while cvs Klaxon, Regatta and Vista were of feed quality. In the winter sown sowing rate trial (SR) cvs Igri, Marinka and Halcyon were chosen to represent the full range of malting quality (bad to good) in two row types while cv. Plaisant is a six row feed type. Cv. Blenheim, with good malting quality, as chosen to contrast with cv. Klaxon in a nutrient culture experiment (SOLX).

Cvs Tyne and Prisma were chosen as contrasting types for detailed examination of growth, nitrogen uptake, dry matter partition, grain yield and quality in relation to nitrogen distribution in a series of experiments conducted in a polythene tunnel (PTX). Both cultivars are semi-dwarf types but cv. Tyne is an early maturing type with small grain size and erect leaves attributable to the effect of the erectoides dwarfing gene. In contrast cv. Prisma possesses the *denso* dwarfing gene which results in the extension of the stem at a higher internode than in nutans types. Cv. Prisma is notable for a short strawed type because it has a large grain size. While cv. Tyne has poor quality, when judged from UK rather than Scottish Trials, cv. Prisma has good malting quality.

The origin of each of these cultivars is:-

Cultivar	Pedigree[1]
Blenheim	Triumph x Egmont
Doublet	Triumph x Goldspear
Halcyon	Warboys x Maris Otter
Heriot	Trumpf x HB855
Igri	820 x 1427 x Ingrid

Klaxon	RPB16–71 x Nackta
Marinka	(Alpha x SVP67.4) x Malta
Natasha	Triumph x Aramir
Plaisant	Ager x Nymphe
Prisma	(Triumph x Cambrinus) x Piccolo
Regatta	PF52213 x Claret
Vista	Claret x PF52213
Tyne	(Goldmarker x Athos) x (Goldmarker x Magnum)

[1] Pedigrees from "National Institute of Agricultural Botany Descriptions of Varieties of Wheat, Barley, Oat, Rye and Triticale 1991".

The main characteristics of each cultivar as established in National List and Recommended List Trials[1] are:–

Cultivar	Habit[2]	Mildew Resistance	Yield	Malting Quality
Blenheim	S	C	C	A
Doublet	S	C	D	A
Halcyon	W	B	C	A
Heriot	S	B	C	B
Igri	W	B	C	D
Klaxon	S	C	B	C
Marinka	W	C	B	B
Natasha	S	C	C	A
Plaisant	W	D	A	C
Prisma	S	D	B	A
Regatta	S	A	A	C
Vista	S	A	A	C
Tyne	S	A	A	C

[1] Taken from "National Institute of Agricultural Botany Classified List of Cereal Varieties 1992/93".

[2] Habit W = winter, S = spring.
Mildew resistance, Yield and Malting quality A = good, D = poor.

3.2 Field experiments

In 1988 two trials were grown to provide information on the relation between yield, quality and nitrogen fertilizer application. A spring sown trial (VNT), containing cultivars with good malting quality and feed types, was laid out in a split plot design and given treatments of 80, 100 and 120 kg ha^{-1} of nitrogen fertilizer.

A winter barley trial was sown at seed rates of 48, 96 and 192 kg ha^{-1} to impose environmental effects on tiller development (sowing rate trial, SR). Prior to combine harvesting, plants were pulled from marked quadrats and grain on the main-stem was separated from that borne on the tillers and their nitrogen content determined separately.

Plots were harvested from both trials with small plot combines and grain samples dried to 12% moisture before storage. Samples from the VNT were fractionated by sieving into four size classes.

3.3 Controlled Nutrient Uptake (PTX)

3.3.1 Year 1988

A single span polyhouse with both ends open and measuring 6.4 m by 19.2 m was used to protect the nutrient culture system from rain. Twelve beds, each 5 m long by 1m wide, were filled to a depth of 150 mm with standard horticultural perlite (Hall, Wilson & McGregor, 1984). The beds were lined with polythene and after initial wetting with nutrient solution applied to the surface (Hall & Wilson, 1986), future applications were done by supplying solution to the higher end of the bed thrice weekly and allowing it to flow under the bed down the gradual gradient. Dams, approximately 40 mm high, were placed every metre to maintain solution in the bottom of the bed while the excess flowed over into the next compartment and ultimately out of the lower end of the bed.

A single cultivar, Blenheim, was sown into dibbed holes 50 mm deep at a density of 200 seeds/m^2. The beds were divided into three replicates and four nutrient treatments were imposed; 3 mM (nitrogen applied) and 10 mM throughout, 3 mM switching to 10

mM, and 10 mM switching to 3 mM. The switches were made around anthesis. Observations of development and growth were made at regular intervals through to maturity on samples of 16 plants per replicate.

Crops were grown to maturity and grain yields equivalent to 5 t/ha were achieved. The main purpose of the first season was to evaluate the culture system. Problems encountered were related to maintaining uniform conditions both in time and space within each bed. Fluctuating moisture conditions during emergence resulted in a protracted period of emergence and on average only 86% plant establishment was achieved. In order to maintain moist conditions in the bed it was found necessary to apply nutrient solutions at least three times a week. A systematic gradient of nutrient concentration developed down the bed despite applying nutrient solutions in sufficient quantities to cause excess to overflow from the end of the beds.

3.3.2 Years 1989 and 1990 (PTX)

Because of the difficulties in 1988 in maintaining uniform conditions a pilot system with continuous recirculation was set up and tested after the end of the growing season. A bed. This was continuously refreshed using a trickle feed system above and on one side of the bed and an outflow gutter underneath and on the opposite side (Figure 3.3.2F1). Both the trickle feed and outflow gutters ran the full length of the bed. The outflow from the bed was recycled from the collection tanks back to the header tanks (Fig. 3.3.2F2). Any losses of water were automatically topped up from the mains supply. Stable, moist conditions were maintained throughout the depth and length of the bed. However, germination and emergence tests were still lower than expected. The standard grade perlite was covered with a shallow layer of horticultural sand and then the sown grain covered with seed grade perlite to a depth of 50 mm. Germination and emergence reached acceptable levels with these modifications to the system.

The single span polythene tunnel was also used in the 1989 and 1990 seasons. Twelve beds were filled to a depth of 150 mm with standard horticultural perlite. The beds

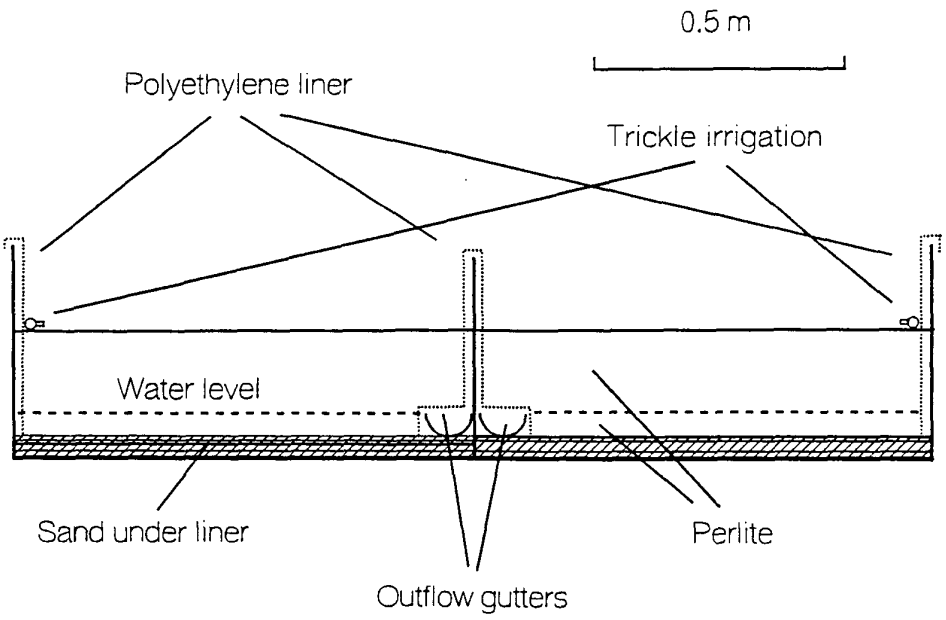


Figure 3.3.2F1 Cross-section through a perlite bed as used in 1990. The bed is divided into two halves along its length, to reduce the risks of nutrient gradients developing across the bed. Sand is used under the polythene liner to level the base of the bed. The seeds are sown onto a thin layer of horticultural grade sand (not shown) and a final 50 mm layer of seed grade perlite placed over the seeds.

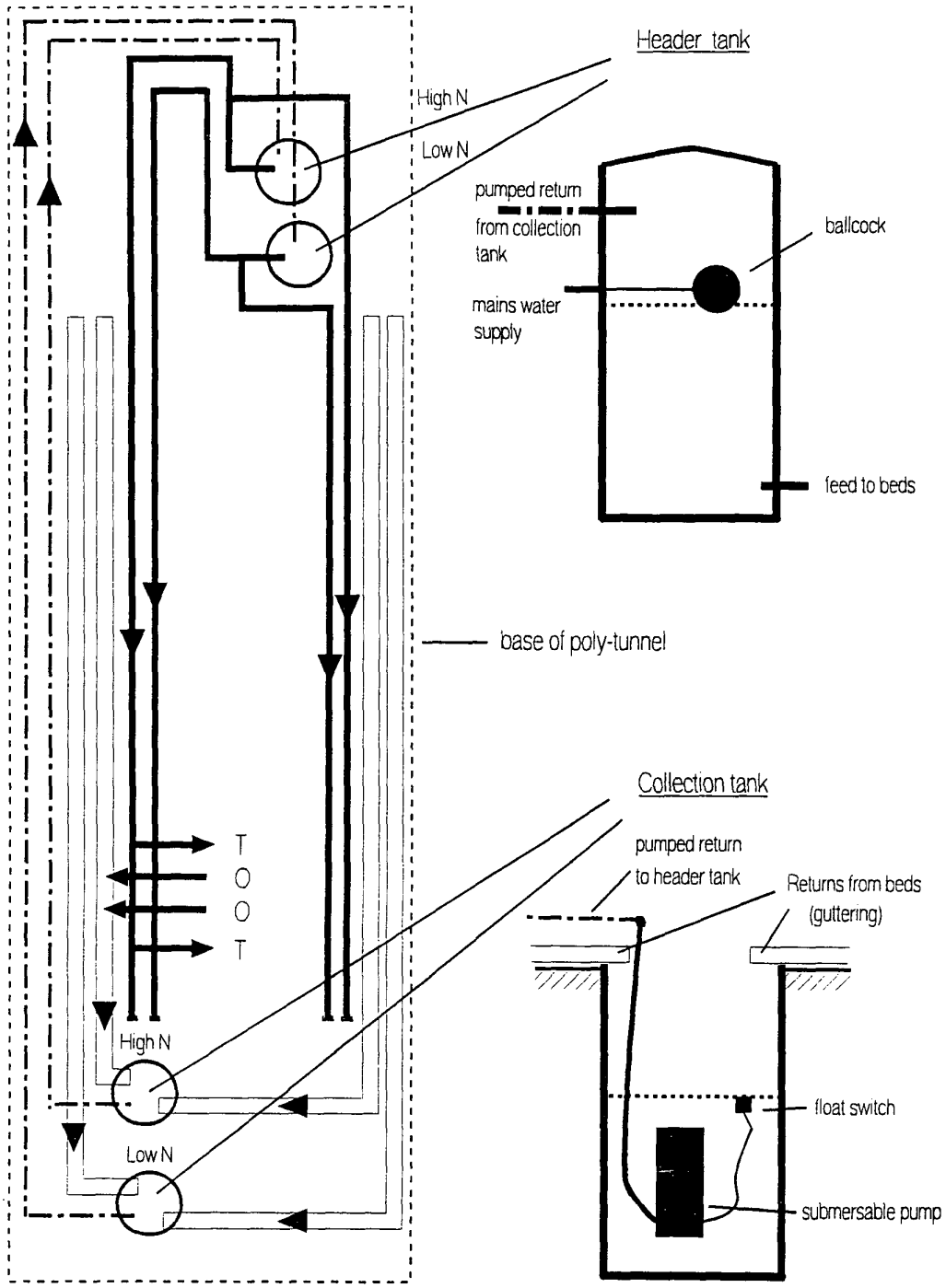


Figure 3.3.2F2 Diagram (not to scale) of the nutrient recirculation system used in 1990. The take offs (T) for trickle irrigation and outflows (O) for one bed are shown. There are six sets on each side of the poly-tunnel.

were lined with polythene and the initial wetting was with nutrient solution applied to the surface. The cultivars were sown at a density of 250 seeds/m^{-2} by placing seeds on the surface of the perlite on top of a thin layer of horticultural grade sand and then covering them to a depth of 50 mm with seed grade perlite. The beds were wetted and covered with polythene until germination had occurred. The experimental plans for the two years are shown in Figure 3.3.2F3. The beds were divided into three replicates and two nitrogen treatments were imposed on each of two cultivars (Tyne and Prisma); in the high nitrogen treatment when the solution dropped to 0.5 mM it was replenished. At the same time the low treatment was replenished by one third of the nitrogen added to the high level. Sulphuric acid was added to both treatments, as required, to bring pH down to 6.5. Conductivity of both treatments was also maintained between 1 and 2 mS cm^{-1}. Observations of development and growth were made at regular intervals through to maturity on samples of 16 plants per replicate. The time of the year on which samples were taken were:-

Day of Year and elapsed time

	1989	Time	1990	Time
Sowing	110		90	
Harvest 1	146	36	132	42
Harvest 2	159	49	146	56
Harvest 3	172	62	159	69
Harvest 4	185	75	173	83
Harvest 5	200	90	187	97
Harvest 6	230	120	227	137

At the final harvest the plants from a defined area of each bed were harvested and the modal stem number for each determined.

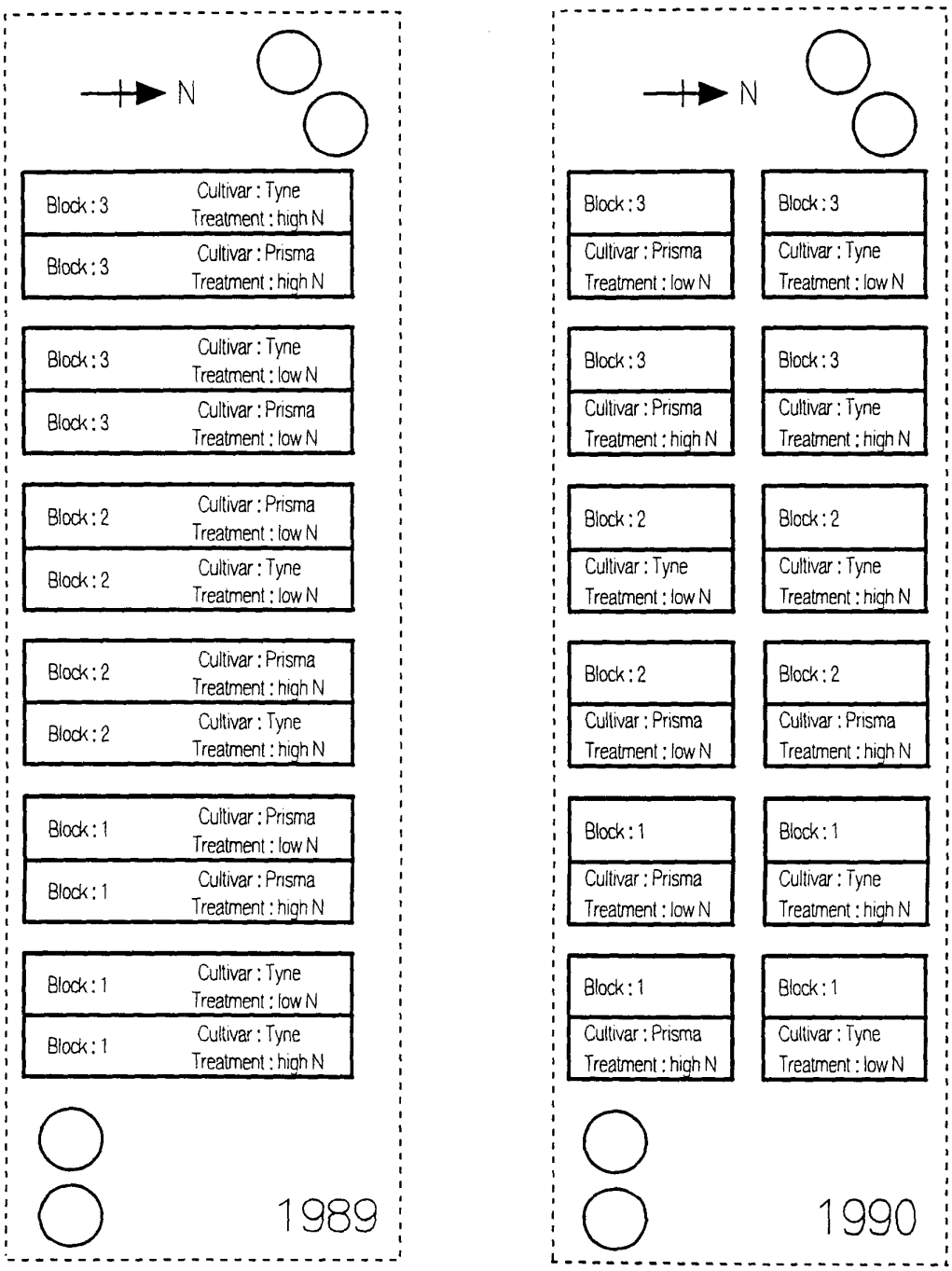


Figure 3.3.2F3 Site plan of the controlled nutrient experiments (PTX) showing the arrangements of the three blocks and the combinations of cultivar and nitrogen (N) treatments in years 1989 (left) and 1990 (right). The outer, dashed rectangle is the base area of the poly-tunnel.

Separation of grain by grain position

At final harvest 30 modal (having modal stem number) plants were harvested, air–dried and the ears on them separated into main stem ears and tiller ears. The tiller ears were then ranked by weight and coded T1, the heaviest; T2 the next heaviest and so forth.

The grain from each ear type (plot x stem type [MS, T1, T2, ...]) were separated by grain position into separate vials. 30 ears giving a maximum of 30 grains at each grain position. The middle grain from each ear in a sample was first removed and placed in vial number 15 and the next grain down placed in vial 14, 13, 12 and so on; likewise the next above was placed in 16, 17, 18, 19 etc. There were never more than 30 grain on an ear. Once a sampled was separated the vials were renumbered, the lowest grain position holding at least one grain being numbered 1.

The number and weight of air dried grain at each grain position was then recorded.

Growth analysis – Definitions

Leaf

The lamina surface from the tip to the ligule. The leaf sheath (between point of attachment on the stem and the ligule) is included with the stem.

Stem

Prior to ear emergence, this includes all the stem from the base to the tip, including all leaf sheaths and the developing ear structures. After ear emergence, the ear structure was removed from the stem material and analyzed separately.

Ear

The ear includes all material from the collar upwards.

Rachis

Includes all the ear structure except the grains.

Non–reproductive biomass

The weight of both leaf and stem material (excludes ear and root).

Total plant

The sum of leaf, stem and ear material. Roots are not included.

Main-stem

Leaf, stem and ear borne on the initial or primary stem emerging from the seed.

Tillers

Leaf, stem and ears borne on all stems excluding the main-stem. This includes both primary and secondary tillers. There were few secondary stems and no tertiary or higher order stems.

In both years samples of 4 adjacent plants in a row were taken at random from within 4 predefined regions of each bed to ensure that the bed was uniformly sampled with out bias. In 1989 these were kept as individual replicates whereas in 1990 the 4 samples were then bulked to give one replicate per bed. There were 6 harvests and on 4 (1989) or 3 (1990) harvests measurements of development were made. Measurements of growth and nitrogen concentrations were made at all 6 harvests in both years. The ear was only separated into rachis and grain at harvest 6 (the final harvest).

Measurements of development

At harvests 2, 3, 4 and 5 in 1989 and 2, 3 and 4 in 1990 one plant per replicate was selected at random for measurements of development. The stem types present on the selected plant were recorded (Figure 3.3.2F4). Then the number of leaves fully emerged and those emerging from the sheath of the leaf immediately below were recorded for each stem type. The plant was then returned to the replicate for growth analysis.

Measurements of growth

The stems from the 4 plants (16 plants in 1990) in each replicate were first separated into main-stems and tillers. The two groups of stems were then further separated into leaf, stem and ear (ears were not separated out prior to their emergence i.e. not present in harvests 1 and 2 in both years).

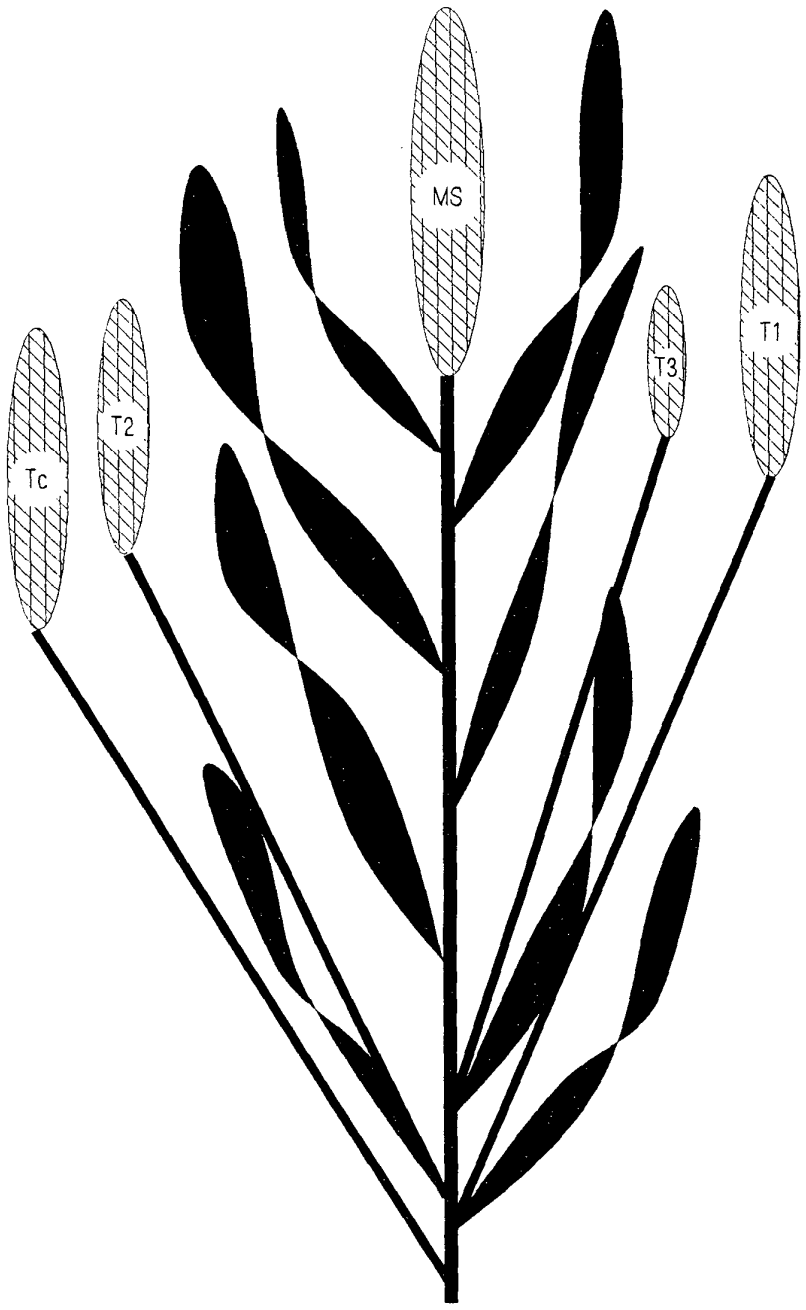


Figure 3.3.2F4 Schematic showing the classification of stem types: MS, main-stem; Tc, coleoptile tiller; T1 - T3, primary tillers at leaf positions 1 - 3 on the main stem.

The leaves were sub-divided further into *live* and *dead* leaves. A leaf was classified as dead when more than half its surface area was judged to be yellow or brown i.e. senescent. The number of stems, ears and leaves (live and dead separately) were recorded. The fresh weights of each component was then recorded and then leaf areas were measured.

Fresh weight and counts

The number and fresh weights of each component were recorded first.

Leaf area

The area of one side of each leaf. Only the area of live leaves was recorded. Dead leaves, although contributing to the over all interception of light by the canopy, are usually located in the lower part of the canopy and contribute little to the growth rate of the crop. In addition the dead leaves are often curled and twisted reducing their effective leaf area. A Skye Instruments Video Digitiser was used to measure leaf area. The leaves were laid out on a flat surface, taking care that leaves did not overlap, and then held flat by a covering layer of perspex while the image was scanned and total area estimated. At later harvests, when the leaves were more numerous and larger leaf samples were sometimes divided into 2 or 3 lots for measurement and their areas totalled. In 1990, when the fresh weight of a leaf sample exceeded 8 g a representative sub-sample of known fresh weight (5 g) was taken for measurement leaf area and then the total leaf area calculated by multiplying by the total fresh weight divided by the sub-sample fresh weight.

Dry weight

In 1989 the whole of the sample for each component was dried by placing in an oven at 100°C for 48 hours. The dried samples were then removed from the oven and immediately weighed. In 1990, when the fresh weight exceeded 50 g a representative sub-sample of known fresh weight (20-30 g) was taken for drying and then the total dry weight of the original sample estimated by multiplying the sub-sample dry weight by the total fresh weight of the sample divided by the sub-sample fresh weight.

Nitrogen concentration

Having recorded the dry weights, the samples were then ground to a fine powder using a steel ball mill in agate lined cup. A period of 2 months was required to complete the grinding of all the samples. The samples were then stored until nitrogen analyses could be carried out. Immediately prior to analysis the ground samples were redried in a freeze drier and the total nitrogen concentration of a sub-sample measured using mass spectro-photometry.

3.3.3 Germination Tests

Pilot tests were carried out to optimise the consistency of germination on agar. Full scale tests were delayed until post-harvest dormancy was absent when it was possible to be sure that grain was completely viable. The agar based system was compared with standard germination tests to ensure that the water supply was optimised.

Germination tests were carried out on grain separated from the modal plants collected at final harvest. Five grain positions within an ear type were tested. The positions were bottom, lower quartile, mid-quartile, upper quartile and top. The bottom and top were defined as the third grain position in from the extreme grain bearing position (position 1 and the highest position holding at least one grain) subject to the condition that there were at least 20 grains present (this was true in the majority of cases), if not then the lowest and highest grain positions having at least 20 grains present were taken as bottom and top. If the range of grain bearing sites is defined as the position of the top most position bearing at least one grain. Then the lower, mid- and upper quartile are positions 1/4, 1/2 and 3/4 of the range.

Each grain to be tested was weighed individually on a balance accurate to 1 mg. Tweezers were used to handle the grain. Up to 50 grains were stored individually in a compartmented tray ready for transfer to a petri dish. Germination tests were started on Monday and carried out in 14 cm glass petri dishes. 40 ml of dissolved agar (0.75% by weight) was added to each dish which were then allowed to cool for half an hour. An acetate sheet was taped under each dish to provide a unique dish number and

placement grid for a randomisation of the numbers 1 to 50 with one dish used per bed. Immediately prior to starting a germination test a further 20 ml of agar was pored on top of the set agar to create a thin layer to 'stick' the grain into a fixed position. A skin was allowed to form on this new agar (the temperature of the agar was less than 30°C when tested with a thermocouple) and the grain from the tray transferred to the corresponding locations in the petri dish. Grain were placed crease down, all with the same horizontal orientation with tweezers.

The time to nearest minute was noted as the final grain was laid on the plate and then immediately and carefully 4 ml of distilled water was added with a Gilson pipette. Any grain that became dislodged were re-positioned. The cover plate was replaced and sealed with NESCO film and the dishes were incubated at 15°C. From the next morning observations were made 4 times a day for the 4 days remaining in the week i.e. at 8:30–9:30, 10:30–11:30, 13:30–14:30 and 16:00–17:00). Care was taken to recheck any doubtful grain and to avoid observer bias. Finally on the 7th day (Monday) total germination was recorded. This is referred to as the lower time resolution. Having observed the timing of the peak germination the test was then repeated at finer resolution. During the phase of peak germination an additional 3 observations were made during the night (20:30–21.05, 0:30–1:30 and 4:30–5:30). This test is referred to as the finer time resolution.

The germination rates of grain from the MS and T1 and T2 were tested first. The grain from each year were tested separately. An individual test comprised 12 petri dishes (1 per plot). Each dish comprised 45 grains (3 stem types, 5 grain positions replicated 3 times) from the corresponding plot. The lower then finer time resolution tests were carried out on these grain in both years.

Germination was also tested in T3 and T4 ears in both years but lack of resources permitted only one germination test at the lower time resolution. Individual grain replication was increased to 5 per grain position on a given stem and the number of grain positions examined reduced to 3. These positions were bottom, middle and top.

(The lower and upper quartiles were omitted and were frequently close to the top and bottom positions. As T3 and T4 were usually missing in Low N treatments, the tests were restricted to High N treatments only. Grains from the MS were also included to act as a standard of comparison. Both 1989 and 1990 were done simultaneously. Thus with 5 replicate grains per position on each of the stem types there were 45 grains per High N treatment tested in each year. The results were consistent with the trends observed in MS, T1, T2 comparisons.

3.4 Solution culture (SOLX)

Plants were grown inside a glasshouse, minimum air temperature of 16°C, in 45 l tanks containing complete nutrient solution with pH at 6.5, which were aerated. The solutions were not automatically replenished, but replaced entirely every week. Seedlings of cv. Klaxon (feed quality) and cv. Blenheim (good malting quality) having a root length of c. 20 mm were transferred to the nutrient solutions which were labelled with ^{15}N for the first week of growth only. This was to allow the nitrogen absorbed during this period of growth to be later measured in the harvested crop. Two nitrogen treatments were imposed: 'steady-state', in which the availability of nitrogen was aligned closely with the projected demand assuming a constant nitrogen concentration in the plant; and 'high-low', in which the availability of nitrogen was initially high then reduced to a low, constant concentration to simulate the pattern of availability in field soils following fertilizer application. Five replicate plants of each cultivar were harvested from each treatment after 7 days, and on 13 other occasions thereafter, until maturity (105 days after transfer). Ears were separated from shoots and roots. Samples were dried at 100°C for 48 h and dry weights recorded. Finely ground samples were taken for analysis of total N and ^{15}N concentrations.

4.0 RESULTS

4.1 *Field Experiments*

4.1.1 *Variety x Nitrogen Trial* – (VNT)

Grain samples from the spring barley VNT (Table 4.1T1) showed a consistent trend for grain from the 2.5–2.75 mm fraction to have higher nitrogen content than the 2.25–2.50 mm fraction. This pattern appeared to be consistent over a range of top dressing from 80 to 150 kg(N)ha^{-1}. Cv. Tyne, the only genotype in which this was not seen, was also the only erectoid.

At low top dressing levels (Table 4.1T1a) all the values were within a narrow range that would have been acceptable for malting. The highest level of top dressing resulted in high grain nitrogen content (Table 4.1T1b) and the highest levels of nitrogen were present in the 2.50–2.75 mm fraction. When the results of nitrogen analyses of unfractioned grain was examined, statistically significant genotype and nitrogen effects were seen for grain nitrogen content, thousand corn weight, yield and hot water extract (Table 4.1T2). Nitrogen application increased grain yield and nitrogen concentration but reduced thousand corn weight and hot water extract. Over all cultivars the average yield of grain nitrogen represented between 119 and 86% of that applied as fertilizer. As plants were not examined it is not possible to comment on differences in the partitioning of nitrogen between leaf, stem and grain but the increase in grain yield did not justify the higher application rate.

All numbered tables are located in Appendix A2 and are numbered by the results section they relate to.

4.1.2 Sowing rate trial (SR)

Grain nitrogen concentration was lowest in cv. Halcyon with no significant difference between the other cultivars. There were no differences due to sowing rate. Over all the cultivars the average N concentration in the grain from the main-stem and tillers was not different. However, in cvs Plaisant and Halcyon main-stem grain had lower N concentration than the tillers (Table 4.1T3). This relation was reversed in cvs Igri and Marinka.

4.2 Controlled nutrient uptake (PTX)

The physical layout of the 1989 and 1990 experiments have already been described in the Materials and Methods section (3.3.2). Particular problems arose in the execution of the work in both years. In 1989 one half of one bed of the cultivar Prisma at the high nitrogen level could not be sampled. In addition the irrigation system was not as efficient as might have been desired and required frequent cleaning to ensure even nutrient supply to all beds. In 1990 the irrigation system was improved but nutrient recirculation was delayed until the crop emerged. In 1989 nitrogen and water were stopped when maximum grain size was reached i.e. before the crop turned yellow. In 1990 water and nitrogen were supplied until the crop was completely ripe. While these minor variations in procedure were not all designed careful observation of the results provided a useful insight into crop performance.

The results of the experiments were subjected to statistical analysis but this is problematic when the data are not orthogonal. For example nitrogen treatments affect tiller number so that low nitrogen treatments will always have lower tiller numbers than high nitrogen treatments. As can be seen from the following sections the main-stem, tiller 1 and tiller 2 have been compared over both levels of nitrogen in both years. This is accompanied by similar analyses, at the high nitrogen level only of tiller 3 in 1989 and tillers 3 and 4 in 1990.

4.2.1 Nitrogen uptake and total dry matter production

The changing amount of nitrogen in the plant (excluding roots) with time is shown in Figure 4.2.1F1. There was significantly and substantially less nitrogen taken up by the Low N treatments in both years (Table 4.2.1T1). The amount of nitrogen taken up in the High N relative to the Low N treatment by final harvest is close to the intended ratio of 3:1. Averaged over the two cultivars the amounts by final harvest were 23.0 and 7.8 g(N) m^{-2} (ratio 2.9:1) and 29.0 and 10.0 g(N) m^{-2} (ratio 2.9:1) in 1989 and 1990 respectively (Table 4.2.1T2). In both years there is a suggestion that cv. Prisma has taken up more nitrogen than cv. Tyne by harvest 4 (close to anthesis) in the High N treatments, but this difference was not significantly greater than the background variation in either year.

Despite the earlier sowing (see Page 19) in 1990, the initial rate of nitrogen uptake was slower in 1990. It is not until day 140 that the amount taken up exceeded that in the previous year. The second contrast between years is in the amount of N taken up after anthesis (harvest 4) in the High N treatments. There was little or no uptake during this period in 1989, 21.5 g(N) m^{-2} at harvest 4 compared to 23.0 g(N) m^{-2} at final harvest averaged over the two cultivars (Table 4.2.1T2), an increase of only 1.5 g(N) m^{-2}. In contrast, there was a similar amount taken up by harvest 4 in 1990 (20.0 g(N) m^{-2}) but there was more nitrogen taken up after anthesis resulting in 29.0 g(N) m^{-2} by final harvest, a post anthesis increase of 9.0 g(N) m^{-2}. These differences reflect differences in management between the two years. In 1989 the recirculation of nutrient solution was started immediately after sowing. In 1990, as in the previous year, the perlite was presoaked to saturation with nutrient solution before being placed in the beds. However, recirculation was not started until the plants were emerging. Although the plants are small at this stage and the absolute requirement for nitrogen is small, this early difference had a distinct effect on early uptake and growth. The second contrast in management occurred during grain filling. Replenishment of the nutrient solution was stopped half way through grain filling and then recirculation was stopped a fortnight

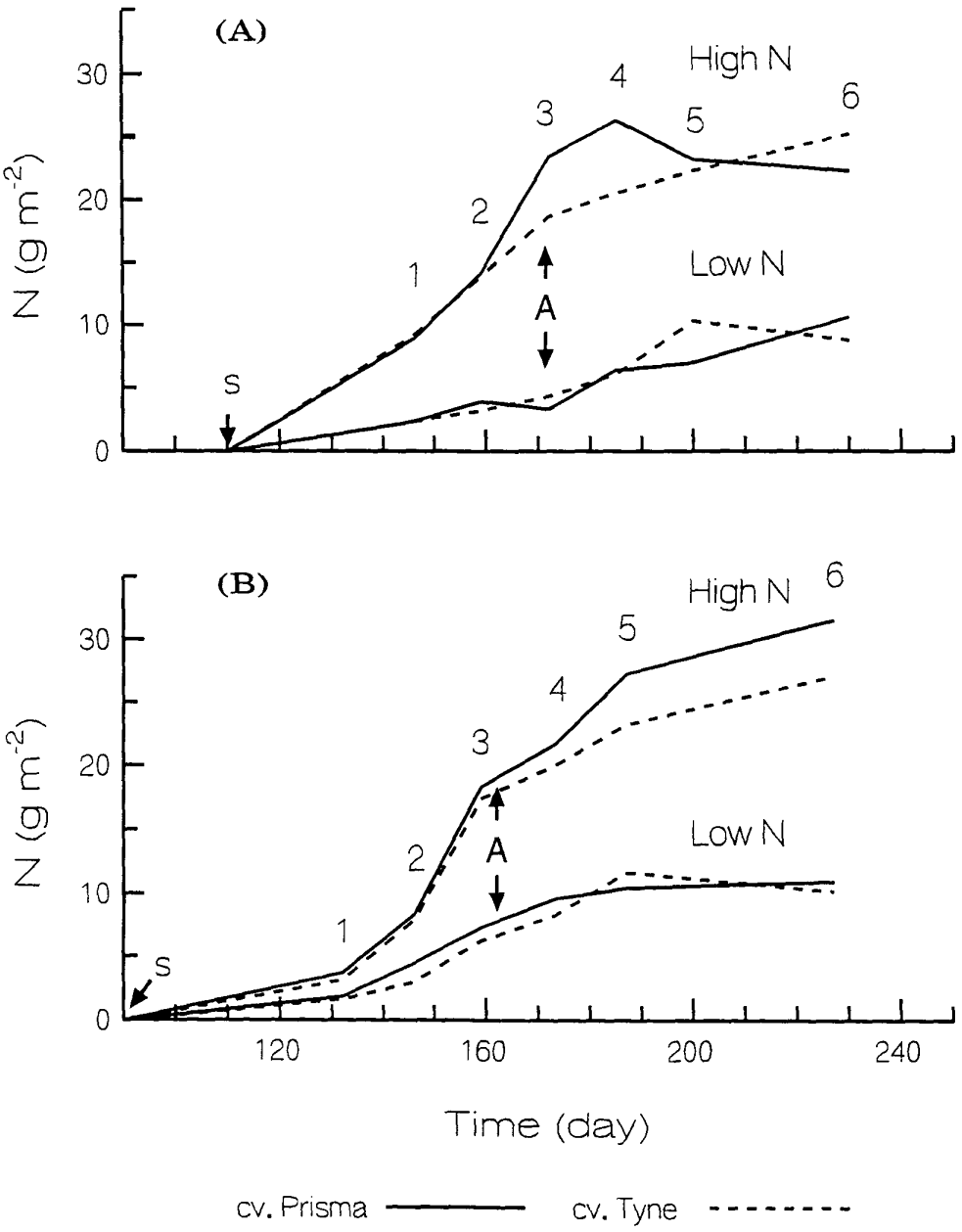


Figure 4.2.1F1 The increase in total plant nitrogen content with time for cv. Prisma and cv. Tyne with Low and High Nitrogen supply in (a) 1989 and (b) 1990. The times of sowing (S), harvest (1...6) and anthesis (A) are indicated.

later, allowing the crop to dry and mature. This is commonly the case in the field, when water is often limiting before anthesis and there is little of no nutrient uptake thereafter. In 1990, recirculation and replenishment of nutrient solution was maintained throughout grain filling. These differences provide interesting insights into the importance of early and late nitrogen uptake and its consequences for growth rate and grain quality.

The controlled recirculation of nutrients has provided the necessary control of uptake, eliminating consequences of feedback on root growth and function and separating nutrient effects from those of water. This would be difficult and expensive to achieve in the field.

The consequences for plant growth are clearly evident (Figure 4.2.1F2). Again there is a consistent and significant reduction in total plant dry weight due to nitrogen, at every harvest date in both years (Table 4.2.1T3). The cumulative effect of nitrogen on final plant dry weight is smaller than that on nitrogen uptake. Averaged over the two cultivars, the plant dry weights at final harvest were 1.64 kg(DW) m^{-2} in the High N treatment and 0.88 kg(DW) m^{-2} in the Low N treatment (ratio of High N to Low N, 1.9:1) in 1989 and in the following year were and 2.08 and 1.11 kg(DW) m^{-2} (ratio of High N to Low N, 1.9:1) respectively (Table 4.2.1T4). Whereas nitrogen uptake was reduced by two thirds, plant dry weight was reduced by one half. Thus nitrogen, which is closely linked to photosynthesis, in the green tissues is used more efficiently in terms of plant growth when supply is limited.

As with nitrogen uptake there is the suggestion that plant dry weight is also greater in cv. Prisma up to anthesis (harvest 4) in both years. This difference is significant in 1989 and close to being significant in 1990 (Table 4.2.1T3 and 4). However, by final harvest no significant difference was detectable.

When plants have an optimal supply of nitrogen i.e. plant growth is maximal and any reduction in nitrogen uptake leads to a reduction in growth, then the change in the concentration of nitrogen with the increasing dry weight of whole plant exhibits a

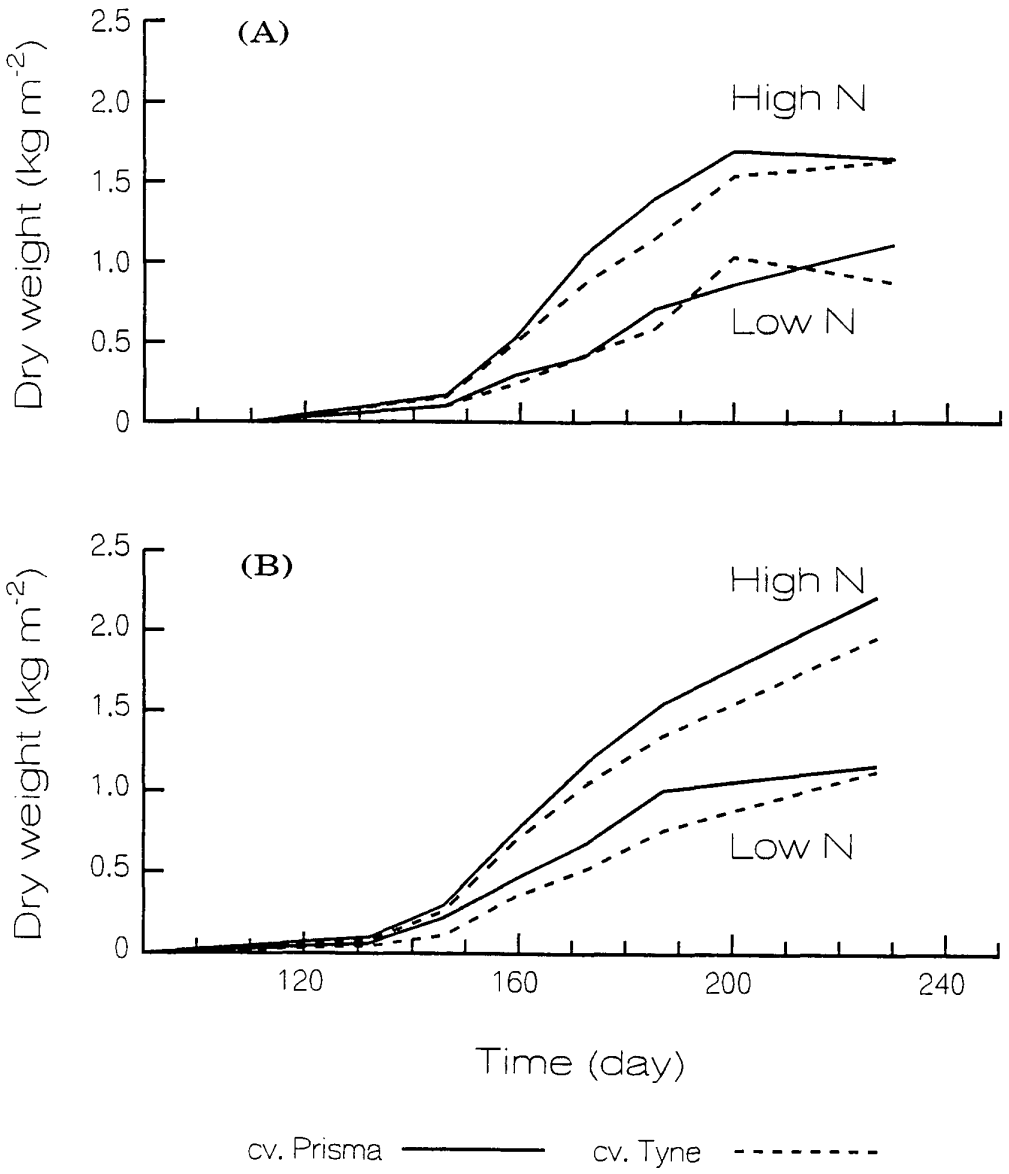


Figure 4.2.1F2 The increase in total plant dry weight with time for cv. Prisma and cv. Tyne with Low and High Nitrogen supply in (a) 1989 and (b) 1990.

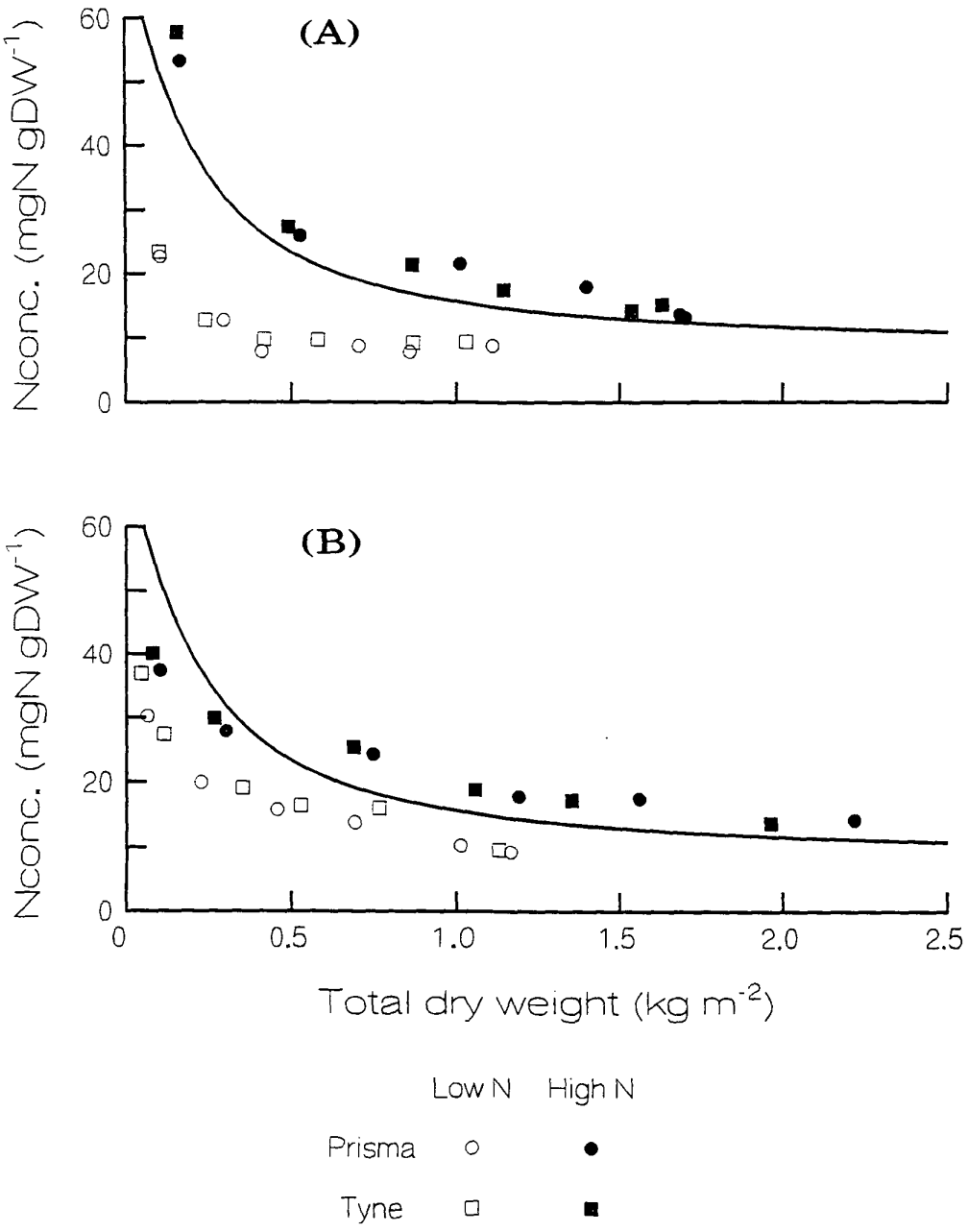


Figure 4.2.1F3 The change of total plant nitrogen concentration with increasing plant dry weight in (a) 1989 and (b) 1990. The solid line represents the minimum nitrogen concentration at which growth is not limited (Marshall and Porter, 1991).

characteristic relation which is seen in many arable crop species (solid line, Figure 4.2.1F3). This was first noted by Greenwood (1982) and quantitative relations and model were proposed (Greenwood *et al.*, 1985a, b). A similar relation was derived by Marshall & Porter (1991) based on the ideas of Monteith (1977, light limited linear growth rate) and Ingestadt (1982, nitrogen limited relative growth rate), which is consistent with these earlier findings. This is the relation shown in Figure 4.2.1F3. Plant dry weight increases with time and the proportions of structural and storage tissues (with low concentrations of nitrogen) increase and so the average nitrogen concentration over the whole plant falls. For all harvests in 1989 and all but the first two harvests in 1990, the nitrogen concentrations of the whole plant are on or above the optimal line. This is further evidence that the supply of nitrogen in the High N Treatments was adequate, if not super-optimal, to sustain maximum growth. The first two harvests in the High N treatments in 1990 are noticeably below the optimum (left most points in Figure 4.2.1F3b). Thus not only nitrogen uptake but also growth rate in this period may have been restricted by not starting the recirculation of nutrients until emergence.

In both years, the concentrations in the Low N treatments are substantially below that required for optimum growth. The initial concentrations in these treatments were lower in 1989 than in 1990, but by final harvest were similar. The combined effects of the two thirds reduction in nitrogen supply on uptake (2/3 reduction) and dry weight accumulation (1/2 reduction) resulted in a one third reduction (2/3 x 1/2) in the final nitrogen concentrations averaged over the whole plant (excluding roots) in both years.

The differences between years lead to a large differences in maximum leaf areas achieved (Figure 4.2.1F4) in the High N treatments. In 1989 the leaf areas were greater in the main-stem and particularly the tillers (difference between main and total leaf area) than in 1990. This would appear to be due to the initial differences in nitrogen supply. In addition, cv. Prisma produced a larger leaf area than cv. Tyne in the High N treatments in both years, although only the effect of nitrogen on leaf area was found to be significant in either year (Table 4.2.1T6, consistency over years was not tested

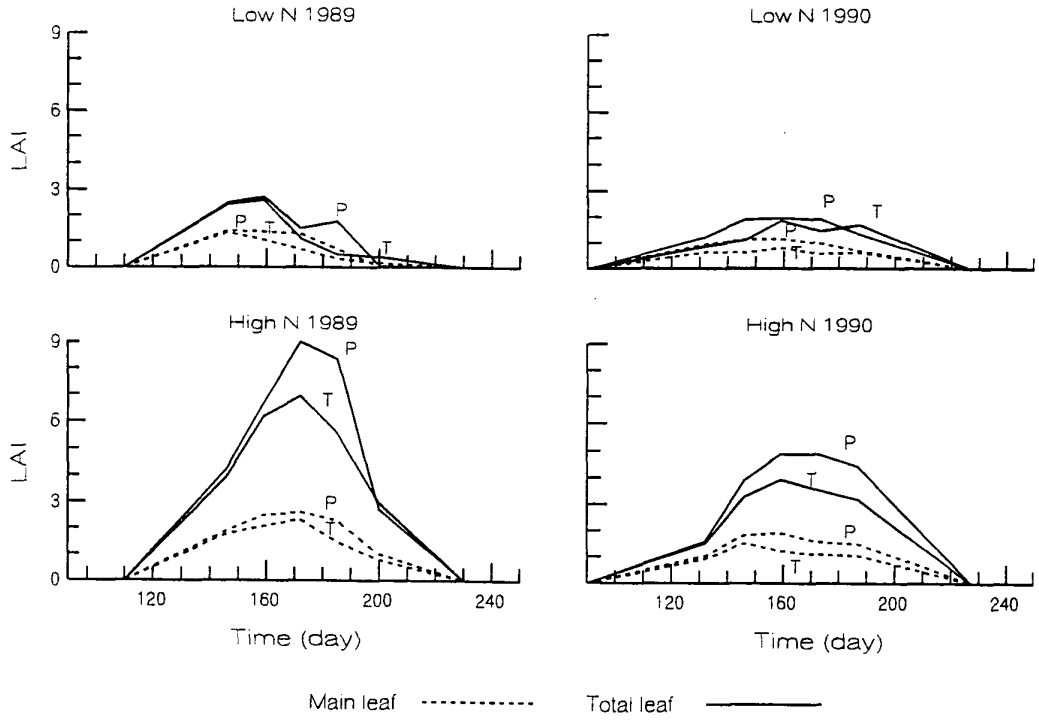


Figure 4.2.1F4 The time-course (day number in the year) of leaf area index (LAI) on the main-stem and whole plant in cv. Prisma (P) and cv. Tyne (T).

for). Although there were large differences between years, the effect on the quantity of radiation intercepted is much smaller. When a canopy reaches a leaf area index (LAI) of 3 then it is intercepting nearly all the radiation incident upon it. Any further increase in leaf area has little or no effect on the amount intercepted. In 1989 the period when the canopy was closed (LAI>3.0) was similar for the High N treatments of cvs Tyne and Prisma and lasted for 55 days. In the High N treatments in 1990 cv. Tyne reached canopy closure later than cv. Prisma and died more quickly so the periods of closed canopy were 40 and 52 days respectively.

In the Low N treatments the differences between both total and main-stem leaf areas over the two seasons were much smaller than those observed in the High N treatments. There was little or no difference between cultivars.

The proportion of leaf dry weight which was senescent (more than 50 % of the leaf lamina yellow or brown) increased steadily with each harvest (Figure 4.2.1F5). All leaf material was dead by the final harvest (harvest 6) in both years. In 1989, the proportion of senescent leaf was consistently and significantly greater in the Low N treatments (Table 4.2.1T7) over the first 5 harvests. There were no systematic nor significant differences between cultivars. The rate of senescence in 1990 was slower than in the previous year. The early differences in nitrogen supply between years, while restricting leaf expansion did not influence rates of senescence. The later was influenced by the difference in nitrogen supply after anthesis.

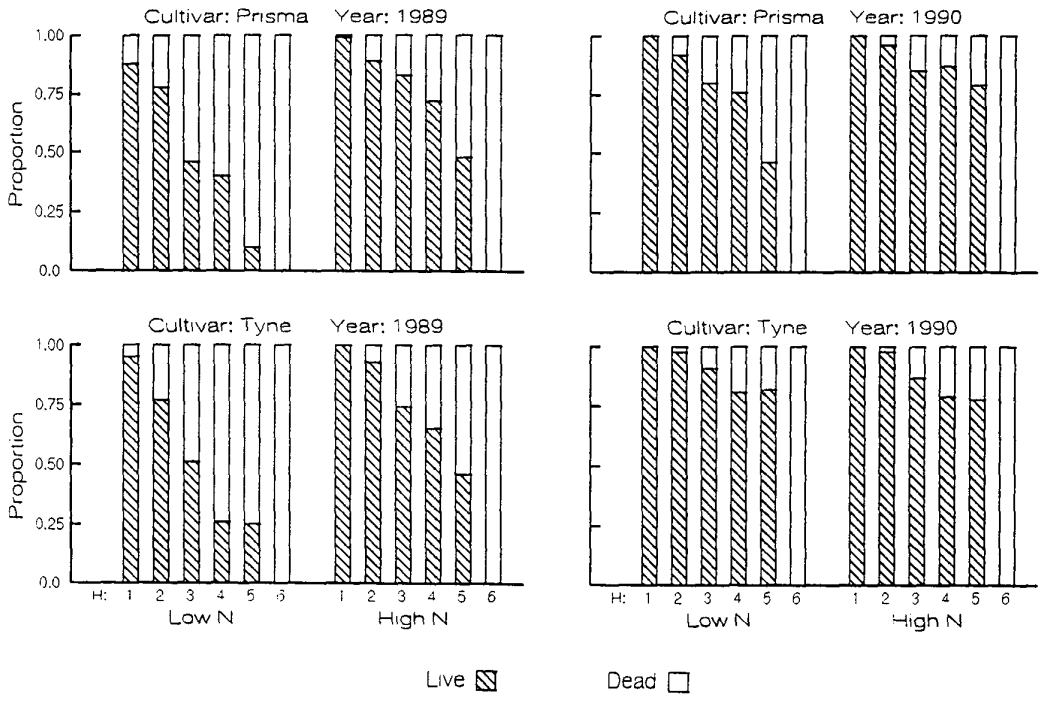


Figure 4.2.1F5 Proportions of total leaf dry weight that are either live or dead (dead = less than 50% of lamina green).

4.2.2 Development of the plant

Data on plant development and its final outcome were collected by plant dissection and during growth analysis (Section 3.3.2). Resources did not permit complete dissection and observation of the formation of primordia at the stem apex so no estimates were made of the rate of development or final number of primordia. Plant dissection was carried out for 4 harvests in 1989 (Figures 4.2.2.F1–2) and 3 in 1990 and aimed to determine the development of stems and leaf number per stem. As each leaf unfolds the potential tiller in the axil is differentiated and begins to grow. The fate of a particular tiller depends on plant growth, water supply and nutrient uptake. Finally the time of emergence from the subtending leaf sheath is critical. If the canopy is closed the tiller is subject to severe competition for light and is unlikely to form a fertile ear. In 1989 T3 emerged after canopy closure so plants from high nitrogen treatments with the modal number of ears were composed of MS, Tc, T1 and T2.

The formation of tillers during plant development (Table 4.2.2T1) was affected by nitrogen treatment. There was no consistent cultivar or cultivar by N interaction, which can be attributed to the effects of regular plant spacing and a lack of root competition for water. In this respect the experimental system contrasts strongly with field trials (Table 4.1T2a).

The number of leaves on the main–stem of both cultivars was similar in both seasons (Table 4.2.2T2a) with a maximum of about 8. Counts are not given for harvest 6 because senescence made direct counts misleading. Indeed, by harvest 5 there was an apparent drop in leaf number which cannot in fact happen! There were significant differences due to N treatment (Low N fewer leaves) and cultivar (cv. Tyne fewer leaves than cv. Prisma) in the second harvest. In subsequent harvests there tended to be no significant differences. The coleoptile tiller leaf number (Table 4.2.2T2b) contrasted with the main–stem and showed greater differences due to nitrogen treatment in the later 1989 harvests. The same result was found for the number of leaves on primary tillers 1 and 2 (T1, T2)(Table 4.2.2T2c,d). Few leaves were developed on the third tiller,

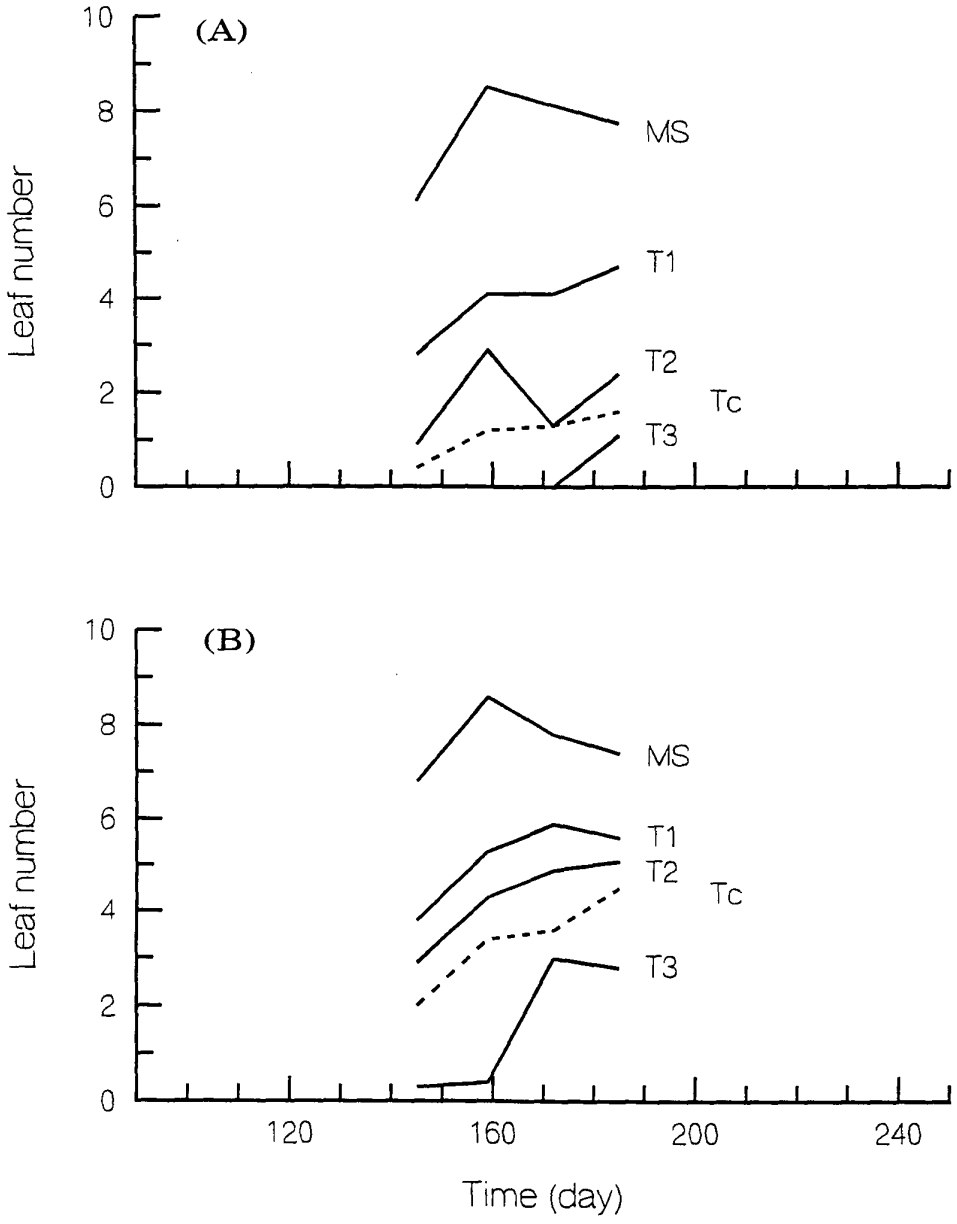


Figure 4.2.2F1 The time-course of leaf number by stem type (MS, Main-stem; T1 - T3, Tillers 1 - 3; Tc, Coleoptile tiller, dashed line) in cv. Prisma, 1989, in (a) Low N and (b) High N treatments.

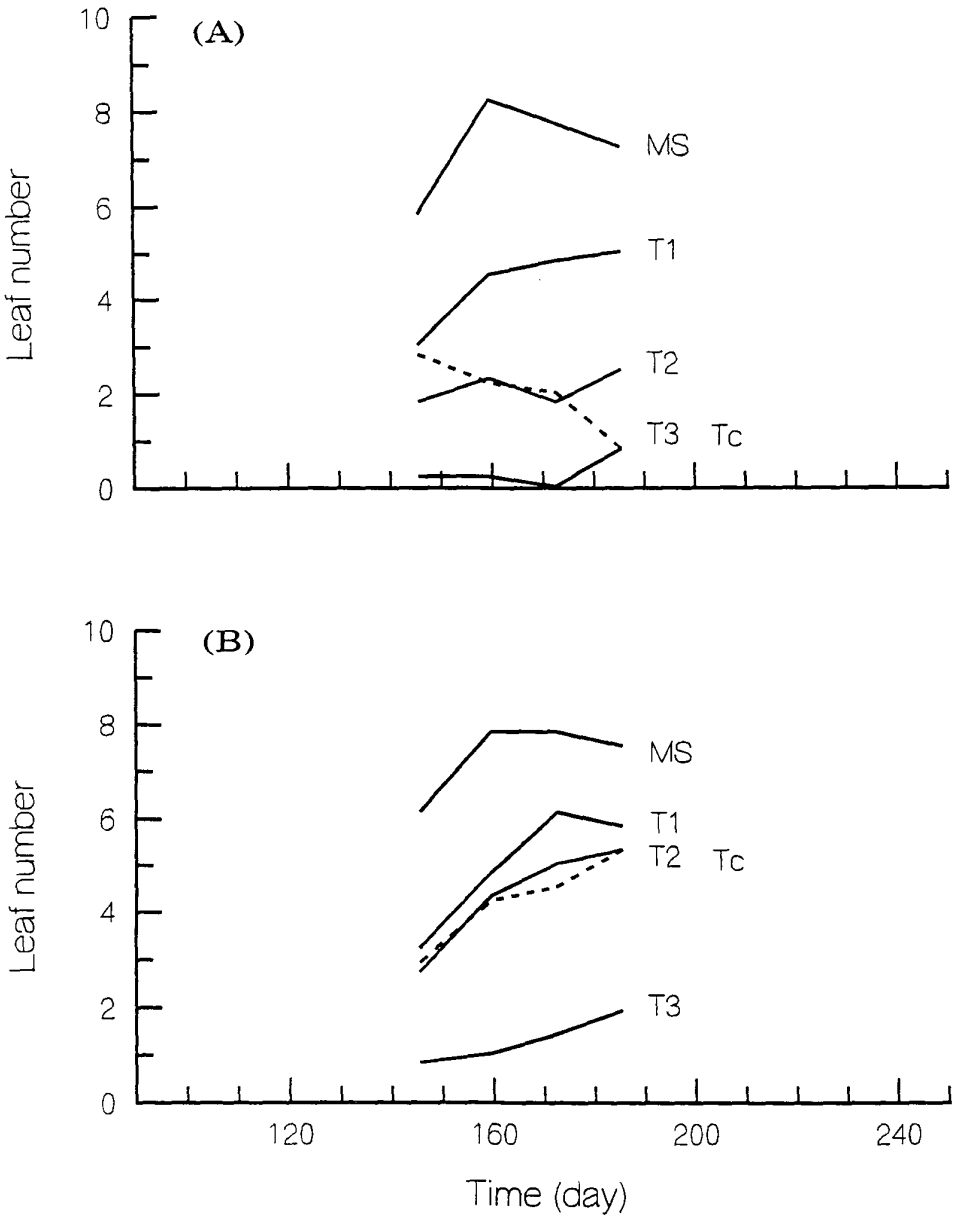


Figure 4.2.2F2 The time-course of leaf number by stem type (MS, Main-stem; T1 - T3, Tillers 1 - 3; Tc, Coleoptile tiller, dashed line) in cv. Tyne, 1989, in (a) Low N and (b) High N treatments.

which consequently showed no consistent effects of treatments (Figures 4.2.2F1–2, Table 4.2.2T2e). The secondary tiller at the first leaf site (T1,1 not shown) also showed no consistent effects of treatments.

The somewhat incomplete development data do not allow a full evaluation of the relationship between leaf number per stem and the fate of that stem. The later emergence of a tiller from the subtending leaf sheath effectively compresses the time for the formation of leaves and spikelet primordia. At a threshold time the tiller will not be viable and will not form an ear. The number of leaves and the rate at which they are formed on a stem allow it to be assigned to viable/non–viable category. In 1989 (Figures 4.2.2F1–2) the low nitrogen treatment appeared to give one viable primary tiller (T1) and thus an expectation of up to two ears per plant. The number of stems found in the dissection of harvest 5 was 3.5 for cv. Prisma and 3.1 for cv. Tyne (Table 4.2.2T1) and plants from the growth analysis samples in harvest 6 in fact had 1.7 ears for cv. Prisma and 1.8 for cv. Tyne (Table 4.2.2T3).

The High nitrogen treatment did not result in such a clear differentiation between the tillers for leaf development. High leaf numbers occurred on the coleoptile tiller (Tc), T1 and T2 but in cv. Prisma the final leaf number for T3 was also greater than 2. Thus 4 ears per plant could be expected from the leaf data and the stem number in harvest 5 dissections was 4.7 for cv. Prisma and 4.6 for cv. Tyne. The actual number of ears found in the growth analysis samples dissected from harvest 6 was 3.1 for Prisma and 4.2 for cv. Tyne (Table 4.2.2T3). It is possible that the effect of a more competitive T3 in cv. Prisma was to lock up resources, i.e. carbohydrates, that otherwise could have been re–mobilised during the processes of ear filling. However, there were no significant differences between the cultivars for the number of stems per plant dissected from samples at harvest 5 (Table 4.2.2T1) nor at harvest 6 for the number of ears per plant (Table 4.2.2T3b).

4.2.3 Partitioning of dry weight

As was shown earlier in section 4.2.1 the effect of nitrogen shortage was to reduce overall dry matter production by one half. What is also evident is, that whether crop growth ceased at anthesis as in 1989 or continued after anthesis as in 1990, there was a considerable reduction in the dry weight of non-reproductive biomass (NRB) during grain growth (Figure 4.2.3F1). There were noticeable differences in the way the main-stem and tiller tissues responded to nitrogen. In the main-stem, cultivar effects, where present, were more significant than those due to nitrogen (Table 4.2.3T1). The main-stem NRB in cv. Prisma was on average some 33 to 40% heavier than in cv. Tyne. The main-stem ear was 29% heavier at final harvest in cv. Prisma in both years. In contrast, with one exception, there were no detectable cultivar effects in the tiller tissues, either in NRB or the ears. The nitrogen effects were the dominant feature in the tillers. Low N reduced NRB to 38 and 42% of that in High N in 1989 and 1990 respectively. This is in contrast to the main-stems where the reduction was only to 85 and 76% in 1989 and 1990 respectively. The ear weights were similarly affected by nitrogen with the tillers showing reductions to 54 and 47% in contrast to main-stem ears showing no reduction and reduction to 80% in 1989 and 1990 respectively.

The maximum weights of NRB in the main-stem were observed at harvest 4 (around anthesis) in both years, except for the Low N treatment in 1989 which was observed later, at harvest 5. In the tillers the maximum weights of NRB were recorded at harvest 5, although the indications are that the true maximum was a little earlier in the High N treatments. Indeed the maximum in the High N treatment in 1989 was recorded at harvest 4. The absolute reduction by final harvest in weight of NRB from its maximum was similar for main-stems in both Low N and High N treatments within each year, and if anything greater in Low N (in 1989, 78 and 62 g m^{-2} respectively and in 1990, 101 and 91 g m^{-2} respectively). Thus there was a greater proportional reduction in the Low N treatments, 30 compared to 22 % in the High N treatments. In the tillers there was greater absolute reduction in the High N treatments, especially in 1989 (37 and 152 g m^{-2} in Low N and High N). The difference in 1990 was less (71 and 92 g m^{-2}

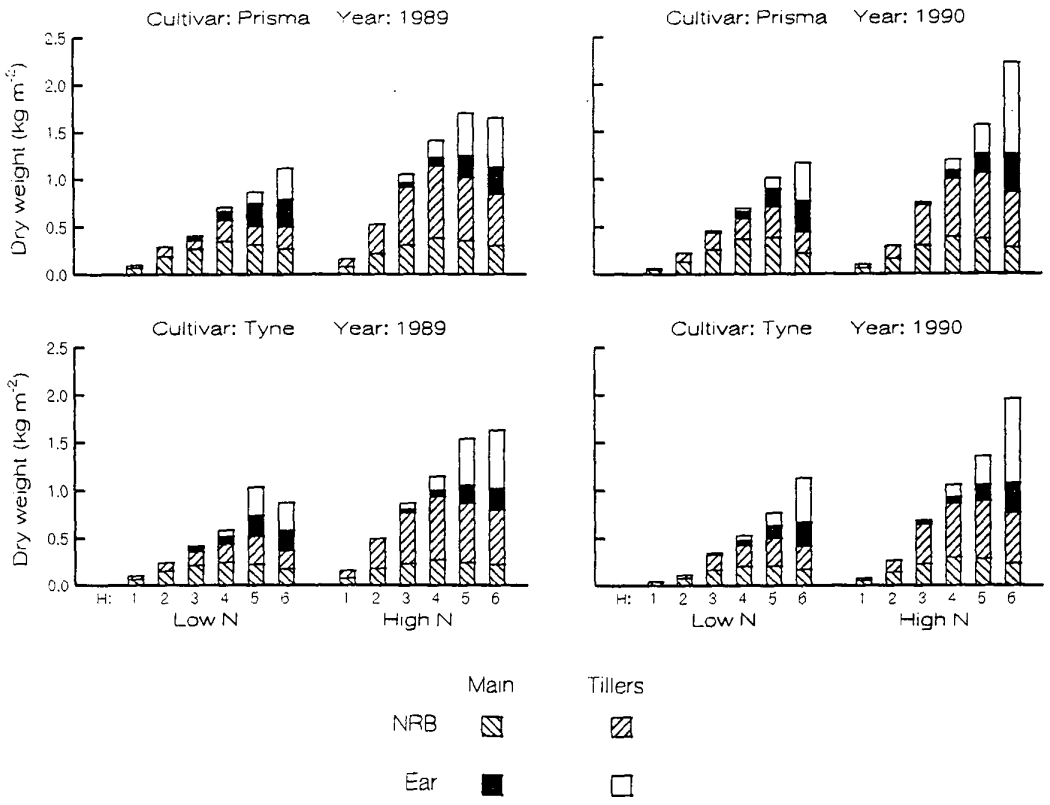


Figure 4.2.3F1 Cumulative graphs of dry weight of non-reproductive biomass (NRB, (stem and leaf tissues) and ears separated into main and tiller stems at each harvest (H).

respectively) reflecting the continuing nitrogen supply during grain growth in that year. The proportionate reductions in the tillers were either similar or considerably less than in the main-stem. In 1989 it was the Low N that had the greatest proportionate reduction whereas in 1990 it was the opposite (1989, 15 and 22%; 1990, 23 and 14% for Low N and High N respectively).

Partitioning of dry weight between the main-stem and tiller (Figure 4.2.3F2) was significantly affected by nitrogen treatment in both seasons at all harvests (Table 4.2.3T2). In 1989 the proportion of dry weight in the main-stem remained relatively constant in time within each nitrogen treatment from around harvest 3 onwards. In contrast, in 1990 there was a gradual decline in the proportion i.e. the proportion of dry weight in the tillers increase steadily with time. By final harvest the proportion of dry weight in tillers was 43% compared to 68% (1989) and 59% compared to 70% (1990) in Low N and High N respectively. Differences between cultivars were less than between nitrogen treatments, and varied in significance (Table 4.2.3T2). However, they were consistently lower in cv. Prisma at all harvests in both years. At final harvest the proportions, average over nitrogen treatments, were 53% compared to 59% (1989) and 61% compared to 68% (1990) in cvs Prisma and Tyne respectively.

Nitrogen increases the amount of leaf tissue produced in a plant. It is often thought that this is due not only to an effect on plant growth rate but also to changes in partitioning between tissue types. This is clearly not the case in these experiments (Figure 4.2.3F3). Within a year there were no significant differences due to nitrogen in partitioning between stem and leaf tissue during canopy expansion (Table 4.2.3T3). The only significant differences due to nitrogen detected were in later harvests in 1989 in leaf tissue. They were small (no more than 4 % and typically less than 2 %) and more probably reflected differences in rates of leaf senescence which were faster in 1989 (see earlier section, proportion of dead leaves increased more rapidly in 1989 due to earlier cessation of nutrient replenishment, Figure 4.2.1F5). Ear dry weight at final harvest varied between 49 and 57% of the total plant dry weight in 1989, and was slightly

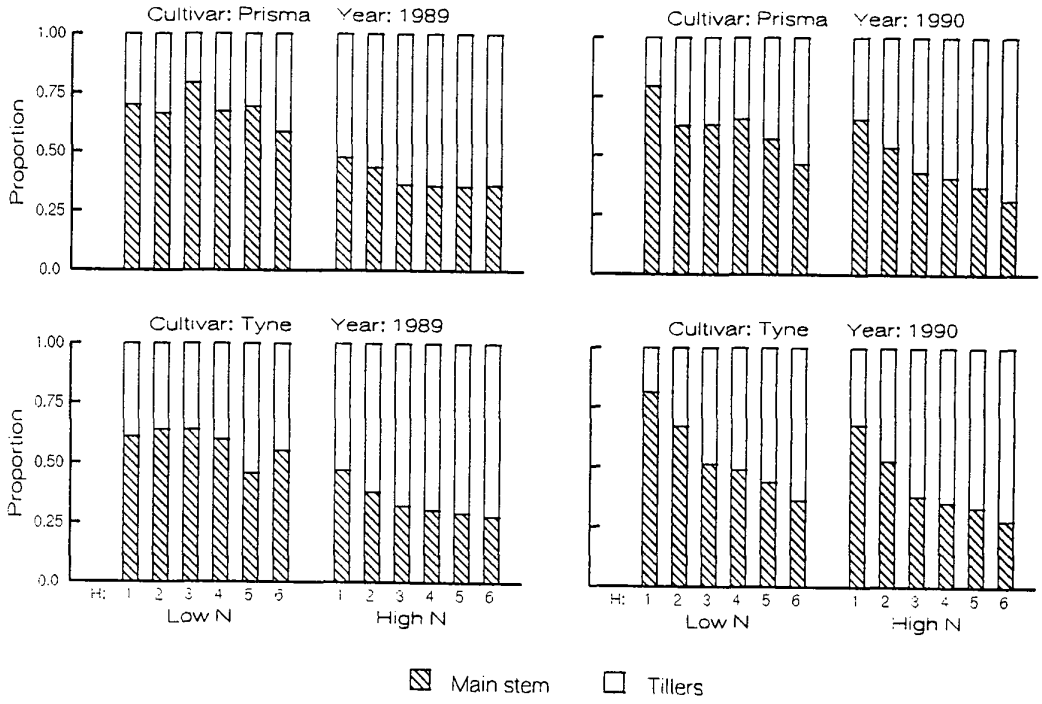


Figure 4.2.3F2 Proportions of total plant dry weight that reside in the main versus tiller stems at each harvest (H).

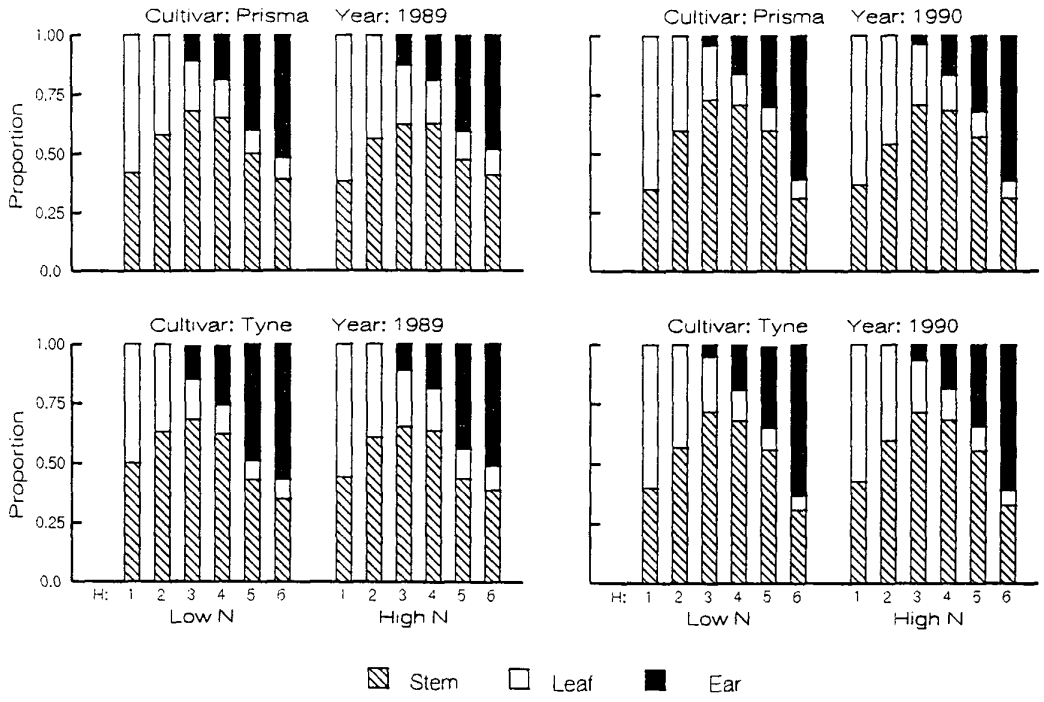


Figure 4.2.3F3 Proportions of total plant dry weight which reside in stem, leaf and ear tissues (averaged over main and tiller stems) at each harvest (H).

higher in 1990, varying between 61 and 63%. There were no consistent differences in partitioning between cultivars.

A similar picture emerges when the partitioning between tissue types within the main-stem and within tillers is examined (Figure 4.2.3F4 and 5). The significant differences in proportion of leaf tissue detected in 1989 (averaged over main and tiller stems) was only detected in the main-stem, and in this case was present throughout and consistently 5 - 7% greater in High N than Low N (Tables 4.2.3T4 and 5). Again differences between cultivars were not consistent over years, except at the first harvest with cv. Prisma having a slightly greater partitioning to leaf growth. The only consistent and significant differences in tiller stems were observed at harvest 5. Cv. Tyne was consistently earlier in its partitioning to ear growth than cv. Prisma. Differences between timing of ear growth were also evident when main and tiller stems were compared. Looking at the proportion of dry weight in ears at harvest 3 in both years (Figures 4.2.3F4 and 5) it was clear that ear growth on the main-stem is slightly earlier than in tillers.

On the main-stem only the later harvests in 1989 showed significant differences in the partitioning of dry weight (Figure 4.3.3F5). Within tillers (Figure 4.3.3F5) dry weight partitioning showed no significant effects and overall tiller ear represented 50-60% of the total dry weight.

In summary, the major effect of nitrogen was on the overall dry matter production, which was manifest in the total amount of dry weight present in the tillers. Once inside either tiller or main-stem the proportions partitioned to tissue types (leaves, stems and ears) was unaffected by nitrogen. Partitioning of dry weight to the ears was slightly earlier in the main-stem than in the tillers. And comparing main-stems of the two cultivars, a slightly greater proportion was initially (harvest 1) partitioned to the leaves in cv. Prisma. The only cultivar differences observed in the tillers was in the slightly earlier partitioning to ears in cv. Tyne.

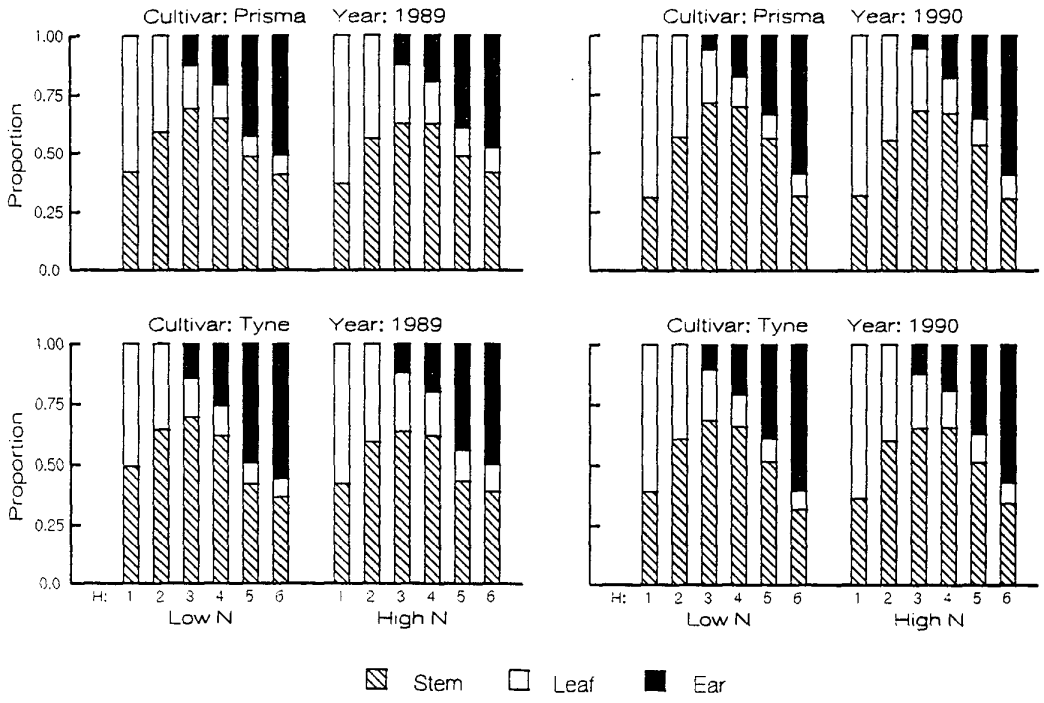


Figure 4.2.3F4 Proportions of the total dry weight in the main stem which reside in the stem, leaf and ear tissues at each harvest (H).

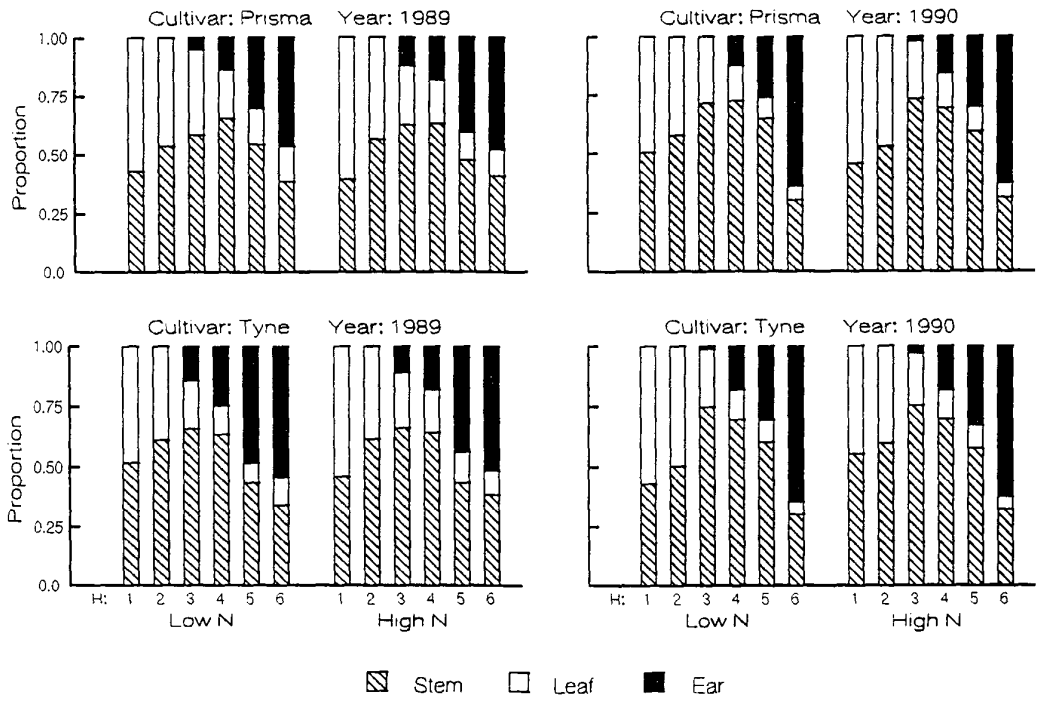


Figure 4.2.3F5 Proportions of the total dry weight in the tillers which reside in the stem, leaf and ear tissues at each harvest (H).

4.2.4 Partitioning of nitrogen

The difference due to nitrogen treatment on the total amount of nitrogen taken up, as stated previously (section 4.2.1), was relatively greater than the effect on dry weight accumulation (3:1 compared to 2:1, High N:Low N). The presence or absence of significant effects on the absolute amount of nitrogen in NRB and ears, separated into main-stem and ears, mirrored those of dry weight (compare Table 4.2.4T1 with the corresponding table for dry weight, Table 4.2.3T1 in the previous section). As was evident with dry weight, whether crop growth ceased at anthesis as in 1989 or continued after anthesis as in 1990, there was a considerable decline in the amount of nitrogen in the non-reproductive biomass (NRB) during grain growth (Figure 4.2.4F1). There were similar contrasts in the way the main-stem and tiller tissues responded to nitrogen. In the main-stem, cultivar effects where present, were more significant than those due to nitrogen, excepting harvest 1 (Table 4.2.4T1). The main-stem NRB in cv. Prisma contained on average 9% more nitrogen than in cv. Tyne, and although equally significant, was considerably less than the relative differences observed in the previous section between average dry weights of the two cultivars (33 to 40% heavier). There was 39% more nitrogen in the main-stem ear in cv. Prisma than cv. Tyne at final harvest in both years. This difference was greater than the corresponding relative difference for dry weight (29%) - both differences (nitrogen and dry weight) between cultivars reached a maximum at final harvest.

As with dry weight, with two exceptions (NRB at harvest 1 in both years), there were no detectable cultivar effects in the tiller tissues, either in NRB or the ears. The nitrogen effects were the dominant feature in the tillers. At final harvest, Low N reduced the nitrogen in the NRB to 15 and 29% of that in High N in 1989 and 1990 respectively. In main-stems the nitrogen effect on NRB was less - reductions to 32 and 57% in 1989 and 1990 respectively. The quantities of nitrogen in the tiller ears were reduced to 41 and 27% in contrast to main-stem ears, showing smaller reductions to 75 and 61% in 1989 and 1990 respectively. There is an interesting contrast between the two years: when nitrogen supply is reduced during grain growth (as in 1989) the

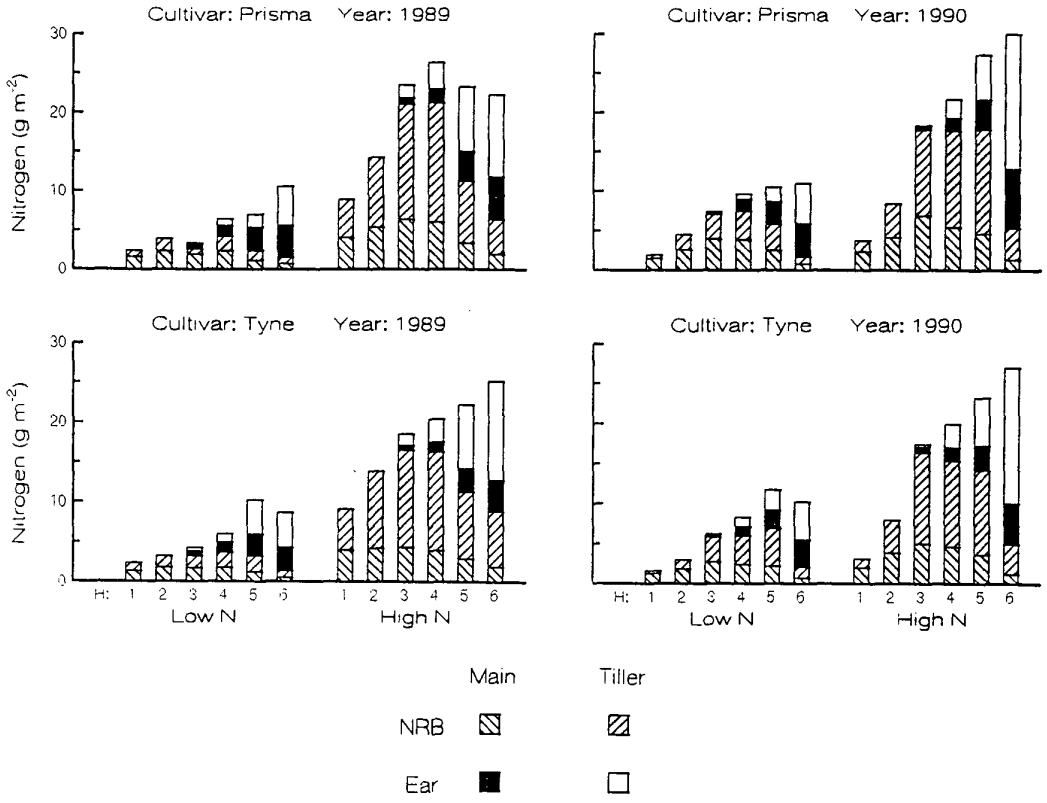


Figure 4.2.4F1 Cumulative graph of nitrogen contents of non-reproductive biomass (NRB, stem and leaf tissues) and ears, separated into main and tiller stems at each harvest (H).

effect of Low N, relative to High N, on the amount of nitrogen in the NRB is enhanced whereas the effect in the ears is diminished and vice versa, when nitrogen supply is maintained throughout grain growth (as in 1990). This phenomenon was present in both tillers and main-stem, moreover it was not reflected in the dry weights of either NRB or ear tissues (see section 4.2.3).

The maximum nitrogen contents of NRB in the main-stem and the tillers were observed at harvest 4 (around anthesis) in 1989, and a little later in 1990, harvest 5 (Figure 4.2.4F1). The absolute reduction by final harvest in nitrogen content of NRB in main-stem from its observed maximum, in the Low N was slightly greater than one half that observed in the High N treatment in both years (in 1989, 1.46 and 3.43 g(N) m^{-2} for Low N and High N respectively; in 1990, 2.58 and 4.66 g(N) m^{-2} respectively). Likewise in the tillers, the absolute reductions were greatest in the High N (in 1989, 1.05 and 8.12 g(N) m^{-2} in Low N and High N; in 1990, 2.88 and 7.98 g(N) m^{-2} respectively). However, the proportionate reductions within main-stem and tillers were very similar in both nitrogen treatments and years (Table 4.2.4T2). The reductions were slightly greater in 1990 compared to 1989. The average reduction in nitrogen content over the two years was 73% for main-stems and 63% for tillers (Table 4.2.4T2). They are much greater than the corresponding values for reductions in dry weight, which were typically less than 20% and variable (see Section 4.2.3).

Partitioning of nitrogen between the main-stem and tiller (Figure 4.2.4F2) was significantly affected by nitrogen treatment in both seasons at all harvests (Table 4.2.4T3). The patterns of partitioning mirrored those of dry weight in the same tissues, with the proportion of nitrogen going to the tillers being systematically greater than that for dry weight (consistent over cultivars, nitrogen and years), albeit a small difference of 0.028 between the proportions (nitrogen and dry weight) throughout. In 1989 the proportion of nitrogen in the main-stem remained relatively constant in time within each nitrogen treatment from around harvest 3 onwards. In contrast, in 1990 there was a gradual decline in the proportion i.e. the proportion of nitrogen going to the tillers increased steadily with time. By final harvest the proportion of nitrogen in tillers in

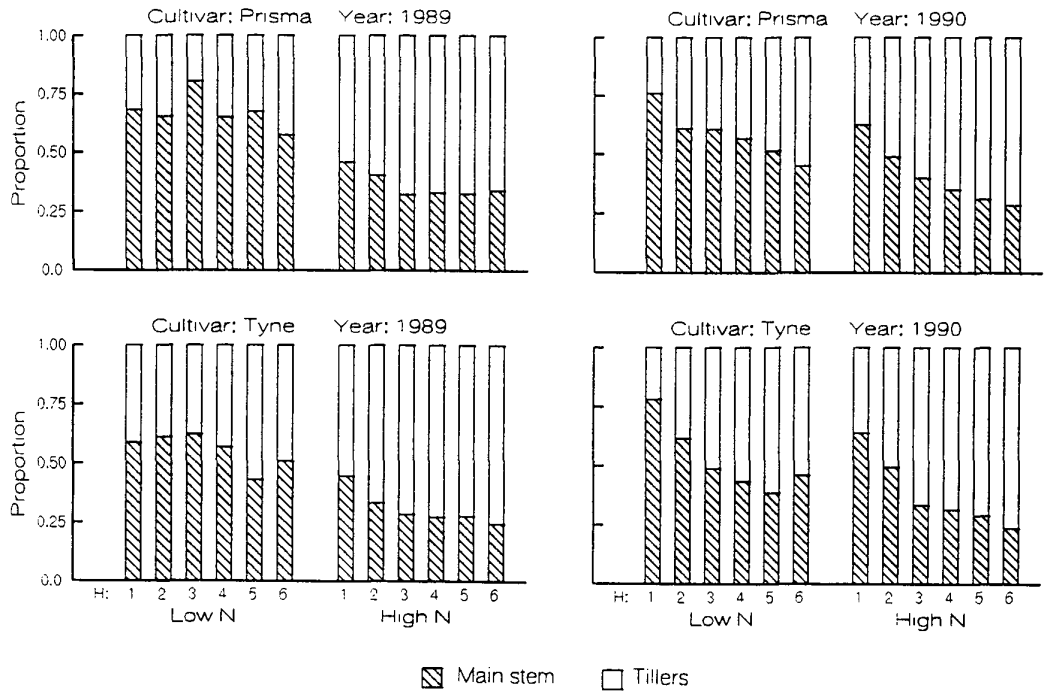


Figure 4.2.4F2 Proportions of the total plant nitrogen that reside in the main versus tiller stems at each harvest (H).

1989 was 46% compared to 71% in Low N and High N respectively, and in 1990 54% compared to 74% in Low N and High N respectively. As with dry weight, differences between cultivars were less than between nitrogen treatments, and varied in significance (Table 4.2.4T3). The proportion of nitrogen found in the tillers tended to be lower in cv. Prisma than cv. Tyne. However, this was not as consistent a difference as found in dry weight – the exceptions being harvests 1 to 3 in 1990 in both Low N and High N. At final harvest the proportions, averaged over nitrogen treatments, were 54% compared to 62% (1989) and 63% compared to 65% (1990) in cvs Prisma and Tyne respectively.

The partitioning of nitrogen between tissue types (stem leaf and ear) was little affected by nitrogen treatments as with dry weight (Figure 4.2.4F3). What significant differences in partitioning between stem and leaf tissue during canopy expansion due to nitrogen that were detected (Table 4.2.4T4) were not consistent over years. Significant differences due to nitrogen, that were present in both years, were detected in later harvests. The biggest differences were at harvest 4 in 1989, as much as 0.20 difference in the proportions of nitrogen found between ears sampled from Low N and High N. The corresponding difference in 1990 was much smaller, typically 0.03. This contrast reflected the difference in uptake between the two years. The demand for nitrogen by the filling grain could not be met by uptake in 1989, and resulted in earlier relocation of nitrogen from the nitrogen rich photosynthetic (leaf) and carbohydrate storage (stem) tissues in the Low N. This is consistent with the higher rates of leaf senescence in 1989 (see earlier section, proportion of dead leaves increased more rapidly in 1989 due to earlier cessation of nutrient replenishment, Figure 4.2.1F5). Ear nitrogen contents at final harvest were similar in both years, varying between 67% and 85% of the total plant nitrogen in 1989, and between 77% and 85% in 1990. There were even fewer significant effects of cultivar detected for nitrogen than was the case for dry weight, and non were consistent. Contrasting the time course of partitioning between tissue types of nitrogen (Figure 4.2.4F2) with that previously for dry weight (Figure 4.2.3F2) highlights three important features; nitrogen in the leaf achieves a greater maximum proportion than dry weight (vice versa in the stem), the partitioning of nitrogen to the

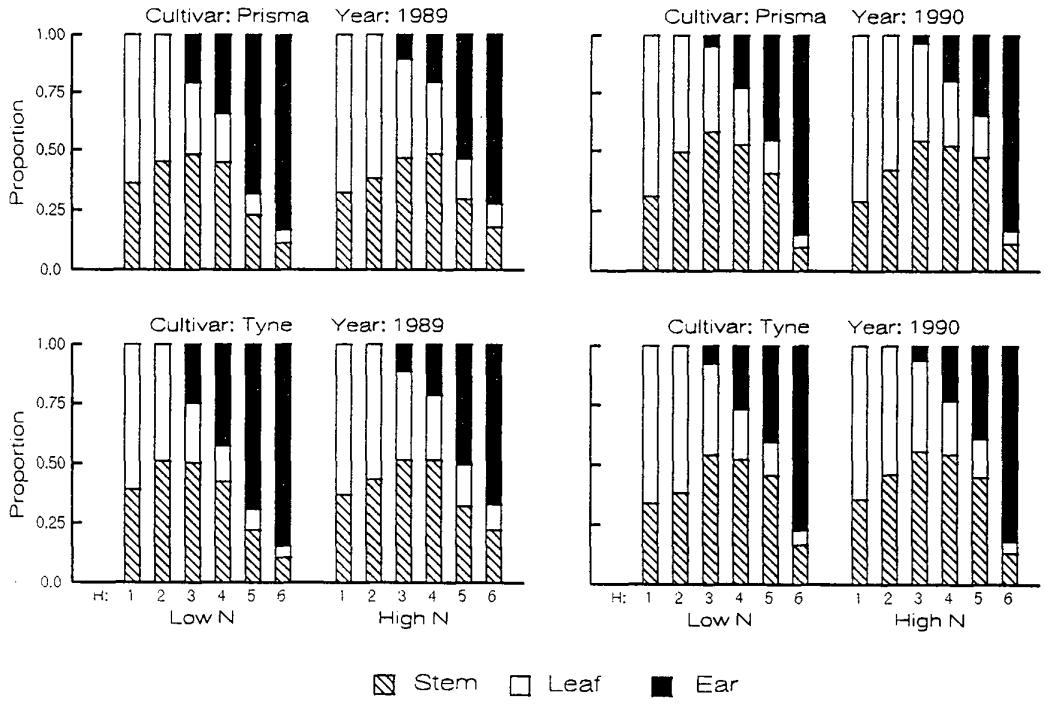


Figure 4.2.4F3 Proportions of the total plant nitrogen which reside in stem, leaf and ear tissues (averaged over main and tiller stems) at each harvest (H).

ear precedes that for dry weight, and a greater proportion of nitrogen than dry weight is apparently moved to the ear from leaves by final harvest.

The patterns of partitioning between tissues (stem, leaf and ear) within stem types (Figure 4.2.4F4 and 5) reflected those just discussed, averaged over the whole plant. The additional feature being the difference in timing of ear nitrogen between main-stem and tillers, which was even more pronounced than that for dry weight. Partitioning of nitrogen to the ear tissues in the main-stem was clearly ahead of the same partitioning in the tillers. However, by final harvest this difference in partitioning had disappeared. In 1989, with the reduced nitrogen supply during grain filling, significant differences between Low N and High N in the partitioning to leaves and ears was detected in both main-stem and tillers (Table 4.2.4T5 and 6). This difference was more pronounced with nitrogen than with dry weight, which could only be detected in the main-stem (see Figure 4.2.3F4 and 5). Few significant effects of cultivar were detected and none were consistent.

In summary, like dry weight, the major effect of nitrogen was on the total amount taken up and the changing proportion of nitrogen found in the tillers. Once inside, a stem type, nitrogen level had little effect on the proportion of nitrogen partitioned to the different tissues. However, differences in the implementation of treatments between the two years did lead to differences between Low N and High N in the timing of partitioning to the ears in 1989 (Low N being earlier than High N). Few significant, and even less consistent, effects due to cultivar were found. The contrasts highlighted between partitioning of nitrogen and dry weight were consistent with leaves being the main tissue source for nitrogen, and stems the main tissue source for carbon during grain growth i.e. in addition to the nitrogen taken up and carbon fixed during that time.

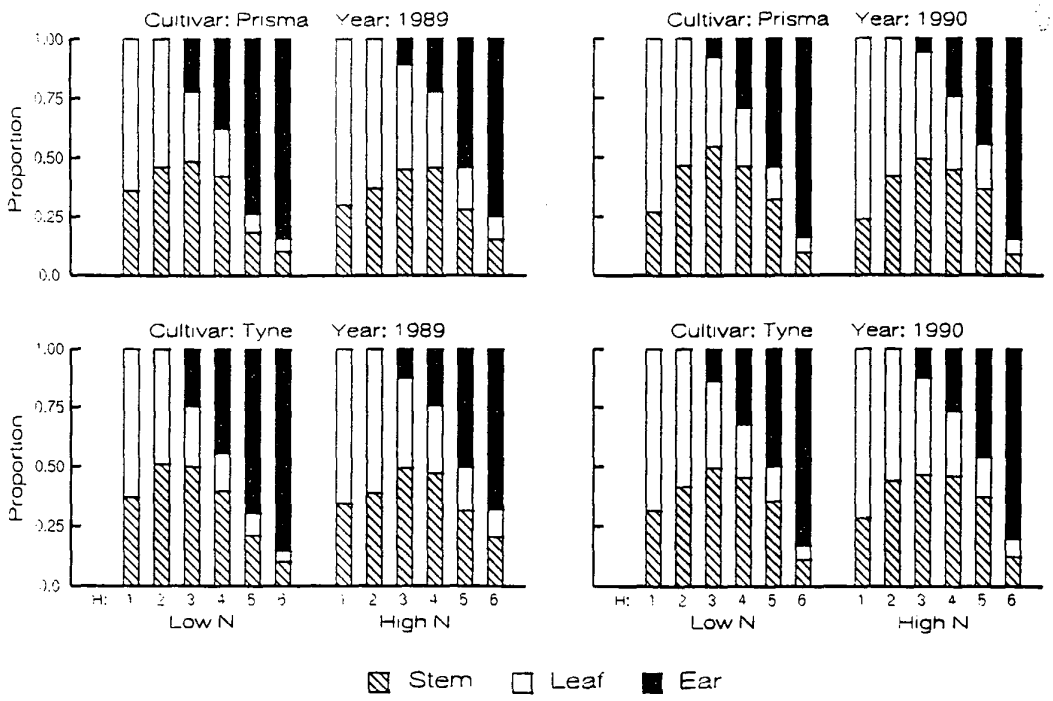


Figure 4.2.4F4 Proportions of the total nitrogen in the main stem which reside in the stem, leaf and ear tissues at each harvest (H).

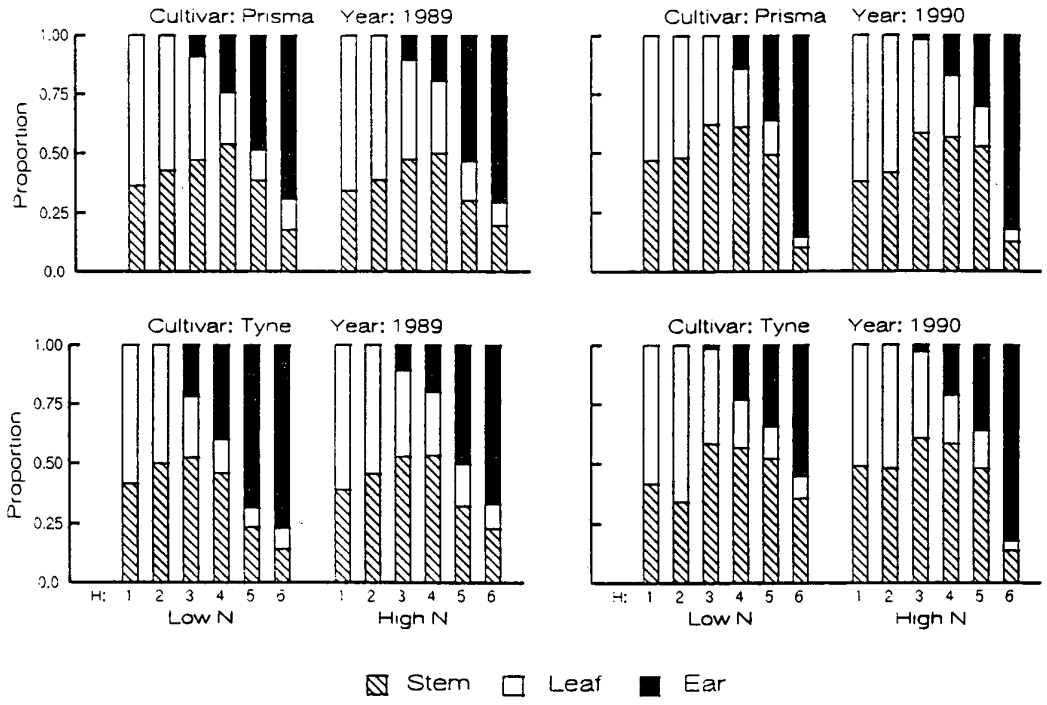


Figure 4.2.4F5 Proportions of the total nitrogen in the tillers which reside in the stem, leaf and ear tissues at each harvest (H).

4.2.5 Concentration of nitrogen

In the previous two sections we considered the net movement of carbon (dry weight) and nitrogen into and out of the three above ground tissue types in both main-stem and tillers. In simplest terms, the balance of these two elements within a tissue determines the nitrogen concentration of that tissue. At a gross scale, the nitrogen concentration of the whole plant is an indicator of whether the plant's uptake of nitrogen is optimal for growth (see Figure 4.2.1F3). This will be developed further in the Discussion (Section 5). Looking in more detail, the role of nitrogen varies between the different tissues. In leaf tissue its primary function is to contribute to the photosynthetic capacity of the crop canopy. In the stem it is also associated with photosynthetic apparatus, and in addition can act as a temporary storage for nitrogen. The photosynthetic apparatus can also be dismantled and the nitrogen associated with it redistributed elsewhere in the plant. In the ear, the vast majority of the nitrogen ultimately ends up in the grain and forms a nitrogen reserve for the initial growth of the new seedling. As with nitrogen, so the role of carbon varies between tissue types. In the leaf it is principally there as structural support. Assimilates that are produced are rapidly transported elsewhere in the plant. In the stem carbon is present both as structural support and as storage. Storage tends to reach a maximum just before grain growth commences. Thus the nitrogen concentration in a tissue is not simply a passive, instantaneous balance of the net inflow of carbon and nitrogen, it is the integration of the entire history of the plant, with active feedbacks on growth rate and sources of carbon and nitrogen if required in the future.

In Section 4.2.1 it was shown that at the level of the whole plant the nitrogen treatments imposed resulted in approximately one third less nitrogen being taken up in the Low N compared to the High N treatments in both years. Secondly that the effect of this difference in nitrogen uptake on growth was less i.e. plant dry weight was reduced by only one half and not two thirds. Thirdly, there was little or no difference between cultivars in these effects. As a consequence nitrogen concentrations, averaged over the whole plant (roots not included), in the Low N treatments, were approximately two

thirds of that in the high N treatments at the final harvest – time courses being very similar in both cultivars. Earlier in the season the relative differences were greater in 1989 and less in 1990 (see earlier Figure 4.2.1F3). Again these effects were similar in both cultivars.

The effects of nitrogen uptake and cultivar on the nitrogen concentration of the three tissue types in both main–stem and tiller stems is now examined. Figures 4.2.5F1 through to 4 each show the concentrations in the leaf, stem and ears on both main–stem (solid line) and tillers (dashed line) for a particular nitrogen level and cultivar. Figures 4.2.5F1 and 2 contrast High N and Low N for cv. Prisma, and Figures 4.2.5F3 and 4 do likewise for cv. Tyne. Throughout the concentration of nitrogen in the leaves (live + dead) was higher than in the stems in all treatments. The first observation of nitrogen concentration in the ear (shortly after anthesis) was always greater than the stem and usually less than in the leaf – the exception being the Low N in 1989 (Figures 4.2.5F2a and 4a). In contrast to the steady declines of nitrogen concentrations in the leaf and stem tissue, the concentrations of nitrogen in the ear were notably steady over time, in all treatments.

Without exception the nitrogen concentrations in the leaf and the stem tissues in the High N treatments were consistently higher in the tillers compared to the main–stems. In the Low N treatments the difference was smaller, and some times not present. Similar but smaller differences were also observed between the ears from main–stem and tillers in High N. Averaged over cultivars and years, at final harvest, ears borne on tillers were higher in nitrogen concentration by 1.9 ± s.e. 0.5 mg(N)/g(DW), that is greater by 0.19 %N, than ears borne on main–stems in High N. The difference appeared to be greater in cv. Tyne – an average of 2.7 mg(N)/g(DW) over the two years compared to an average of 1.1 mg(N)/g(DW) for cv. Prisma. There was no detectable difference between ears on main–stems and tillers in the Low N treatments.

A second feature, as was noted in previous sections, was the contrast between years. The initially slower supply rate of nitrogen in the 1990 experiment is reflected in the

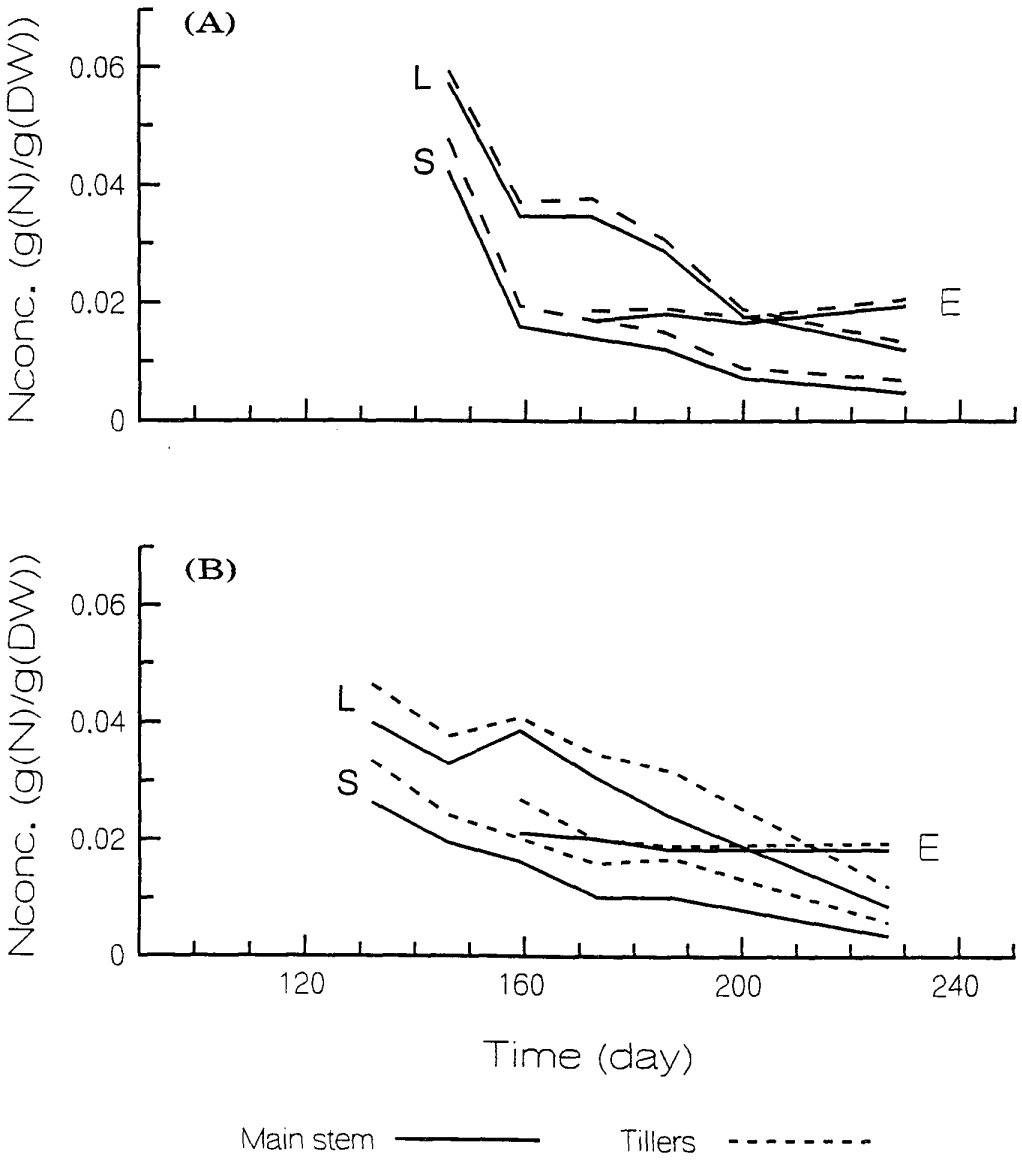


Figure 4.2.5F1 The change in nitrogen concentration of total leaf (L, live+dead), stem (S) and ear (E) with time (day number in the year) in main and tiller stems in cv. Prisma, High N in (a) 1989 and (b) 1990.

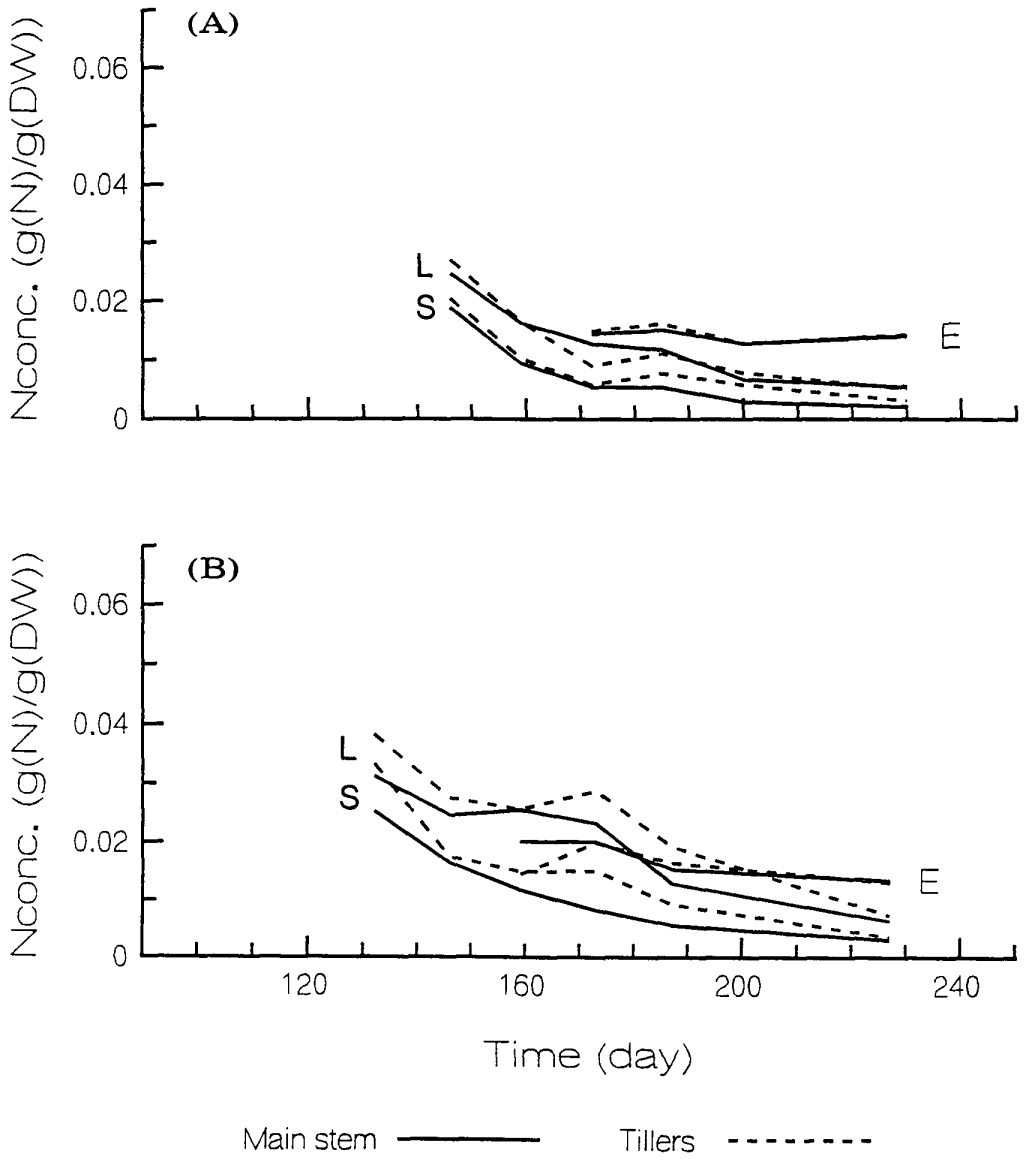


Figure 4.2.5F2 The change in nitrogen concentration of total leaf (L, live+dead), stem (S) and ear (E) with time (day number in the year) in main and tiller stems in cv. Prisma, Low N in (a) 1989 and (b) 1990.

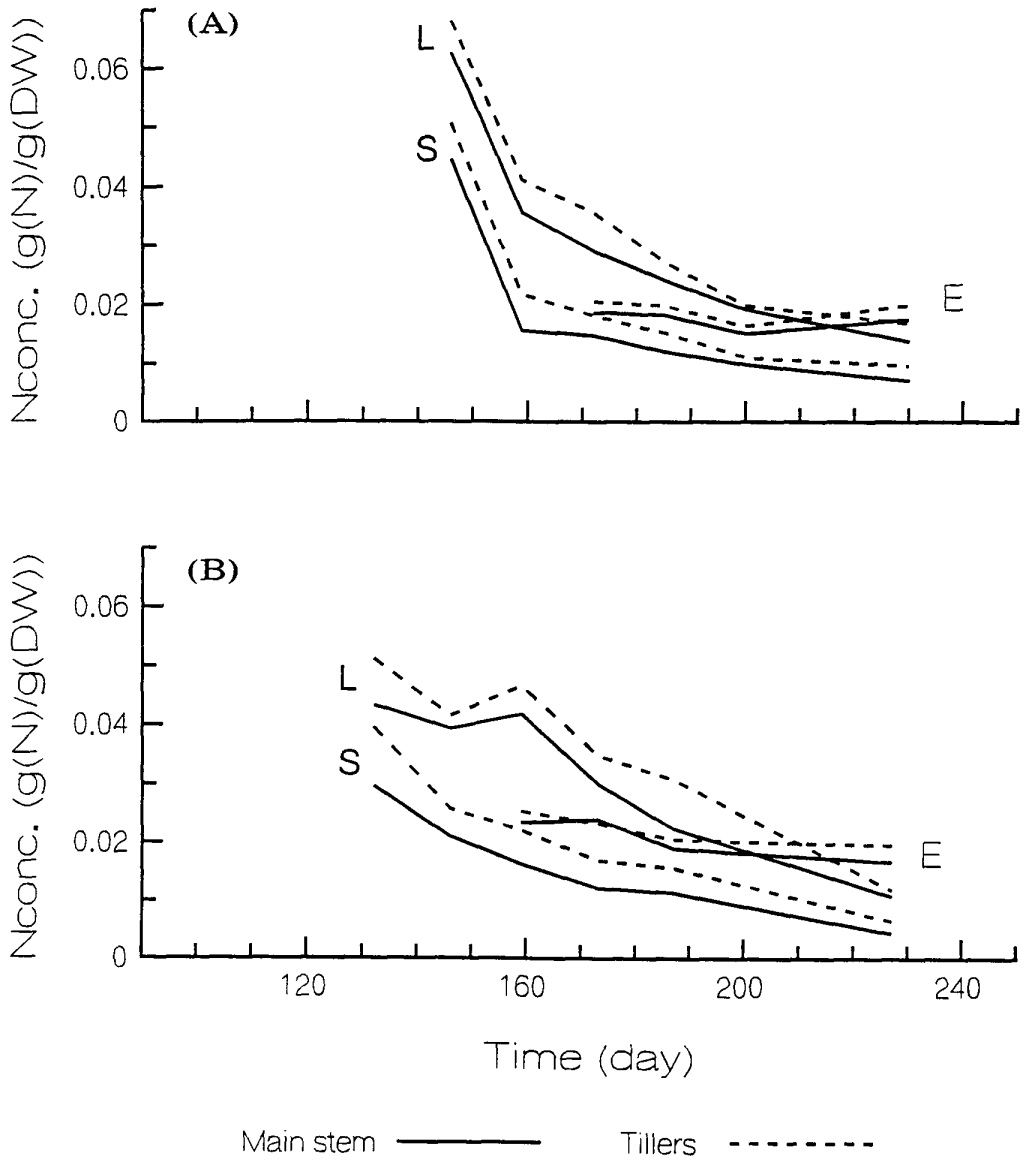


Figure 4.2.5F3 The change in nitrogen concentration of total leaf (L, live+dead), stem (S) and ear (E) with time (day number in the year) in main and tiller stems in cv. Tyne, High N in (a) 1989 and (b) 1990.

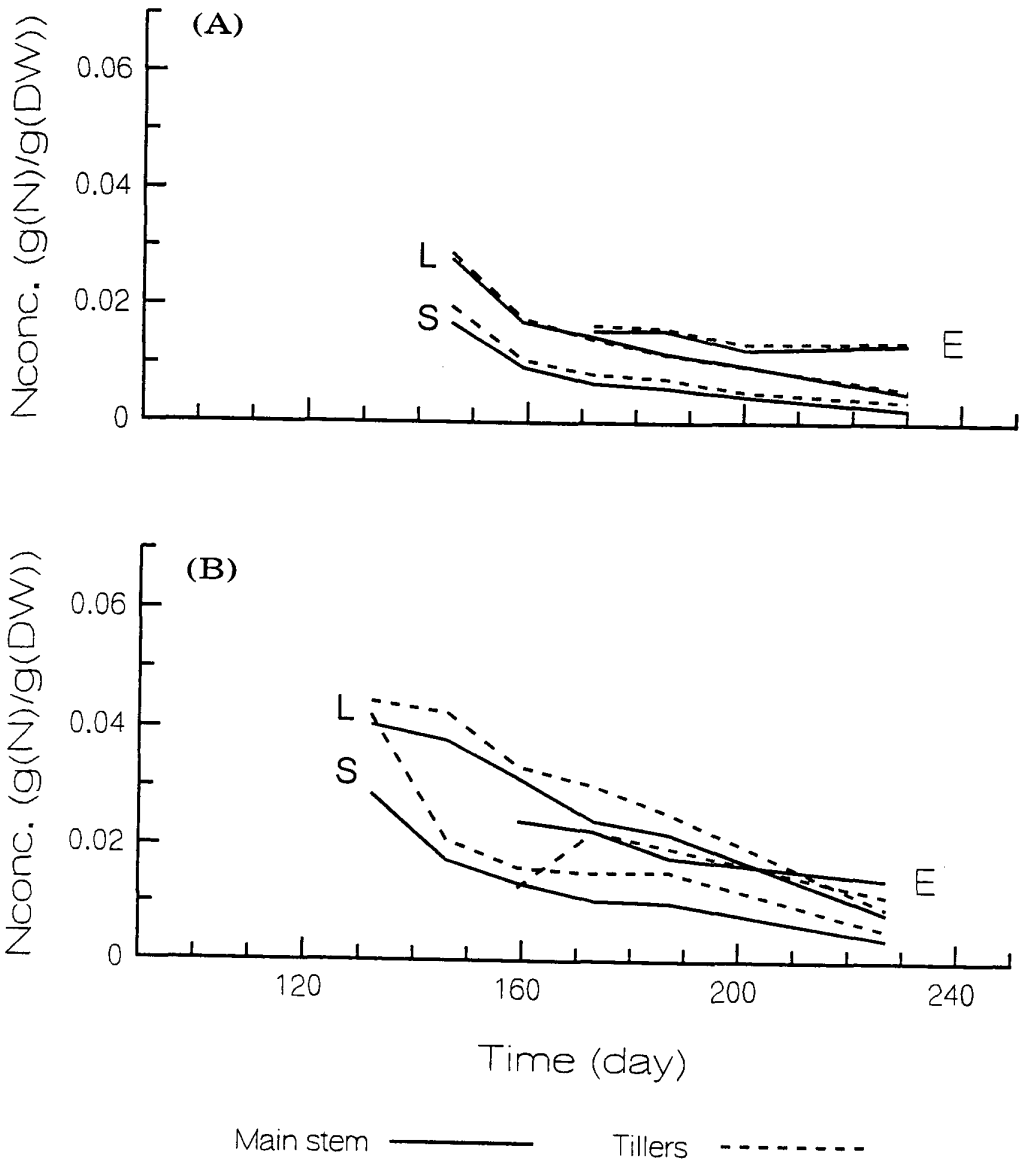


Figure 4.2.5F4 The change in nitrogen concentration of total leaf (L, live+dead), stem (S) and ear (E) with time (day number in the year) in main and tiller stems in cv. Tyne, Low N in (a) 1989 and (b) 1990.

lower nitrogen concentrations early on in the leaf and stem tissues of the High N, in contrast to 1989. However, the same is not true in the Low N, where initial concentrations are greater in 1990. Thus there must have been more nitrogen available in the seed bed in 1990 (the perlite was pre-soaked with nutrient solution but initially there was no nutrient recirculation) than was available through recirculation to the beds in the Low N treatments in 1989.

Table 4.2.5T1 summarises the tests for significant differences due to nitrogen, cultivar and their interaction on the different tissue types. The levels of significance of the main effects of nitrogen were generally greater in 1989 than 1990, in all tissue types whether on main-stem or tiller. This was due, at least in part, to the smaller absolute differences in nitrogen concentration between High N and Low N in 1990 - contrast Figure 4.2.5F1 with 2 (cv. Prisma) or Figure 4.2.5F3 with 4 (cv. Tyne). Greater variability in nitrogen concentration may be a second reason. Despite the tendency for nitrogen concentrations in leaves and stems from both High N and Low N to converge to a mutually low concentration, the final concentrations in these tissues were still different and with the same or greater degree of significance than earlier harvests.

Cultivar differences were less significant than nitrogen. Differences in leaf concentrations in both main-stem and tillers were detected in the early harvests in 1990. Concentrations were lower in cv. Prisma (typically by 5 mg(N)/g(DW)) than in cv. Tyne in the first three harvests in 23 out of 24 possible comparisons (3 harvests x 2 nitrogen treatments x 2 years x 2 stem types). In the main-stems differences were detected during grain growth, particularly around harvest 5 in both years. Again cv. Prisma had a lower concentration of nitrogen in the stem (by 2.2 and 2.6 mg(N)/g(DW) at harvest 5 in 1989 and 1990 respectively). The concentrations at harvests either side of harvest 5 were also consistently lower in cv. Prisma than cv. Tyne, although the absolute difference was less. This may indicate a difference in timing of development between the two cultivars; cv. Prisma being slightly further on. Generally, there was no detectable, significant difference in ear nitrogen concentration between cultivars at final

harvest, however, in 7 comparisons out of 8 (probability = 0.070), over the two years, the concentration was slightly higher cv. Prisma (Table 4.2.5T2).

The nitrogen concentration of the non-reproductive biomass (NRB, leaf plus stem) of the shoot may be a better indicator of the ability of the canopy to photosynthesise than the concentration averaged over the whole shoot, particularly during grain growth. The latter includes an increasing and ultimately large pool of nitrogen not associated with photosynthesis, whereas in the leaf 75 % of the nitrogen is found in the chloroplast. The stem is intermediate. The patterns of decline in nitrogen concentration in the leaf are mirrored in the stem. Figure 4.2.5F5 shows the time course of nitrogen concentration in the NRB. The contrast between years is clearly evident. And the similarity between cultivars is also evident, with the exception of cv. Tyne in the Low N treatment in 1990, which is higher than the corresponding treatment for cv. Prisma. This difference appears to be due to higher concentrations in the leaf rather than stem compared to cv. Prisma (Figure 4.2.5F4 compared to 4.2.5F2). Most surprising, at first sight, is the apparent lack of a major effect of nitrogen on concentration of NRB in 1990. Seeing this figure on its own could easily lead the observer to conclude that there was little difference between the two treatments, and yet final yields had a two-fold difference! This highlights the danger of considering nitrogen concentration of plant tissues on their own, and even worse, taking a single snap shot in time to asses plant status. The levels of significance of the variation due to nitrogen and cultivar generally reflect those of leaf and stem discussed earlier (Table 4.2.5T3).

In summary, the major differences in nitrogen concentration were due to the nitrogen treatments, rather than differences between cultivars. The leaf and stem tissues always had a higher concentration on the tillers than on the main-stem. In the ears this was only true in the High N treatments - there was little or no difference between stem types in the Low N treatments. Nitrogen concentrations in the leaf tissue, which is a major source of nitrogen for the ear, are always greater than in the stem tissue, which is a major source of carbon during grain growth. Whereas concentrations in the leaf and stem tissues decline with time and tend to converge, the ears show little variation with

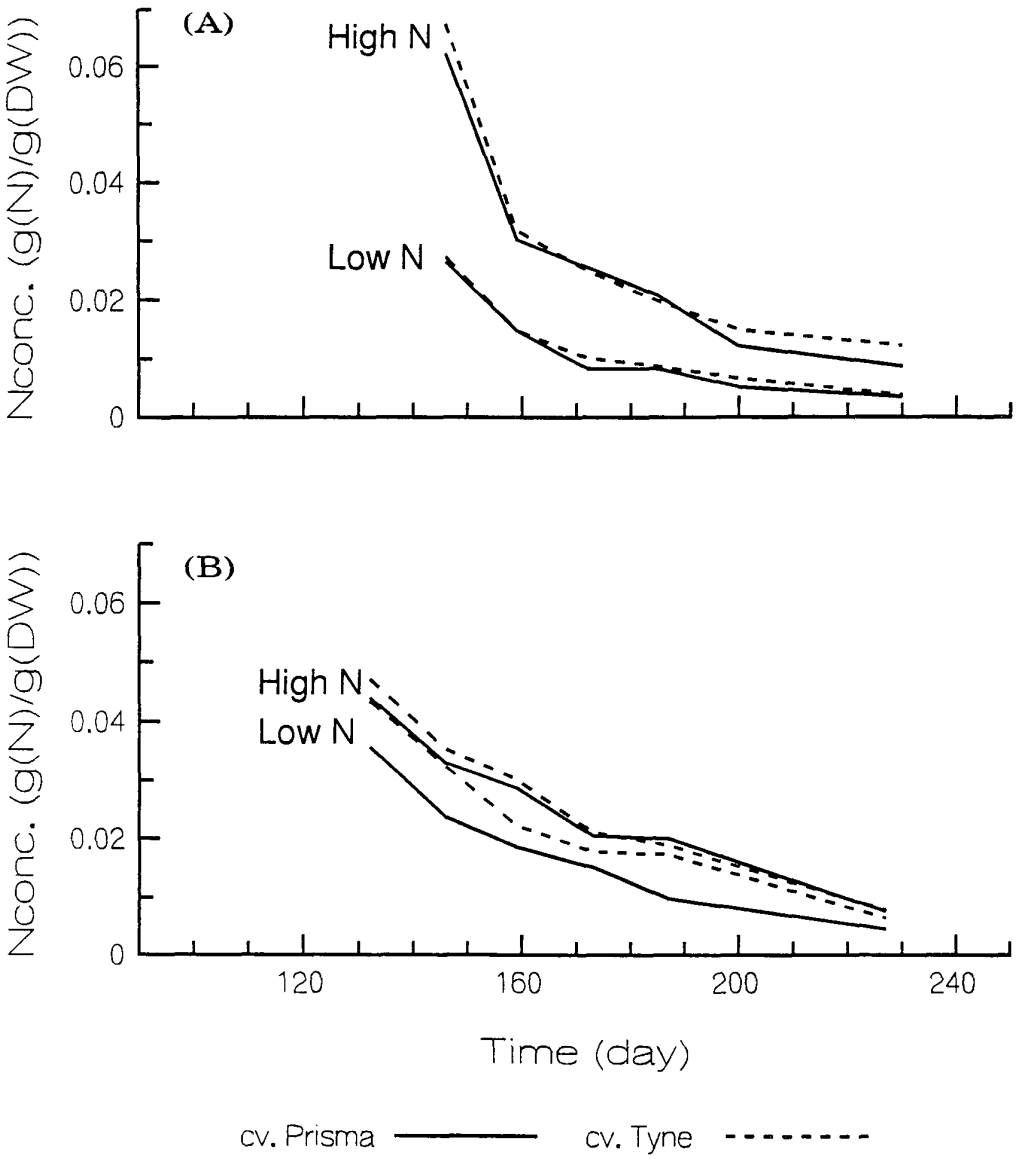


Figure 4.2.5F5 The change in nitrogen concentration of the non-reproductive biomass (leaf+stem) with time (day number in the year) in cvs Prisma and Tyne with High N and Low N in (a) 1989 and (b) 1990.

time and differences between stem types and nitrogen treatments are maintained throughout.

Nitrogen concentration by itself is not a good indicator of the growth status of the plant. Its location and absolute quantities of nitrogen need to be known.

In previous sections, we have seen differences between stem types in timing of dry weight to the ears and likewise for nitrogen. We have now seen differences between stem types in ear N concentration, particularly in High N treatments. This has implications both for seed performance and malting quality which will be addressed in the next section.

4.2.6 Grain quality

The influence of nitrogen fertiliser on the main characteristics determining the value of a bulk grain sample for malting is shown in Figure 4.2.6F1. Given the cultivar and moisture content, the main determinant of the premium paid, because of its direct influence on the HWE, is the average nitrogen concentration of the grain. The average thousand corn weight (TCW), which influences the proportion lost in sieving, is of secondary importance but nevertheless significant. These are the factors as seen by the maltster in setting the buying price from the farmer (solid lines Figure 4.2.6F1). Grain nitrogen concentration is determined by the balance of nitrogen and dry weight partitioned to the grain which in turn is dependent on the quantity and pattern of nitrogen uptake. These aspects have been presented in earlier sections. TCW is determined by the grain number per unit area and the yield. Again both these characters are influenced by the amount of nitrogen taken up.

The implicit assumption made in determining the premium to be paid is that it does not matter how these two averages (nitrogen concentration and TCW of the bulk grain sample) are achieved. If two crops of the same genotype have the same two average values and moisture content then they are deemed to be of the same quality. The question is whether this assumption is valid and if not what are the opportunities for manipulating the quality via management and or breeding. To answer this question one needs to know what and how great are the sources of variation in grain quality within the plant.

The plant is comprised of several stem types, the number of which is influenced by environmental factors such as the nitrogen supply, planting density and water supply as well as the genotype. The variation between stem types and in particular the ears they bear is one potential source of variation. Differences in growth between main-stem and tillers in response to nitrogen supply have been shown. The earlier partitioning of nitrogen and dry weight to main-stem ears compared to tillers is one such example (Sections 4.2.3 and 4.2.4). The second source of variation is within the ear i.e. the

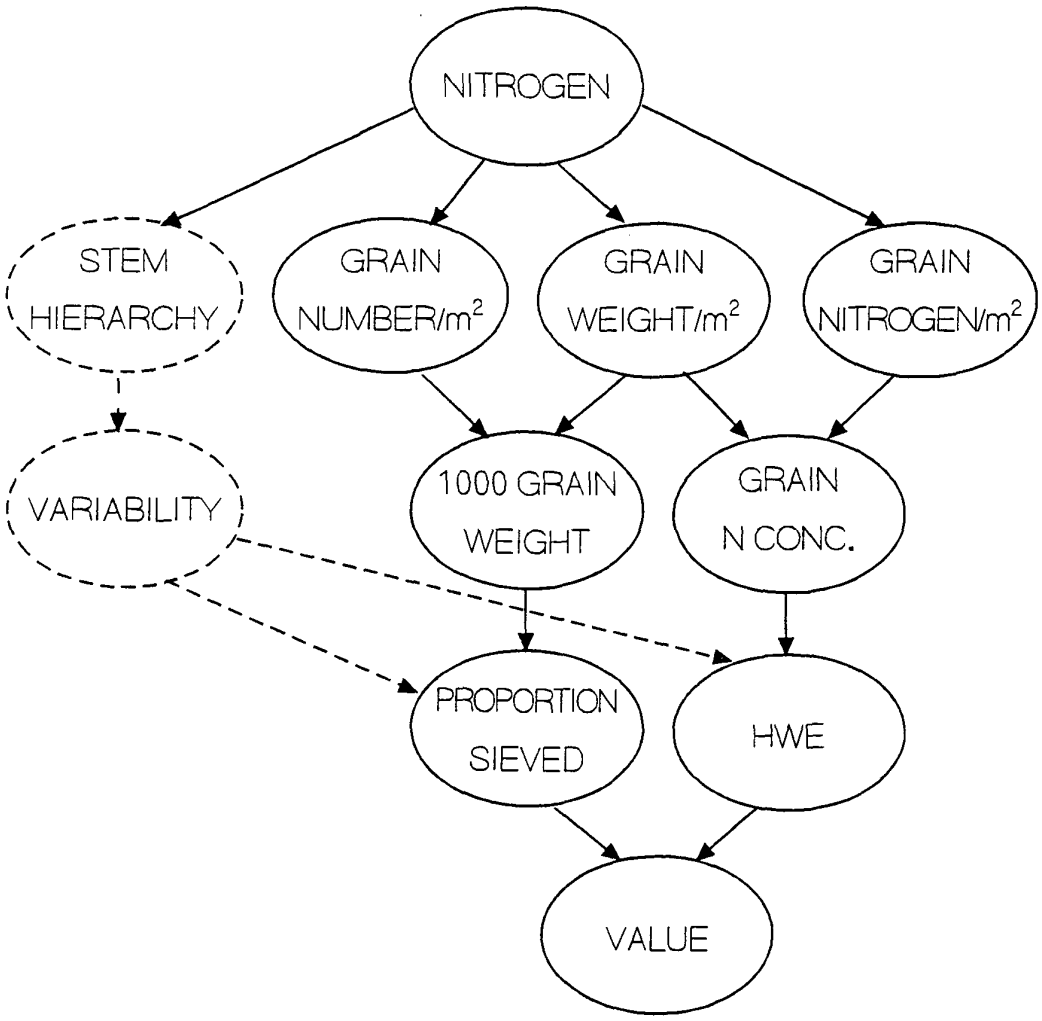


Figure 4.2.6F1 The influence of nitrogen on characteristics determining the commercial value of barley grain samples for malting. The solid lines indicate the current situation for bulk grain samples. The dashed lines indicate sources of variation between bulk samples with the same 1000 grain weight and average nitrogen concentration.

position of the grain on the ear. Several examples of the variation in grain weight with position in the ear are given in the literature (Ellis & Kirby, 1980; Kirby & Riggs, 1978). The scale of this variation may depend on nitrogen fertilisation and ear type. If this is the case then stem hierarchy in the plant has important implications for the variability of quality within a bulk sample and may influence the HWE and proportion lost in sieving (dashed lines Figure 4.2.6F1).

Nitrogen influences individual grain quality through three possible mechanisms: effect on grain size, straight dilution and differences in maturity. In this study these aspects are quantified by grain weight, nitrogen concentration and rate of germination. The variation of these quantities by grain position and between ear types was examined in detail from modal stem material collected at final harvest from the controlled nutrient experiments (1989 and 1990, Section 3.3.2). The other consequence of variation in the time of grain maturity i.e. variable periods of post-harvest dormancy, was not examined as all samples tested for germination were out of dormancy.

Variation of grain weight – Estimation of parameters

It was not possible to find a continuous function that would provide an unbiased description of the change in grain size with position on the ear. The Beta function, although having many of the features of the observed variation, had systematic deviations that led to biased estimates of maximum grain weight and its location and had significant correlations between several of its parameters. Consultation with other experts in the field, including theoretical biologists, led to no suitable alternative.

Thus it was decided to estimate the main features of the distribution separately. The parameters and their methods of estimation are shown in Figure 4.2.6F2. The fitted parameters are:-

R the number of grain bearing positions

W_{max} the weight of the heaviest grain on the ear

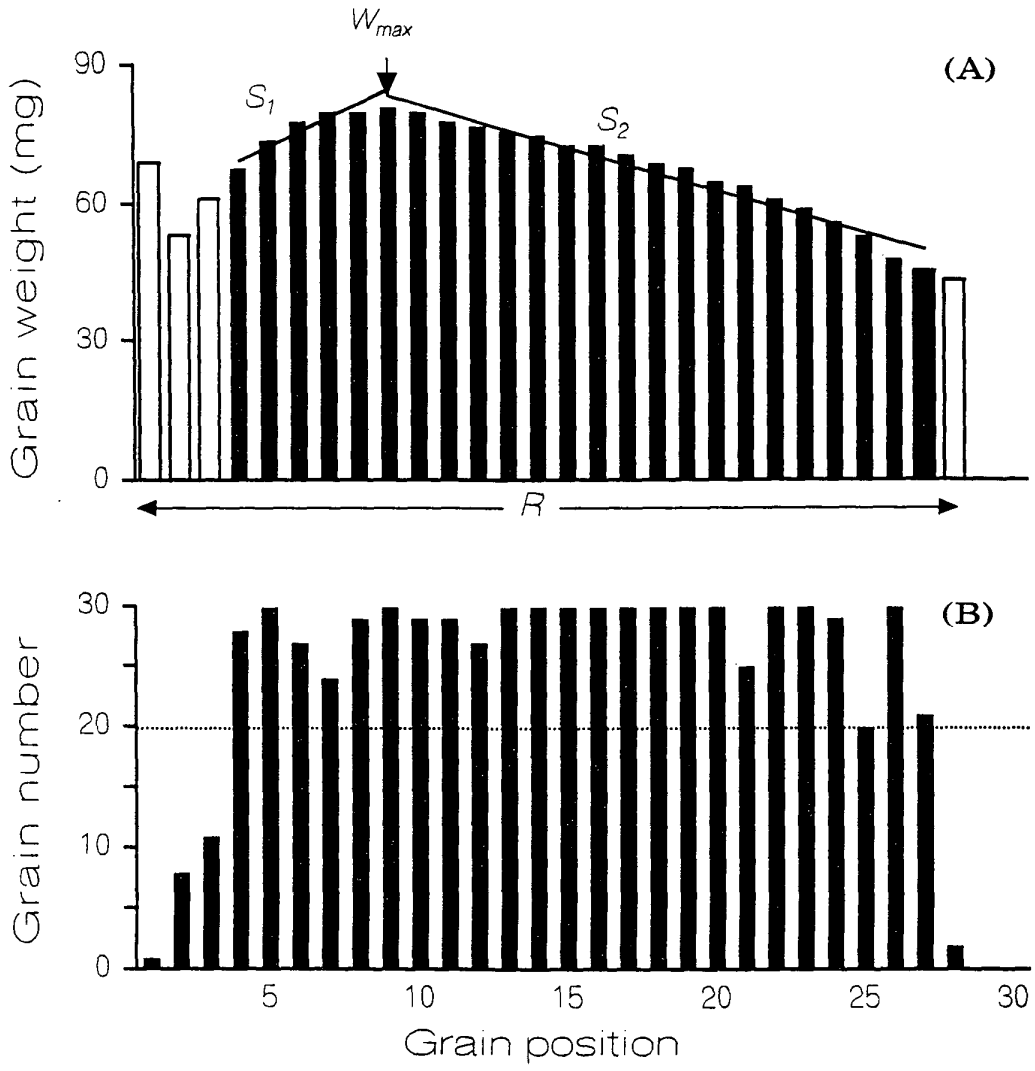


Figure 4.2.6F2 The average grain (a) weight and (b) number with grain position of a main stem ear. The grain from 30 main stem ears were pooled by grain position. The data contibuting to each parameter are indicated by arrows (R, W_{max}) and by sloping lines (S_1, S_2). The dashed line in (b) indicates the 2/3 maximum grain number criterion below which the data is rejected (open bars) for estimation of the slopes, S_1 and S_2.

P_{Wmax} the location of the heaviest grain

S_1 the linear component of the increase in grain weight from the base of the ear up to the heaviest grain

S_2 the linear component of the decrease in grain weight from the heaviest grain up to the top of the ear

The original grain samples were obtained from 30 plants with the modal number of stems (Section 3.2.2) and the grains located at the same position on each ear were pooled. Thus there is a maximum of 30 grains per location on the ear. The later the tiller the greater the probability that it will not be fertile and thus the maximum number of grains at any position will be less than 30. This is more pronounced in the Low N treatment where there are fewer fertile stems per plant. Tillers with fewer than 10 ears per 30 plant sample were not analyzed. Thus in both 1989 and 1990 only MS, T1 and T2 could be analyzed in both the Low and High N treatments. Analyses of variance which include nitrogen as a factor are restricted to these three stem types in both years. In the High N treatments T3 in 1989 and T3 and T4 in 1990 were analyzed. The characteristics of these one or two stem types were analyzed along with the MS in the High N treatment only in 1989 and 1990 respectively.

In a sample of 30 ears on a given stem type there will be variation in the size of individual ears and more importantly in the number of grains. A few of the largest ears will produce grains at extreme locations (base and top of the ear) and will tend to be heavier than the average weight of grains at nearby locations (open bars Figure 4.2.6F2a). These few grains give a distorted image of the overall shape of the variation in weight and need to be omitted from any parameter estimation. An arbitrary criterion of less than 2/3 of the maximum number of possible grains at any one position was chosen as a means of excluding a particular location from the analysis. Thus in the example shown there is a maximum of 30 grains possible and positions with 19 or less grains are excluded. This typically results in 2 to 3 grain positions being excluded from

both extremes. The only exception to this is in the estimation of R, the number of grain bearing sites, which is defined as:–

$$R = P_h$$

where P_h is the highest grain position which has at least one grain present.

Figure 4.2.6F2a shows the average weight of an individual grain at each location i.e. the total weight of the pooled grain at that location divided by the number present. W_{max} is maximum of these average grain weights (excluding extreme positions described above). The location of this maximum, P_{Wmax}, is invariably in the lower half of the grain bearing positions.

S_1 and S_2 are estimated by linear regression using locations which have sufficient grain not to be excluded. Locations from the base up to and including the location P_{Wmax} are used to estimate S_1, and including P_{Wmax} up to the top of the ear for S_2.

Maximum grain weight (W_{max})

While main effects of nitrogen, cultivar and stem type were clearly evident (heaviest grains being produced with High N, on the main–stem and cv. Prisma) there were two significant interactions, Nitrogen x Stem and Cultivar x Stem (Table 4.2.6T1). Thus the magnitude of these main effects is dependent on the level of the interacting factor. These interactions were significant both when considering MS, T1 and T2 and MS, T3 and T4.

Figure 4.2.6F3 shows the interaction of cultivar with stem type. Values for High N, rather than the average over nitrogen treatments, are shown so that the consistent trend across the later tillers (T3 and T4 present in High N only) can also been seen. There is a steady decline in maximum grain size as one moves from the main–stem to later formed tillers. This is not entirely surprising since the definition of T1, T2 etc is based on the ranking by weight of the ears on a plant rather than its position on the plant

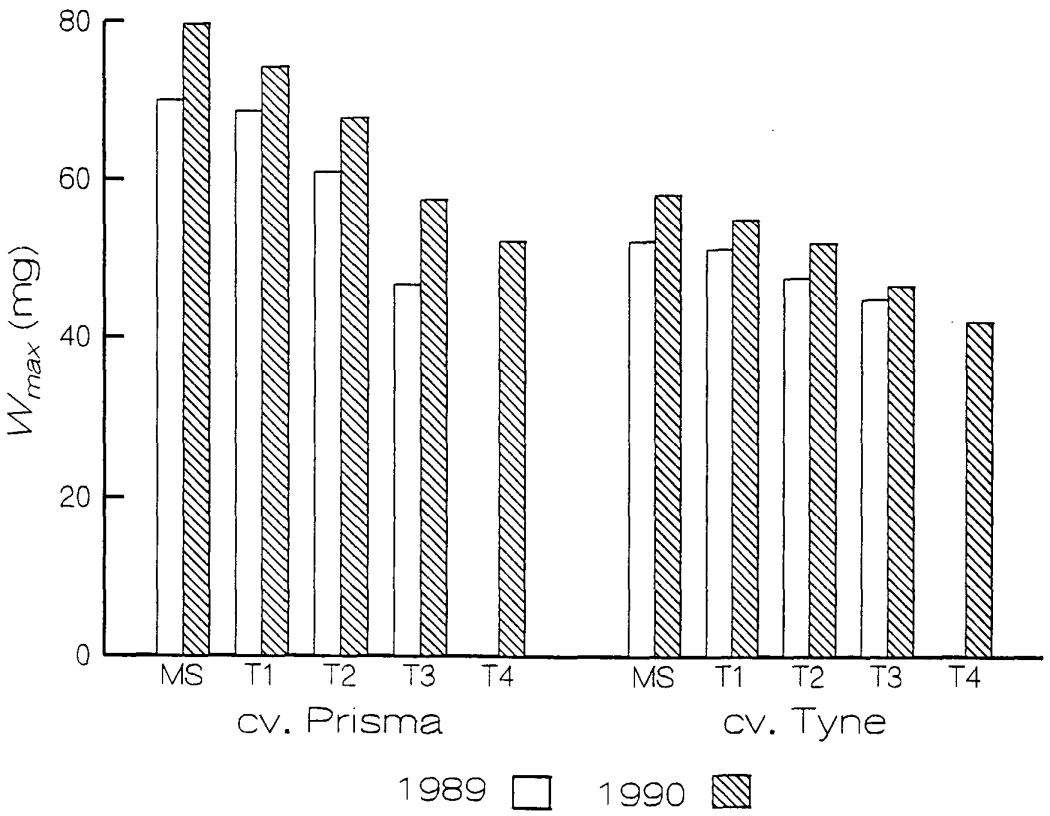


Figure 4.2.6F3 The interaction between cultivar and stem type on the weight of the heaviest grain (W_{max}) on the ear.

(section 3.3.2). This ranking has been shown to be consistent with its location on the plant (Ellis & Kirby, 1980). The decline is steeper in the cv. Prisma which also has the heavier maximum grain size on the main-stem.

The interaction of nitrogen with stem type is smaller than the previous interaction, cultivar with stem type (Figure 4.2.6F4), but no less significant (Table 4.2.6T1). Maximum grain size on the main-stem is little affected by nitrogen. The effect of nitrogen on maximum grain size is evident in T1 with a significantly greater reduction in size in Low N compared to High N treatment. This effect continues to increase systematically with later formed tillers.

Both trends of these two interactions are consistent over the two years. The average effect of cultivar is of similar magnitude to that of stem type and greater than that of nitrogen.

Location of the heaviest grain (P_{Wmax})

No consistent, significant effects of nitrogen, cultivar, stem type or higher order interactions were found. The location of the heaviest grain would appear to be invariant, occurring at the 9th grain bearing position up the ear (s.e. 0.3) in both cultivars in both years on all fertile stems. On smaller ears where the overall number of grain bearing positions is reduced the heaviest grain will occur nearer to the middle of the ear, but still be the 9th grain bearing position from the first grain bearing position at the base of the ear. The large majority of ears sampled have at least 20 grain bearing sites and thus the position of the heaviest grain will be below the middle of the ear in these cases (See Figure 4.2.6F7 for a description of variation in the number of grain bearing sites).

Number of grain bearing positions (R)

As for W_{max}, the main effects of nitrogen, cultivar and stem type are significant – the greatest number of grains being produced with High N, on main-stems and cv. Tyne (Table 4.2.6T2). The first two factors are in the same direction as for W_{max}, but the

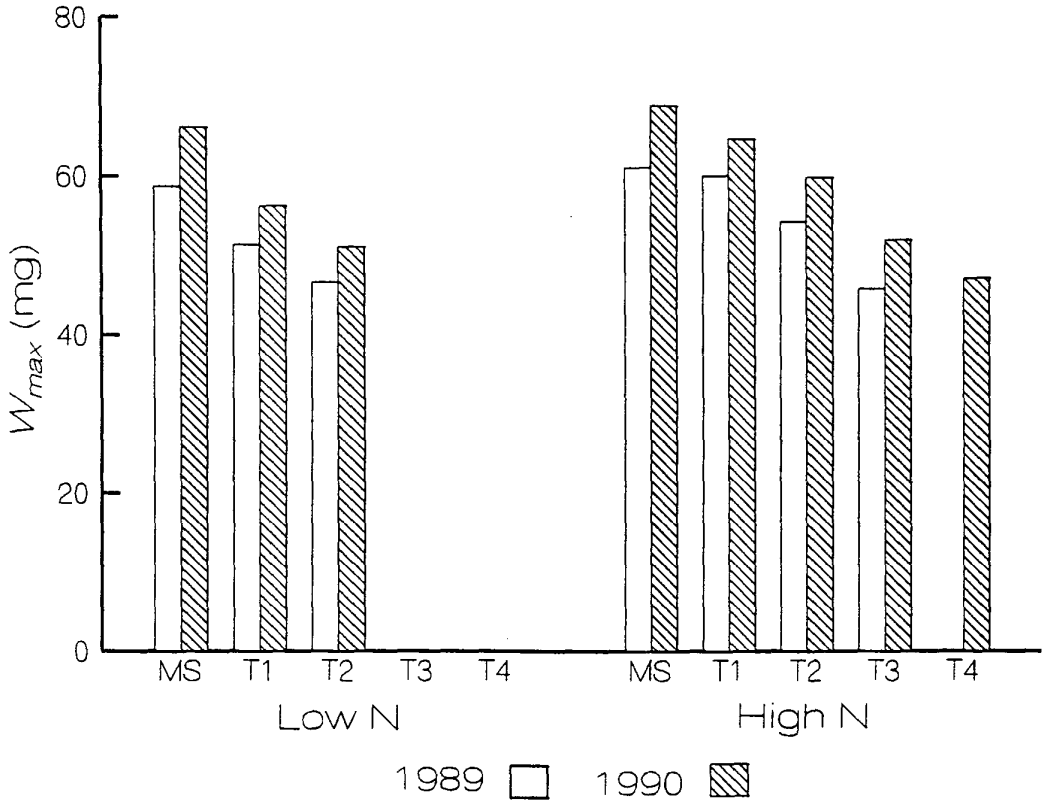


Figure 4.2.6F4 The interaction between nitrogen treatment and stem type on the weight of the heaviest grain (W_{max}) on the ear.

cultivar effect is reversed with fewer grain bearing positions but heavier maximum grain size in cv. Prisma. Again there are two significant interactions which are consistent over years, Nitrogen x Stem (as previously for W_{max}) and in this case Nitrogen x Cultivar.

Nitrogen x Stem interaction is the greater of the two interactions (compare Figures 4.2.6F5 & F6). As for W_{max} the differences due to nitrogen increase with later formed tillers, there being little or no difference between main-stems (MS) from Low N and High N in the number of grain bearing positions.

Both the trends of these two interactions are consistent over the two years. The average effect of stem type is greater than nitrogen which in turn is slightly greater than that between cultivars.

Within a cultivar there is a close relation between the number of grain positions, R, and the maximum grain weight, W_{max}, in both years (Figure 4.2.6F7). The largest number of grain are found on the main-stem and the number is similar on both cultivars. However, W_{max} is generally lighter in cv. Tyne. The differences due to nitrogen at first site appear small - the open and closed symbols (Figure 4.2.6F7) for a cultivar falling about the same general line. Looking more closely reveals increasing effect of nitrogen with later formed tillers. W_{max} is relatively more affected than R. Extrapolating a line through the points for either cultivar to zero grain weight (W_{max}) will intercept the horizontal axis with a positive value.

Linear component of the increase in grain weight up to the heaviest grain (S_1)

There were no consistent effects observed on the value of S_1. The grand means for the two analyses in each year are given in Table 4.2.6T3. The slope is slightly steeper in 1990. Because of the location of the heaviest grain, PW_{max}, and the exclusion of extreme sites the number of grain positions used in estimating S_1 was limited to between 4 and at best 8 positions. Thus there is considerable variation in this estimate and real

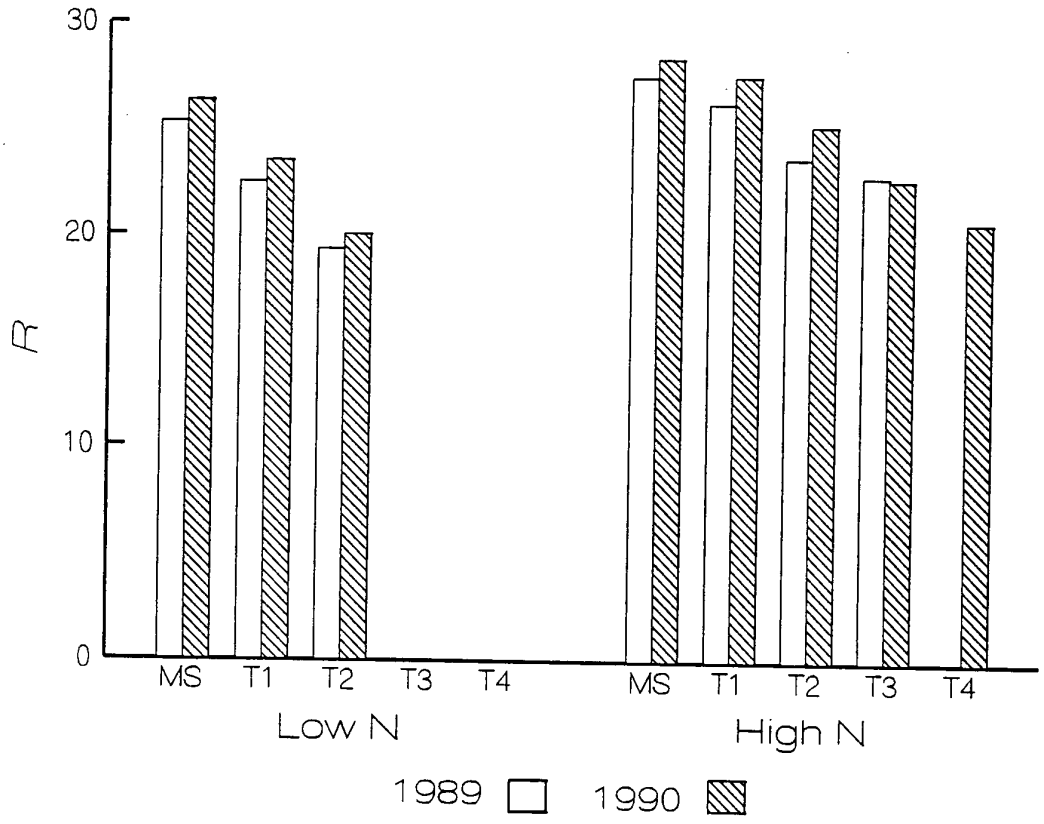


Figure 4.2.6F5 The interaction between nitrogen treatment and stem type on the number of grain bearing sites (R) on the ear.

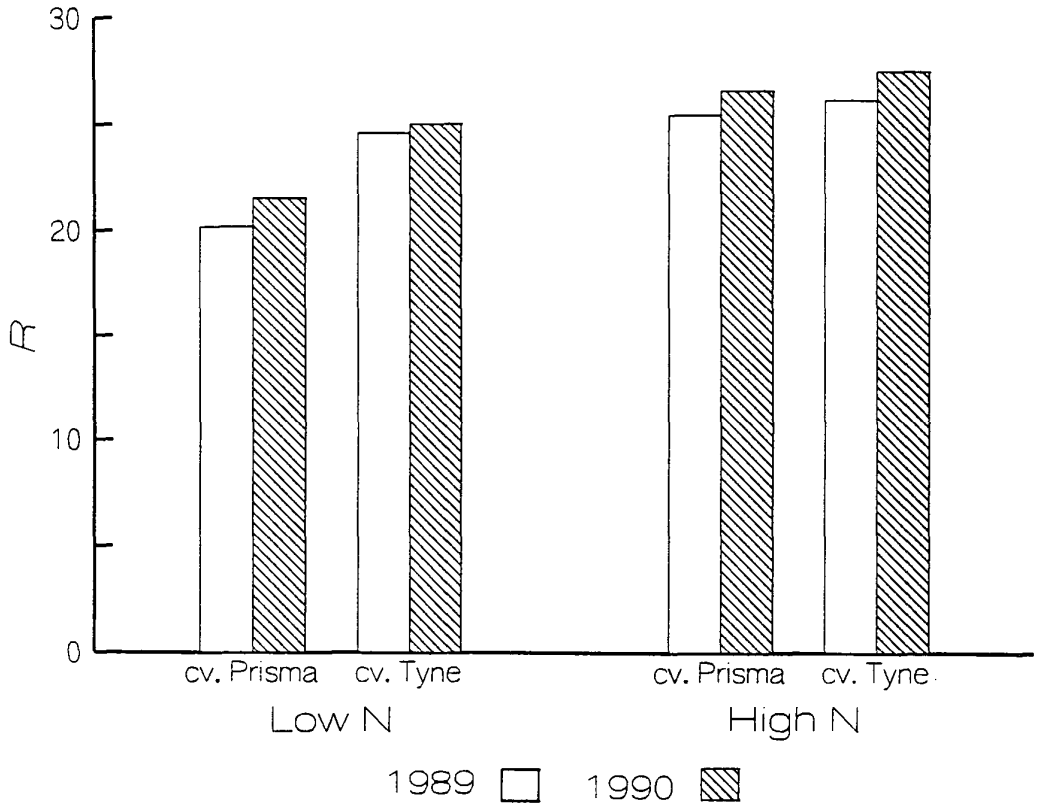


Figure 4.2.6F6 The interaction between nitrogen treatment and cultivar on the number of grain bearing positions (R) on the ear.

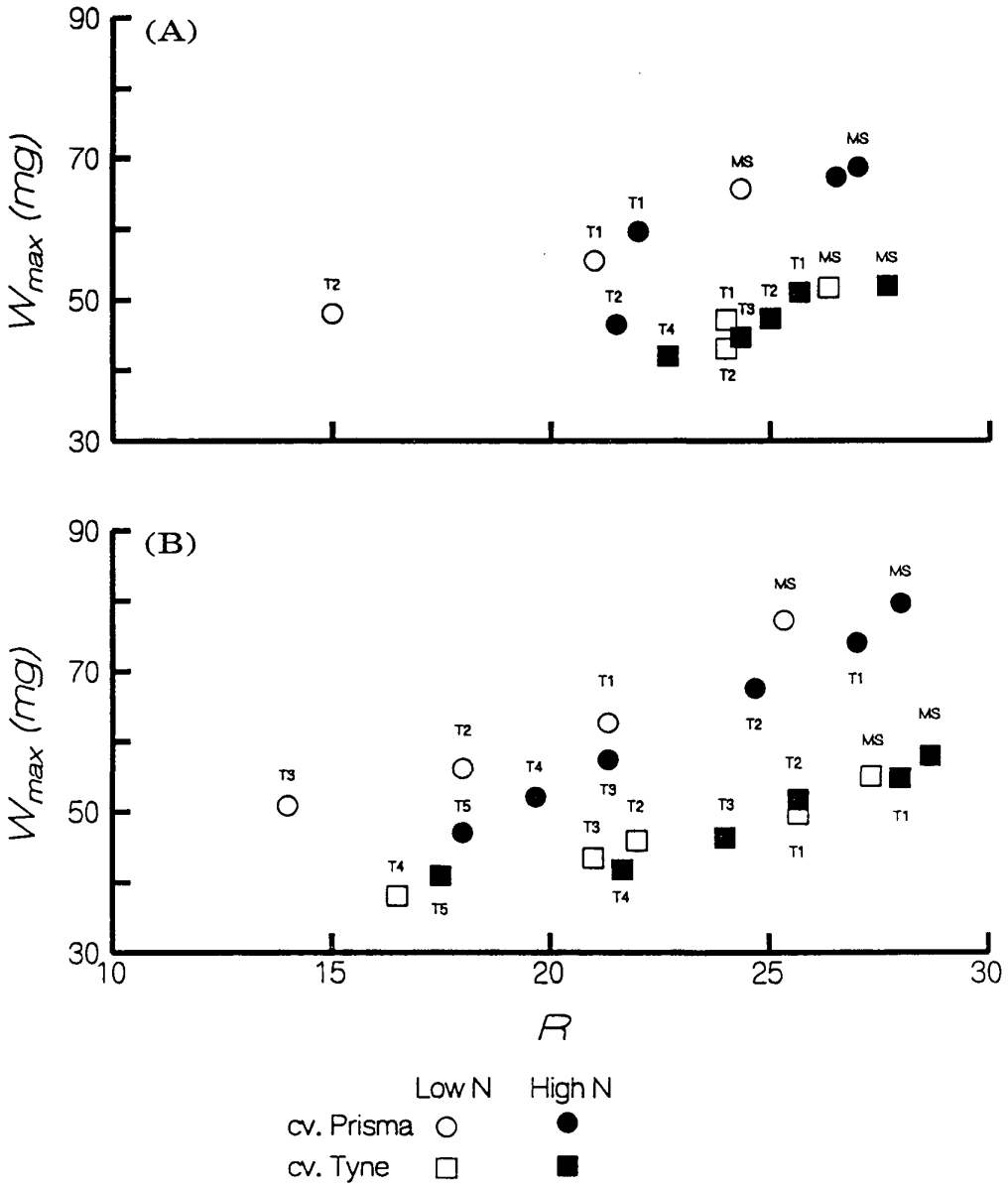


Figure 4.2.6F7 The relation between the heaviest grain (W_{max}) and the number of grain bearing positions (R) on the ear in (a) 1989 and (b) 1990. Each point represents the average for an individual stem type (MS, Main-stem; T1 - T5, Tillers).

effects may have been masked by the variability. The average value of S_1 over the two years is 1.5 mg/grain position.

Linear component of the decrease in grain weight from the heaviest grain (S_2)

There are significant main effects of both nitrogen and cultivar which are consistent over the two years (Table 4.2.6T4). The significance of the nitrogen effect could only be tested on the stem types present in both nitrogen treatments (MS, T1 and T2). The decline was steepest in High N (Figure 4.2.6F8). The cultivar effect could also be tested on later tillers and was significant in 1989 and just failed the 5 % criterion in 1990. The decrease in grain size with grain position is considerably steeper in cv. Prisma than in cv. Tyne in all stem types. The difference between cultivars was about 3 times the difference due to nitrogen. There was no correlation between the heaviest grain (W_{max}) and S_2. There is simply a scatter of points about a mean which is different for the two cultivars (Figure 4.2.6F9).

The combined effects on grain size distribution is summarised in Figures 4.2.6F10 and 11 for cv. Prisma and cv. Tyne respectively. Representative data for main-stem and tiller 3 from High N and Low N treatments in 1990 have been selected. They are the replicate (1 of 3) whose parameter values are closest to the mean set in each case. The dominant features are the effects of nitrogen and cultivar on W_{max} and R. The conservative nature of the location of Wmax is also a striking feature.

Variation of grain nitrogen

Apart from the clear effect of nitrogen uptake on average grain nitrogen concentration other effects are subtle and not always consistent over years. The subtleties arise because of the higher order interactions that are present making interpretation difficult e.g. the interaction of nitrogen by cultivar by stem type (Table 4.2.6T5). Looking at this interaction, the cultivars are responding to nitrogen in different ways (Figure 4.2.6F12). Firstly, the gross effect of nitrogen uptake is greater in cv. Prisma than cv. Tyne. Secondly the variation among stem types also tends to be greater in cv. Prisma than cv.

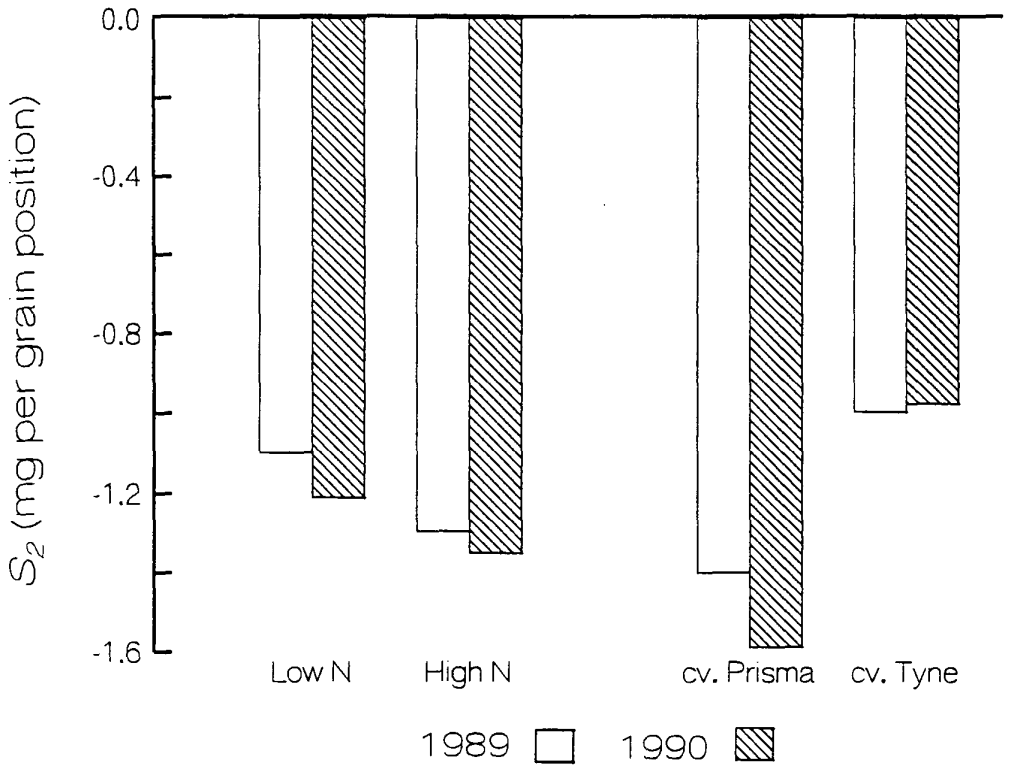


Figure 4.2.6F8 The effects of nitrogen treatment and cultivar on the decline in grain weight with grain position above the heaviest grain (S_2).

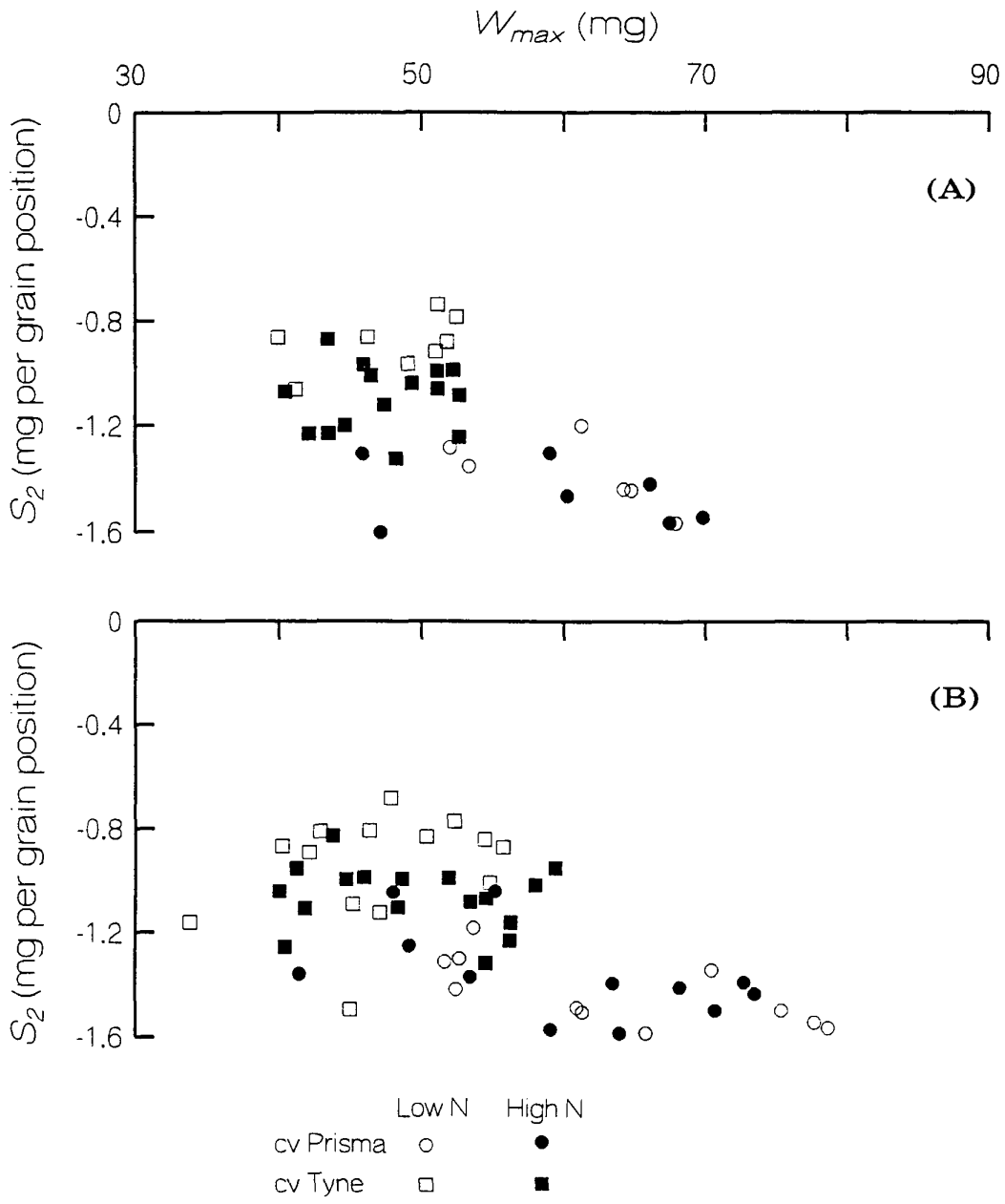


Figure 4.2.6F9 The relation between the linear component of the decrease in grain weight, S_2, and the maximum grain weight, W_{max}, in (a) 1989 and (b) 1990. Each point refers to individual replicates of each stem type (see Figure 4.2.6F7).

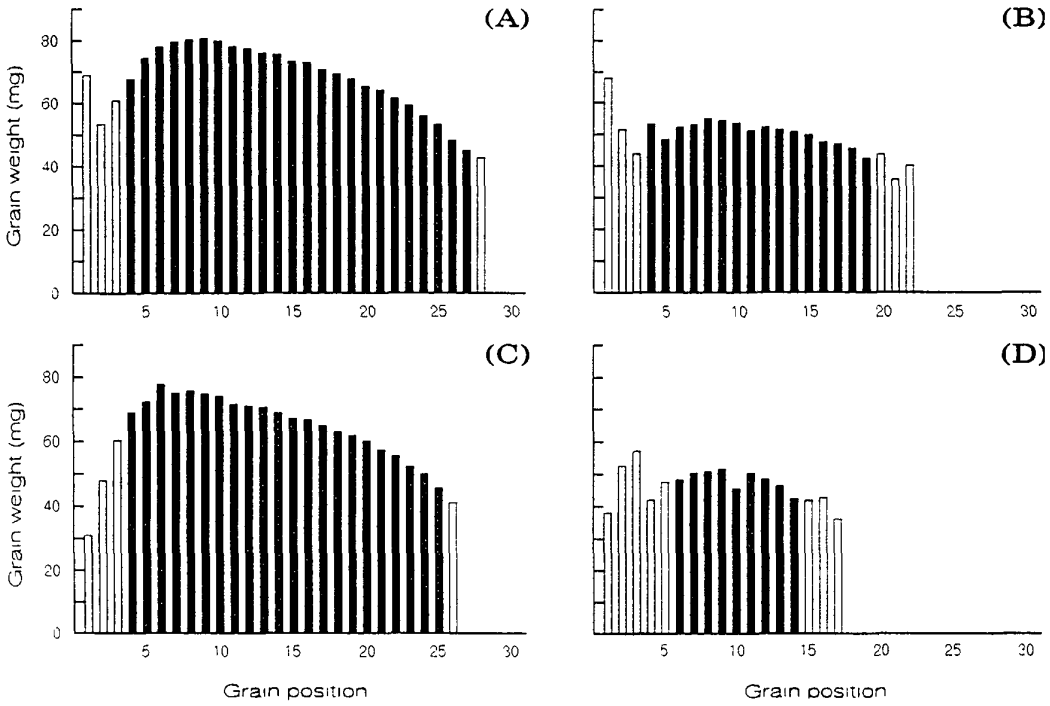


Figure 4.2.6F10 The variation in grain weight with grain position in (a,c) Main-stem and (b,d) Tiller 3 ears from (a,b) High N and (c,d) Low N treatments in cv. Prisma. The open bars indicate grain positions with less than 0.67 probability of being filled. Each distribution is the replicate whose parameters are closest to the treatment mean

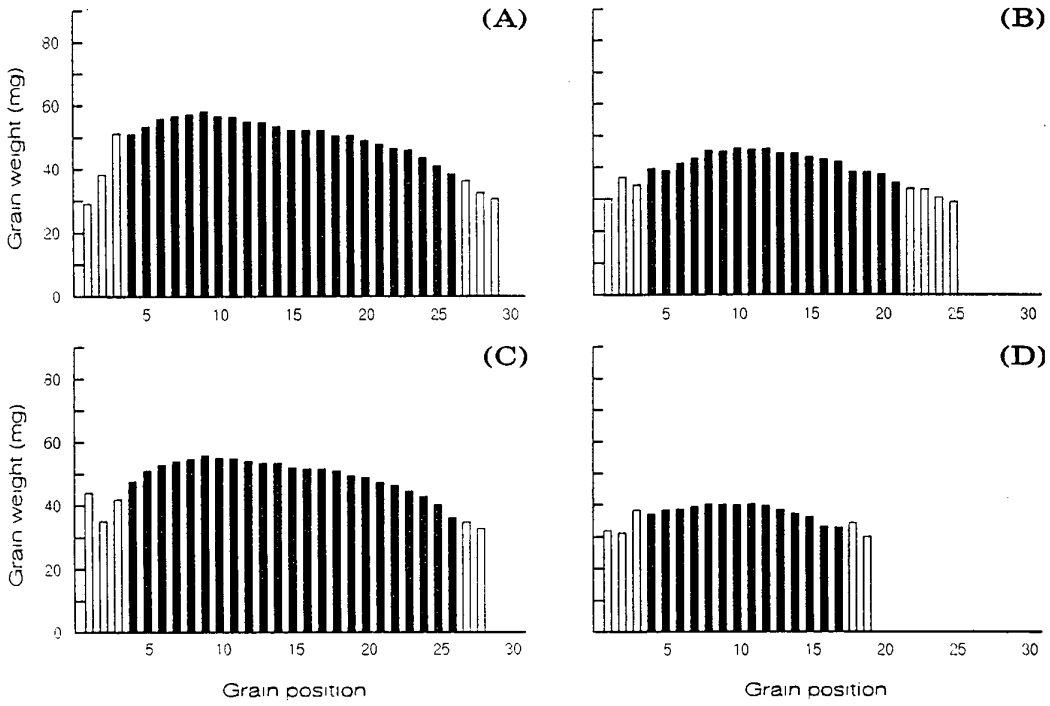


Figure 4.2.6F11 The variation in grain weight with grain position in (a,c) Main-stem and (b,d) Tiller 3 ears from (a,b) High N and (c,d) Low N treatments in cv. Tyne. The open bars indicate grain positions with less than 0.67 probability of being filled. Each distribution is the replicate whose parameters are closest to the treatment mean.

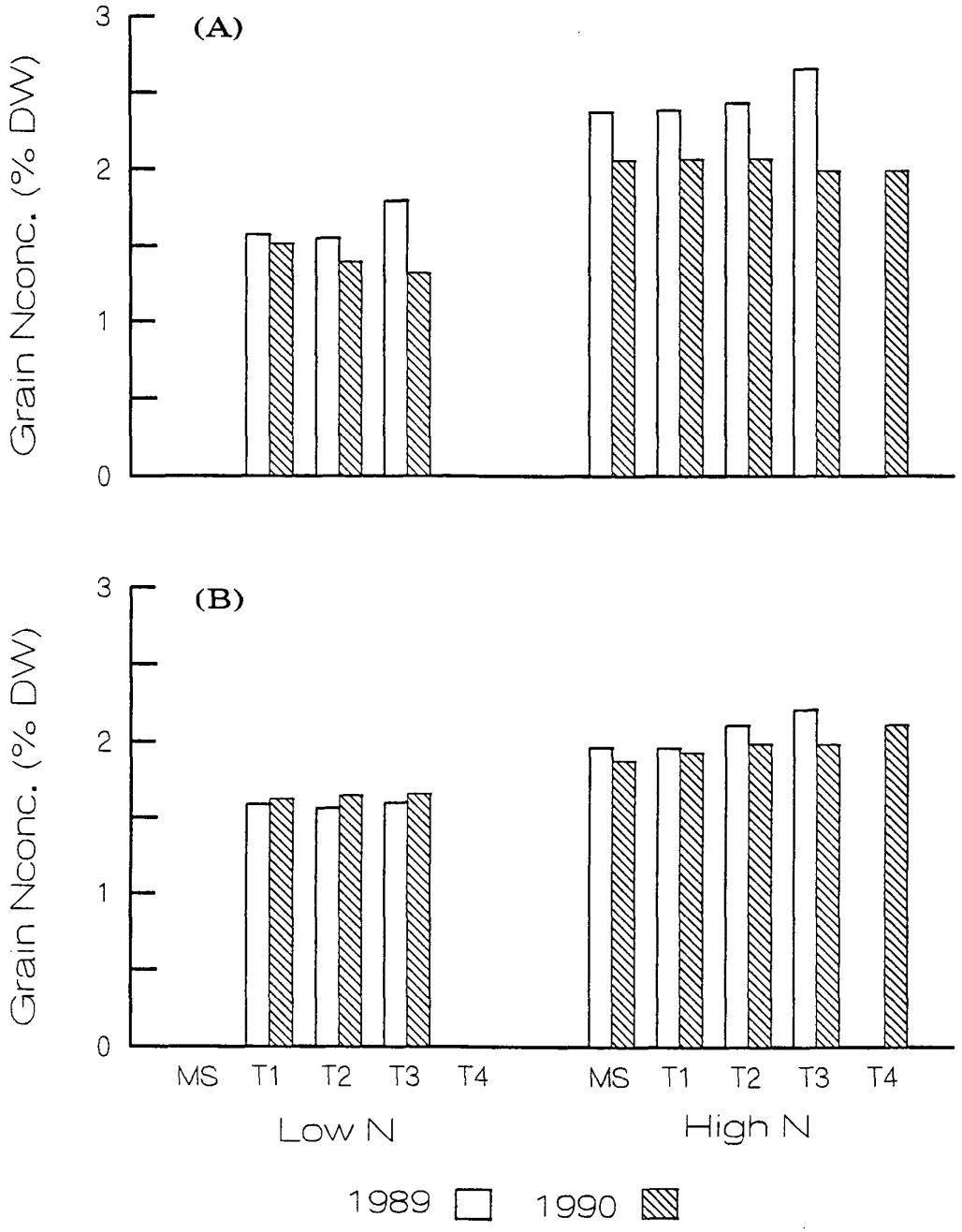


Figure 4.2.6F12 The variation of grain nitrogen concentration with stem type and nitrogen treatment in (a) cv. Prisma and (b) cv. Tyne.

Tyne. However, the trend in this variation is not consistent between years in cv. Prisma whereas it is consistent in cv. Tyne and this represents a genuine genotypic effect which is related to the erectoid habit. The greater variability among stem types in cv. Prisma with Low N compared to cv. Tyne is consistent between years.

There is also significant variation in nitrogen concentration within the ear (Figure 4.2.6F13). Samples of 10 grains were taken from the bottom and top of the ear, typically the third grain bearing position in from the two extreme positions, respectively, and from the lower and upper quartile positions and the middle (see Materials and Methods section 3.3.2). Moving from the base to the apex of the ear, nitrogen concentration falls slightly and then rises systematically from the lower quartile to the top most positions. This effect is small, independent of nitrogen uptake and present in both cultivars. The effect of grain position varies significantly with stem type (Table 4.2.6T5) and is greatest in the main-stem (Figure 4.2.6F14). The effect is smaller in Tiller 1 and all but disappeared in Tiller 2.

The possibility that this variation was related to variation in grain weight was tested by including the average dry weight of the 10 grains as a covariate in the analysis of variation. No significant linear correlation could be found. Thus possible explanations for these observed variations are difficult to find. The effects are the result of subtle changes in the balance of carbon and nitrogen supply and may go as far back as initiation of florets or start at fertilisation and certainly continue through the entire grain filling period.

Variation in time to germinate

A significant variation in the time taken to germinate was found with grain position in MS, T1 and T2. This variation also differed between cultivars. These trends are shown in Figure 4.2.6F15 where the time taken is expressed as a deviation from the mean for the cultivar i.e. averaged over nitrogen treatments and stem types within a cultivar (Table 4.2.6T6). It is possible that this variation is due to the effect of grain weight

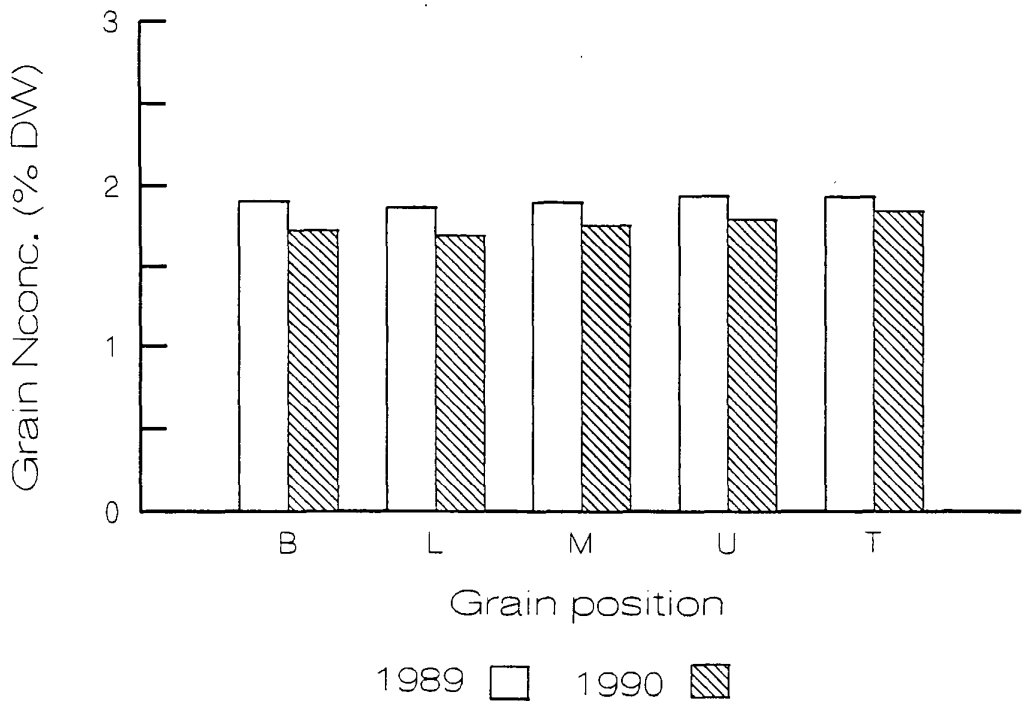


Figure 4.2.6F13 The variation of grain nitrogen concentration with grain position (B, bottom; L, lower quartile; M, middle quartile; U, upper quartile; T - top) averaged over stems (MS, T1 and T2 only), nitrogen treatments and cultivar.

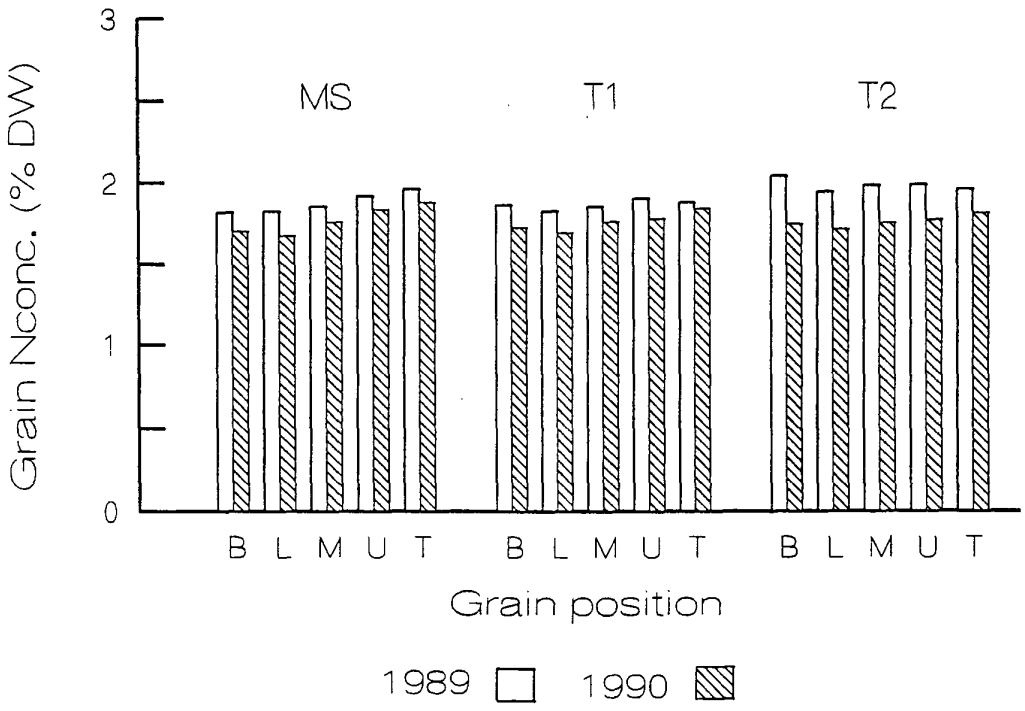


Figure 4.2.6F14 The variation of grain nitrogen concentration with grain position (B, bottom; L, lower quartile; M, middle quartile; U, upper quartile; T - top) and stem type, averaged over nitrogen treatments and cultivars.

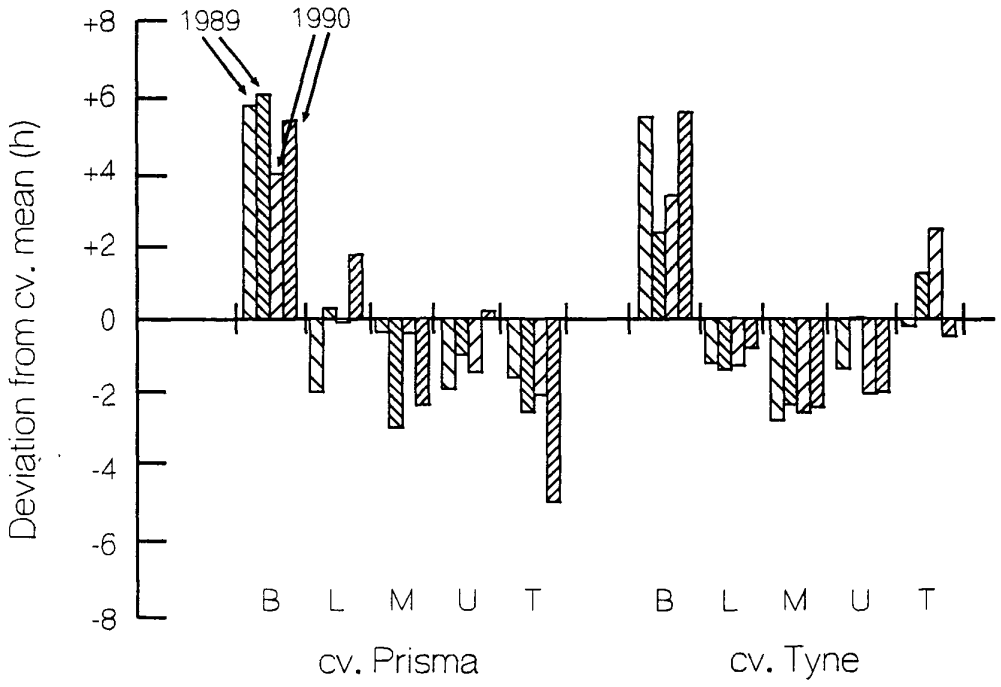


Figure 4.2.6F15 The variation in time to germination of grains taken from five sites on the ear (B, bottom; L, lower quartile; M, middle quartile; U, upper quartile; T,top). The data is averaged over nitrogen treatments and stems: MS, T1 and T2. A positive deviation indicates that the grain germinated earlier than the average. There are a pair of bars for each year at every grain site. The first bar is the lower time resolution germination test and the second the finer resolution (overnight observations).

which also varies with grain position. To test this possibility the variation was re-analyzed using standard ANOVA and including the individual weights of each grain as a covariate (Table 4.2.6T7). The effect of grain weight was highly significant and there were no significant differences in this effect of grain weight across treatment combinations (cultivar x nitrogen). Grain size was found to increase the time to germinate by 17 ± 4 (s.e.) minutes per mg increase in grain weight. In a main-stem ear of cv. Prisma, individual grain weight can vary over a range of approximately 30 mg from the lightest weights at the extremities of the ear to the heaviest grains towards the middle (e.g. Figure 4.2.6F10a). An increase of 30 mg translates into an 8.5 hour delay in germination. The range of grain weights and hence variation in germination time on a corresponding ear of cv. Tyne is less (e.g. Figure 4.2.6F11a), approximately two thirds of that observed in cv. Prisma.

Having removed the effect of grain weight (linear component) on germination time there were two significant effects still present, grain position and the interaction of grain position with cultivar (Table 4.2.6T7). It is now clear that there is a significant, systematic increase in the time taken to germinate as one moves from the base of the ear to the top, and that this increase is greater in cv. Prisma than cv. Tyne (Figure 4.2.6F16). The main effect of grain position was observed in both years and both the lower and finer time-scale. Significant dependency of position effect on cultivar was detected in the finer time-scale tests, and the inclusion of weight as a covariate reduced the probability of observing this interaction by chance in all four runs (Column B in Table 4.2.6T6 and 7). The same effects, and of similar scale, were also observed in T3 and T4 (Table 4.2.6T8 and Figure 4.2.6F17).

The delay in germination in going from the base to the top of the ear is overall about 9 hours in cv. Prisma and 6 hours in cv. Tyne. This is the same scale of effect as that of grain weight and compares with the average time taken over all the seeds to germinate of 40 ± 4.5 (s.d.) hours.

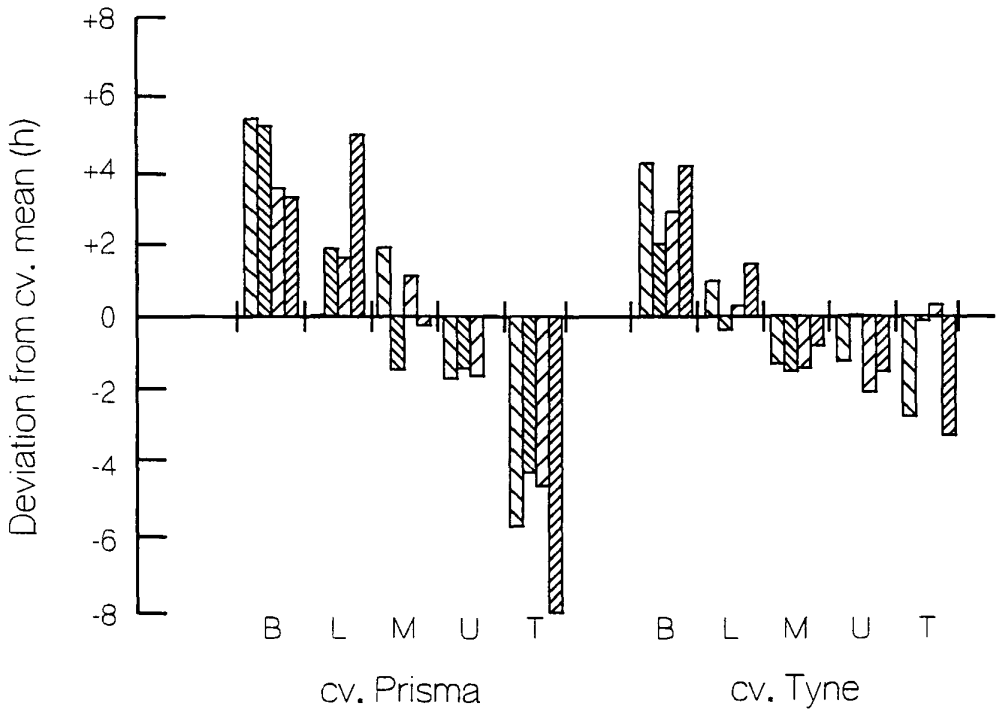


Figure 4.2.6F16 The variation in time to germination of grains taken from five sites on the ear (B, bottom; L, lower quartile; M, middle quartile; U, upper quartile; T,top). The data is averaged over nitrogen treatments and stems: MS, T1 and T2, and the effect of grain weight on germination removed. A positive deviation indicates that the grain germinated earlier than the average. There are a pair of bars for each year at every grain site. The first bar is the lower time resolution germination test and the second the finer resolution (overnight observations).

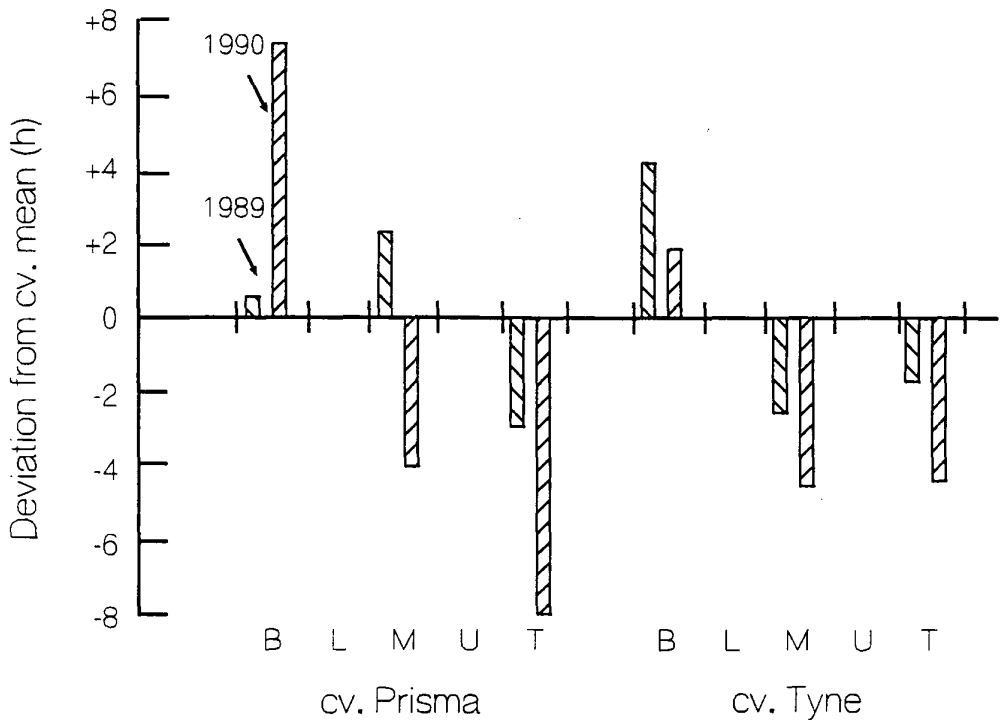


Figure 4.2.6F17 As figure 4.2.6F16 but averaged over stems (MS, T3 and T4). Only the lower time resolution was carried out in these tests which were restricted to three grain sites.

4.3 Solution culture (SOLX)

Table 4.3T1 lists the nitrogen concentrations and contents and dry weights of the ears (grains plus rachis) for both cultivars and nitrogen treatments at the last harvest (Robinson *et al.,* 1991). The 'steady-state' treatments achieved 55% and 59% of the ear dry weight of the 'high-low' treatments in cv. Klaxon and cv. Blenheim respectively. Thus demand for nitrogen during the early part of growth was greater than that estimated from assuming exponential growth with constant plant nitrogen concentration (Ingestadt, 1982). This is further supported by the ^{15}N measurements which show that a considerable proportion (24-32%) of the nitrogen found in the ear at maturity was absorbed during the first week of seedling growth. This indicates a considerable potential for retranslocation both within the vegetative tissues and subsequently from vegetative to reproductive tissues. Cv. Klaxon (feed quality) went on to take up more nitrogen in the 'steady-state' treatment than that required for dry matter production alone, resulting in a higher nitrogen concentration in the ears compared to the 'high-low' treatment. In contrast, uptake of nitrogen by cv. Blenheim (malting quality) appeared to parallel that of dry matter production resulting in similar nitrogen concentrations in the ear under both nitrogen treatments.

5.0 DISCUSSION

The quality of grain is the result of the phasing of developmental events in relation to the acquisition of resources. Changes in the rate of development relative to the acquisition of resources (e.g. warmer temperatures with solar radiation unchanged), and or changes in rates of acquisition of one resource relative to another (e.g. lower fertility affecting uptake of nitrogen more than growth) will result in structural changes in the plant (e.g. smaller leaves, fewer stems and grain) and or grain quality (e.g. grain size, higher nitrogen content). The main links between development, growth and acquisition of nitrogen are shown schematically in Figure 5F1. The diagram illustrates the complexity of the interactions and feed backs that occur between development, growth and the uptake and distribution of nitrogen. While some processes occur in sequence, many occur in parallel and are often strongly interdependent. We do not present an exhaustive representation of reality. The aim is to provide a framework for the discussion which follows. For clarity the discussion is divided into three parts development (region D in Figure 5F1), growth and nitrogen uptake (region G in Figure 5F1) and grain quality (region Q in Figure 5F1).

The research in this programme has concentrated on the effect of nitrogen uptake on the growth, yield and quality of grain produced. In the field water availability is a major source of variability from site to site and season to season. The potential interactions of water with nitrogen, growth and structure of the canopy will be discussed later. Similarly root growth and activity was beyond the scope of this particular research programme. Much of the experimental work (PTX and SOLX) eliminated root distribution and potential uptake as limiting factors. The state of knowledge relating to roots and soil and its application is discussed later.

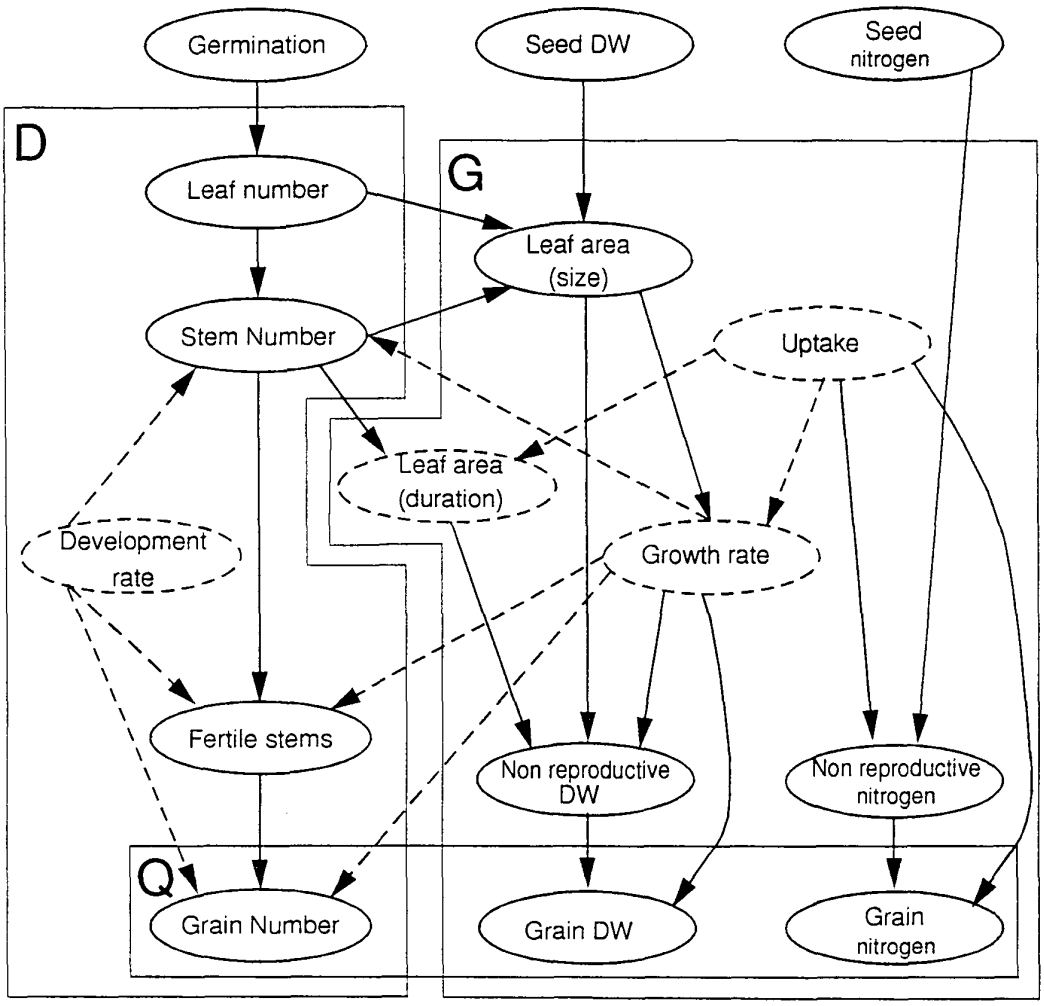


Figure 5.F1 Schematic diagram of the interaction of development, growth and nitrogen uptake on grain yield and quality. Solid ellipses are entities and dashed ellipses are processes. Solid lines are direct causes and dashed lines are modifiers.

5.1 Development

There is a strong quantitative understanding of the effect of environment on timing of developmental events. In particular the influence of temperature on processes such as initiation of leaf primordia, leaf appearance and vernalisation requirement. The influence of daylength is less equivocal - rate of change of daylength was invoked as a means of explaining differences between rates of development in the autumn and spring. However, this has recently been removed from the AFRC wheat model as a mechanism, following a reassessment of the relation between plant tissues temperatures and those in the surrounding environment (Porter, *pers. comm.*). Originally tissue temperatures were assumed to be close to air temperature whereas in reality, prior to stem extension, tissue temperatures are much closer to soil temperatures. Soil is often warmer than air temperature in the autumn but the reverse in the spring. This discrepancy gave rise to an apparent sensitivity to rate of change of daylength. Similar debates surround the influence of water shortage on development - drought is often associated with earlier flowering. However, this again can be reinterpreted as drought reducing transpiration and hence its cooling effect. Tissue temperature and that of the meristems is increased and hence development is accelerated (Keulen & Seligman, 1987). Temperature is the dominant influence on the timing of development.

Within windows of opportunity set by temperature the number of organ types is determined. This is where the major interactions between development and growth occur (Figure 5F1). For example, the number of tillers produced is dependent on the availability of carbohydrates and the rate of development. Sizeable quantities of carbohydrate at very warm temperatures may result in similar numbers of fertile tillers, as do restricted carbohydrate supplies at cooler temperatures. The same is true of grain numbers. The optimum conditions for maximising grain number and yield are fast growth rates (bright sunlight and adequate water and nutrients) with slow rates of development (cool temperatures). Such conditions exist on high altitude plateaus in China where yields of grain crops can achieve 15 tha^{-1} (Monteith, *pers. comm.*). Marshall, Squire & Terry (1992) have investigated the interaction between development and growth in an annual tropical crop, groundnut, and reached similar conclusions. The

principles established in that study are equally applicable to all seed bearing annual crops. Time of sowing is the only and limited tool that the farmer has available to select his environment within which to grow the crop. Therefore the farmer along with the breeder has to adapt the management and genotype to make best advantage of this window and cope with uncertainty from season to season.

5.1.1. The origin of new cultivars and their physiological characteristics

Historical surveys (Feil, 1992) indicate that breeders have produced new, high yielding, barleys that are shorter, earlier to heading, more lodging resistant, higher in harvest index and with modified nitrogen metabolism. Plant breeding programmes have provided farmers with new cereal cultivars which produce grain useful for processing. Plant breeding techniques have evolved to allow complex characters such as yield and quality, to be handled without the necessity for understanding the underlying physiological and biochemical characters (Reinbergs *et al.*, 1976; Thomas, 1987). Thus selection for physiologically important characters is likely to be indirect and through selection for characters of high heritability such as plant height and time of heading.

Differentiation at the stem apex (Kirby & Appleyard, 1984) results in the formation of leaf and floral primordia. In the PTX a maximum of eight leaves developed on the main-stem of both cultivars. This contrasts with field experiments where ten leaves were found in similar cultivars (Kirby & Ellis, 1980). The absolute leaf number on the main-stem is dependent on the vernalization requirement of the genotype and the temperature of the environment. In the field, from autumn, progressively later sowing leads to a decrease in leaf number in spring and winter cultivars (Jones & Allen, 1986). Minimum leaf number occurs from March sowing of spring cultivars but after the end of February leaf number increases in winter cultivars as their vernalisation requirement is progressively less satisfied. The dates of sowing in the PTX (18/4/89 & 29/3/90) were within the range of field experiments while the dates of anthesis (20/6/89 & 11/6/90) were earlier. This is probably an effect of higher temperatures after sowing in the polythene tunnel.

As the leaf primordium develops, an axillary bud is differentiated and may eventually develop and grow into a tiller. Given appropriate environmental conditions, plants with very large numbers of tillers can be grown but in field grown spring barley it is usual to find fertile ears only on Tc and T1–T4. The lower leaf number on the main–stem in the PTX would not have significantly affected potential tiller number.

Between brairding and the start of stem extension floral primordia are differentiated at the stem apex and grow to form spikelets. The differentiation of floral primordia ceases at or soon after the time stem extension starts (Kirby & Ellis, 1980). In the PTX the time of anthesis was virtually synchronous between cultivars within a season so the difference in potential grain number between treatments (Figures 4.2.6F10–11) was mainly due to differences in nitrogen status rather than timing of development.

The fate of a tiller bud depends on the rate of plant growth and the timing of emergence from the leaf sheath. In most UK crops tillers that emerge from the subtending leaf sheath after anthesis suffer severe competition for light and nutrients under the closed canopy. Only rarely do such late tillers form fertile ears in field plots (Kirby & Ellis, 1980). In the PTX it was possible to observe intra–plant competition by the effect on tiller leaf number (Figures 4.2.2.1–4). Even in low nitrogen treatments the first leaf tiller (T1) produced leaves in a regular succession and had a fertile ear (Table 4.2.2.3b). However, higher order tillers often showed fewer than three leaves and less frequently had a fertile ear. The earlier that a tiller is differentiated and emerges the greater the contribution to plant yield. Under commercial crop and experimental conditions grain number per ear and grain weight are reduced proportionately for each step up the stem heirachy (Ellis & Kirby, 1980). PTX results discussed under the 5.3. Grain Quality section are in accord with these findings.

Typically plants from commercial crops at anthesis consist of a main–stem and one to three primary tillers. In experimental field plots (sown at the rate of 250 seeds per m^{-2}, lower than in commercial crops but sown on a regular grid pattern; Kirby & Ellis, 1980) maximum yield resulted from the formation of four tillers (Ellis & Russell, 1984). This

corresponds to the number of stems that were found at the final harvest of the PTX which showed an average of 5.1 stems per plant over 1989 and 1990 (Table 4.2.2.T3a).

5.1.2 Genetic control of plant development

Development in barley and wheat at the whole plant level (Kirby & Appleyard, 1981), even including spikelet abortion (Garcia del Moral *et al.*, 1991), is under genetic control. A large number of genes that control aspects of development have been assigned to a scheme of two phytomeric units (Bossinger *et al.*, 1992). However, for the purposes of this report genes that influence characters of importance in malting quality can be grouped into three broad classes:-

1. Time of flowering
    a) Vernalization requirement
    b) Photoperiod response
    c) Number of leaves
2. Plant stature
3. Ear morphology

For example while there might be no direct relationship between time of flowering and malting quality an indirect effect can arise through effects on grain size. In the PTX we avoided the complication of high vernalization requirement and ear type by only examining two-rowed spring barley cultivars.

Flowering time - Photoperiod

Two genes conditioning early heading in barley have been located to chromosomes 5 (ea_k) and 6 (ea7) respectively (von Wettstein-Knowles, 1992). However, in adapted cultivars such as cv. Tyne and cv. Prisma, time from sowing to heading is a quantitative trait (as it is in winter barley, Hackett *et al.*, 1992). Barley is a quantitative long day plant and responds to longer photoperiod with an increase in the rate of apical differentiation. Thompson & Matthews (1981) found that the rate of spikelet initiation was higher and the survival of spikelets was lowered by longer days. A survey of

cultivars showed genetic differences in response to daylength. While cv. Ymer produced more spikelets in long days cv. Clipper showed a marked drop in spikelet number. Thus high yield in Scotland was expected to be dependent on the appropriate daylength response.

The effects of daylength and temperature are confounded in the field as well as in the PTX and SOLX. In a study contrasting an English and a Scottish site longer daylength compensated for the lower Scottish temperatures so that the rate of differentiation was similar at both sites (Kirby & Ellis, 1980). Because a range of factors favoured the crop in Scotland yield was markedly higher. In contrast, when Thompson (1979) grew a field trial of cultivars that showed a range of response to daylength i.e. variation in spikelet number, he was unable to show a relationship with yielding ability. It is significant that the highest yielding cultivars were Ymer and Lami. The latter is a late semi-dwarf type which showed an average daylength response but tillered more freely than cv. Ymer indicating that there is more than one route to high yield performance. Malting quality of these cultivars was independent of yielding ability and cv. Ymer was of good malting quality but cv. Lami had high levels of ß-glucans and did not perform well. Like cv. Tyne, bred in Southern Scotland, cv. Ymer was bred at a northern site, in Sweden and both contrast with cv. Prisma, bred in the Netherlands.

Flowering time-Leaf number

Leaf number is the remaining variable which affects the duration of the time from sowing to heading. In our field experiments there appeared to be no consistent difference in the numbers of leaves (10) on the main-stem between adapted spring cultivars (Kirby & Ellis, 1980; Ellis & Russell, 1984). Thompson (1979) found a similar result in a wide ranging survey of spring cultivars with the exception of cv. Clipper. As noted above leaf number in the PTX was also consistent over treatments but lower than in field experiments.

Plant stature

Spring barley cultivars with dwarfing genes have been of considerable economic significance in the UK and Japan (Thomas *et al.*, 1991; Nilan, 1964). The most numerous group of dwarfing genes are the erectoides (*ert*) series with more than 31 loci described, although only 9 have been assigned to 5 chromosomes (von Wettstein–Knowles, 1992). Mutants at *ert* loci are characterised by dense ears and short stems but may be both earlier and later to heading than the parent cultivar. The shortening of the rachis internode has been shown to result from a reduction in both cell size and cell number (Stoy & Hagberg, 1967).

While the erectoides mutants have been described as morphologically similar the diverse properties they exhibit suggest that dwarfing can result from more than a single genetical and resultant physiological change. The erectoides mutation in cvs Golden Promise, Midas and Goldmarker (the latter being the source of the gene in cv. Tyne) have not been so well characterised. The gene which shortens the straw in cv. Golden Promise has been located on chromosome 7 (Thomas *et al.*, 1984). The denso dwarfing gene in contrast has been shown to be associated with late heading and higher ß–glucan content than the tall allele.

Ear morphology

Ear morphology is affected by many genes with the outstanding examples being those that determine row number (*V/v* two/six row on chromosome 2) and floret fertility (*I/i* infertile/fertile on chromosome 4). In two row types particular alleles at the *I/i* locus result in the reduction of the sterile florets to small appendages to give the deficiens phenotype.

In spring cultivars adapted to the United Kingdom the largest quantitative effects on ear morphology are seen in the erectoides and semi–prostrate dwarfing types. Studies of the effects of these genes indicate that in addition to reducing height, grain size is also reduced (Thomas *et al.*, 1990 & 1991). Thomas *et al.* (1991) also reported that the

erectoides dwarfing gene is associated with low plot yield. In spring barley these effects are offset by the value of lodging resistance while in winter barley they are exaggerated by the effects of greater disease pressure, especially from *Erysiphe graminis* and *Rhynchosporium secale*.

5.1.3 Yield and grain weight

Yield can be expressed as :-

$$\text{Yield} = \text{Grain number/m}^{-2} \times \text{Weight of a grain}$$

While it has been shown that grain weight is more stable over seasons than yield (Daniels *et al.*, 1982; Gallagher *et al.*, 1975) systematic variation of grain weight has been related to plant structure. Within an ear and between tillers on a plant the weight of a grain can vary by more than 50% (Kirby & Riggs, 1978; Ellis & Kirby, 1980). These differences result from the processes of plant development and grain growth and are genetically determined although simple analysis of variance allocates the effect to environment or error (Giles, 1990).

Grain growth

The genetically controlled phases of grain growth and the main processes that occur in them can be defined as:-

Phase	*Process*
Lag phase	nuclear and cell division
Linear growth	starch deposition
Cessation	grain maturation

In the lag phase, immediately after pollination, little grain growth occurs and excess assimilate is stored in the stem. Stress at this phase dramatically reduces final grain weight (Aspinall *et al.*, 1964; Ellis & Russell, 1984). Pollination is followed by fertilization and the endosperm nuclei divide rapidly before the formation of cell walls.

Cell walls are formed in the endosperm 21 days after pollination and rapid cell division then occurs. The size of the carpel at the end of the lag phase determines the potential grain weight (Scott *et al.*, 1983). Stress, due to drought during the lag phase, can greatly reduce grain size.

Linear growth

The potential grain size, determined in the lag phase, is fixed during the linear growth phase. Reduction in sucrose supply at the start of this phase reduces grain growth greatly but similar stress at the end of the phase has little effect (Aspinall *et al.*, 1964). Stem reserves contribute 10–50% of the total grain fill and are drawn on toward the end of linear growth (Austin *et al.*, 1980). Mineral or drought induced stress in the linear phase of grain growth has the potential to reduce grain size but the exact result will depend on timing of the stress relative to the development stage. In many environments drought stress begins to affect crops at the time of anthesis and is exacerbated by withdrawal of ground water by the crop itself.

Cessation

The decline of grain growth during maturation is not so much due to changes in supply of assimilate but to an inability of the grain to convert sucrose into starch. The endosperm literally becomes so filled with tightly packed starch granules there is no further space for starch deposition (Ellis *et al.*, 1992).

5.2 Growth

5.2.1 Partitioning of carbon

Partitioning of dry matter within the plant is one of the most difficult physiological processes to compare and probably the least satisfactory in any crop simulation model. At the 9th Triennial of the European Association for Potato Research in Interlaken, Switzerland in 1984 a special session on mathematical modelling was held at which the lack of understanding of the processes determining partitioning of carbohydrates was highlighted. Some 10 years later, Ewing (who chaired that special session) & Sandlan (1994) in their opening paragraph point out that "the greatest difficultly in modelling the growth of the potato is associated with partitioning of dry matter to the various organs". They list a considerable range of environmental factors whose effects can vary considerably among genotypes. This presents considerable problems to the modeller both in determining which are the factors which determine the major sources of variation in partitioning (this may vary from region to region) and hence should be included in the model and second obtaining sufficient data to calibrate the partitioning functions for the genotype(s) in question. These uncertainties are not unique to potato. This lack of understanding is a general problem common to all species. Despite continued detailed work by plant physiologists, little or no progress for any plant species has been made since that time in attaining a mechanistic understanding. Thus the modeller has little option but to describe empirically the changing partitioning with time and the responses to changes in the environment. It is not surprising that the values of parameters associated with partitioning often undergo much change when a model is recalibrated for a new environment and/or a different cultivar. This conclusion is as equally valid for predicting barley growth as it is potato.

To date two approaches have been used to describe the partitioning of carbohydrate with time, cumulative and instantaneous partitioning coefficients. The former can be observed directly at any point in time as the ratio of the dry weight of an organ type to the total dry weight of the plant. Empirical equations describe the observed changes in these ratios with time. Where the organ in question is the one to be harvested then the

ratio is the harvest index; for cereals this is the ratio of grain weight to total plant dry weight. The alternative approach uses some form of instantaneous partitioning coefficients in equations which describe the distribution of currently available carbohydrate among the organ types according to their relative strengths. A particular organ may be given first priority (e.g. early on it may be the root) and the remaining carbohydrates are then partitioned among the other organs. A further complication arises in handling the effects of environmental stresses. Both nitrogen and water shortage can shift partitioning in favour of a particular organ. Again these shifts are described empirically. These detailed descriptions have the appearance of being "mechanistic" but in reality are simply more detailed empirical descriptions and possibly less robust than cumulative partitioning coefficients. The majority of crop models use instantaneous partitioning coefficients, even though they are much more difficult to determine experimentally. Ideally one should use ^{14}C tracer techniques, or with the recent advances in stable isotope technology the use of $^{13}C/^{12}C$ ratios at natural abundance or low enrichment levels, to determine the instantaneous coefficients. However, this is expensive both in time and money and hence replication and the number of treatments that can be covered is severely restricted.

An approximate estimate of instantaneous partitioning coefficients can be inferred directly from the observed cumulative partitioning coefficients (Marshall & McNicol, unpublished). No explicit treatment of carbohydrate reserves is possible by this method. They are treated as part of the organ. The instantaneous partitioning coefficient for the *i*th organ,

$$p_i = (1/R)\ dP_i/dt + P_i \qquad (5E1)$$

where P_i is the cumulative partitioning coefficient of the *i*th organ and R is the relative growth rate (RGR) of the crop. P_i is estimated by fitting a polynomial function of time to P_i and dP_i/dt by taking the first derivative of this function with respect to time. R is estimated in a similar fashion by fitting a polynomial to the natural logarithm of crop dry weight and then taking the derivative with respect to time.

All these approaches require destructive sampling and a large degree of replication and treatment combinations. Such information is expensive and rarely available.

The major effect of nitrogen in the PTX was on total dry matter production which was manifest in the total amount of dry weight present in the tillers. Once inside either tiller or main-stem the proportions partitioned to tissue types (leaves, stems and ears) was unaffected by nitrogen. Partitioning of dry weight to the ears was slightly earlier in the main-stem than in the tillers. Interestingly the leaf and stem tissues also had a higher nitrogen concentration on the tillers than on the main-stem. Both these differences are consistent with the tiller development lagging behind that of the main-stem. Cultivar differences were small, a slightly greater proportion of the dry weight was partitioned to the leaves in cv. Prisma during the early expansion. Figures 5.2.1F1 and F2 show the estimated instantaneous partitioning coefficients using equation 5E1 for the four treatments in both years. When growth rate is very slow the first term in equation 5E1 becomes very sensitive to the value of R and estimates of p_i are unreliable. This situation arose after the fifth harvest in all treatments in 1989 and in the Low N treatments in 1990. In reality the p_i values for the ear should be zero until some time between harvests 2 and 3. The small deviations from zero prior to this point are due to the approximations (polynomial functions) used to describe the time courses of R, P_i etc. Unlike the cumulative coefficients the instantaneous coefficients, p_i, can have values greater than unity and less than zero. This situation arises when an organ is increasing in dry weight faster than the crop is as a whole. For this to happen there must be a net re-translocation of dry weight from one organ type to another. This effect can be seen clearly between the stem and the ear tissues in the High N treatments. The time courses are remarkably consistent for each tissue type. The stem by the first harvest is already receiving the greatest proportion of the assimilate. This proportion continues to rise and reaches a maximum shortly before leaf growth ceases. It then declines as ear growth takes over the resources, and by the fifth harvest is, in most cases, going negative. The steepness of this decline is greatest in 1989, particularly in the High N treatments (Figure 5.2.1F1).

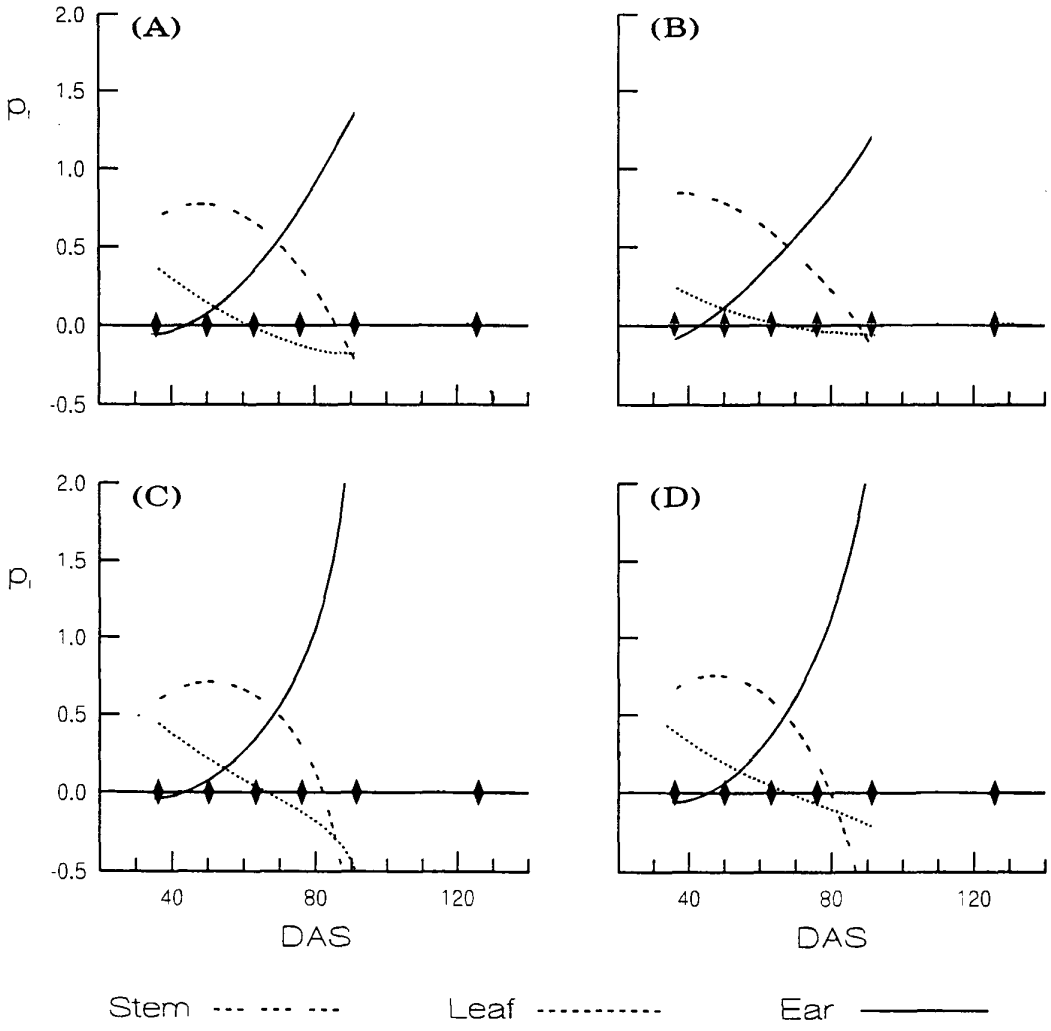


Figure 5.2.1F1 Instantaneous partitioning coeficients of dry weight in 1989, (a,b) Low N (c,d) High N and (a,c) cv. Prisma, (b,d) cv. Tyne. Diamonds indicate the 6 harvests.

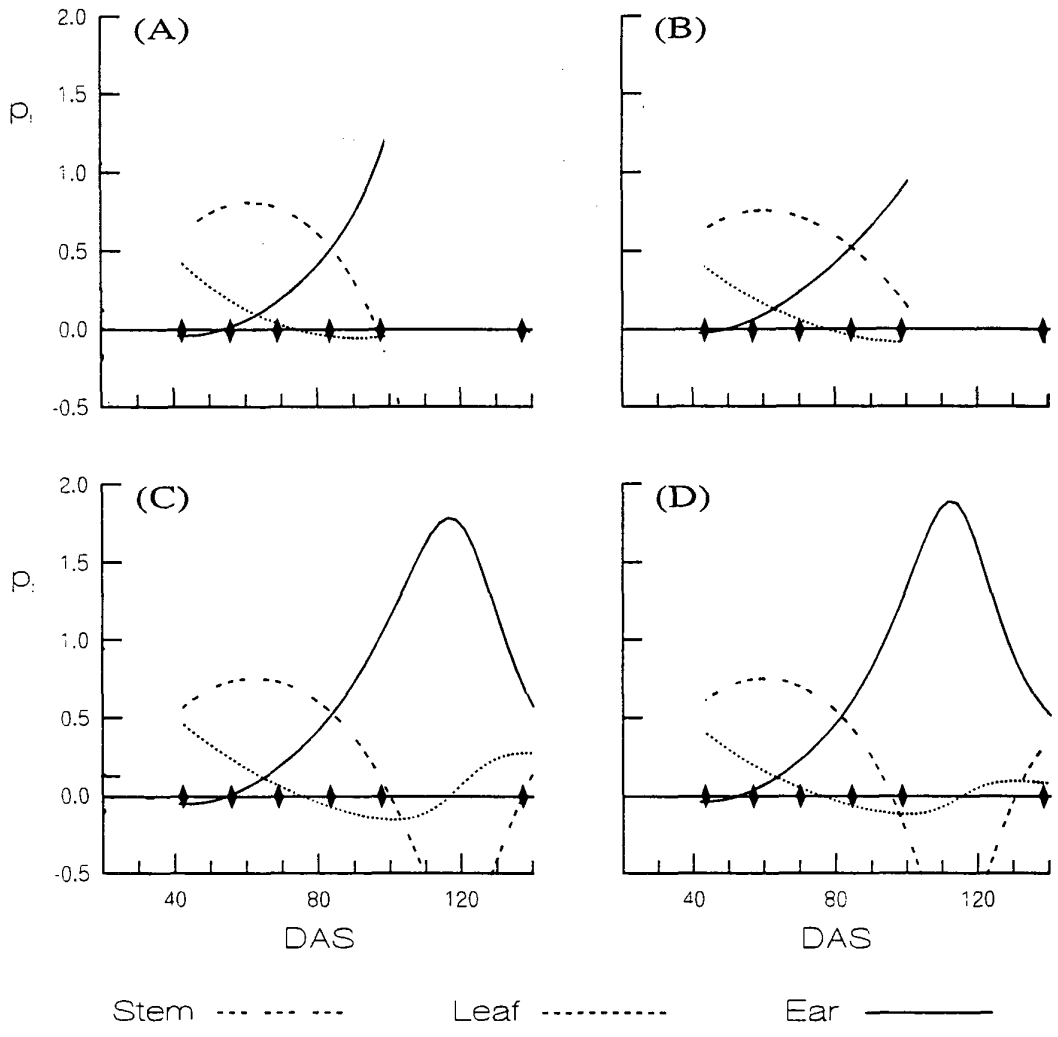


Figure 5.2.1F2 Instantaneous partitioning coeficients of dry weight in 1990, (a,b) Low N (c,d) High N and (a,c) cv. Prisma, (b,d) cv. Tyne. Diamonds indicate the 6 harvests.

The effects on cumulative partitioning of nitrogen were similar to those for dry weight. The main contrast being the much greater proportions of nitrogen residing in the leaves. Hence, during grain growth the leaves were the main tissue source for nitrogen and stems the main source for carbon i.e. in addition to the nitrogen taken up and carbon fixed during that period. Again partitioning of nitrogen to the ear was slightly later in the tillers.

Biological misconception – While estimates of instantaneous coefficients give a clearer indication of when changes in partitioning occur and the proportion which is due to relocation, both instantaneous and cumulative coefficients are essentially descriptive. In themselves they do not provide an understanding. More importantly the approach to partitioning is biologically incorrect. It assumes that decisions on partitioning are made on a global scale (scale of the whole plant) e.g. when a particular organ is deficient in carbohydrate and another organ is better supplied resources should then be relocated. This would require the presence of a global "brain" to make these decisions. This clearly is not the case. As Cheeseman (1993) points out the "decision" as to how much to export, how much to put into structure and how much to retain must reside within the cell. Of course there is no intelligence, it is simply the result of a network of chemical reactions that take place within the cell. The proportions of substrate that flow into structure, is exported etc is determined by the relative concentrations of resources within the cell. These reactions have no knowledge of the size of the cell within which they take place, let alone the organ within which the cell resides. The reason that substrate flows from a relatively sufficient part of the plant to one that is deficient is simply that the deficient cell/organ exports less as a result of its own deficiency than it imports from a more sufficient cell/organ.

The behaviour of crop simulation models is critically dependent upon the procedures defining partitioning of carbon and its redistribution during senescence. Models are especially sensitive when instantaneous coefficients are used and even more so, when the values are determined by the relative sink sizes of the different organ types.

At the outset of this project it had been intended to base the interpretation of nitrogen uptake and carbon assimilation interactions on the use of existing simulation models of cereal growth and one under development specifically for barley. The latter was a three year Ph.D. project funded in part by the then named Department of Agriculture and Fisheries for Scotland (DAFS) (now Scottish Office Agriculture and Fisheries Department (SOAFD)). The Ph.D. viva took place in January 1994. This work was based on the apparently successful model, CERES, produced in the USA under the IBSNAT programme. A major problem became apparent in the processes determining tillering which could not be resolved. It was finally concluded that simulation models were unable to give adequate predictions of cultivar performance. It was difficult to estimate cultivar specific coefficients because the size of differences in these coefficients were small against a background and high variability and interactions present in a field crop. Nevertheless, small differences can on average be of commercial significance.

Since progress on the DAFS model was slower than expected, and its priorities different to this project we had to develop our own simulation model based on the models of Keulen & Seligman (1987) for spring wheat and AFRC winter wheat model. Keulen and Porter both provided us with copies of their models from which we adapted and developed a detailed, mechanistic model of barley development and growth in modular form. Data from an earlier set of experiments funded by ICI were provided by the University of Leeds. However, the sensitivities to partitioning, the use of critical nitrogen concentrations at the whole plant level and the difficulties of calibration of various parameters convinced us that an entirely new approach was required.

Partitioning remains an area of concern and challenge. A conceptual break-through is required if a mechanistic understanding is to be achieved. Cheeseman (1993) is pointing to a possible way forward. For the present, simulation modellers of crop development and growth must make do with empiricisms. This is a major weakness, since the predictions of carbon assimilation and nutrient acquisition are sensitively dependent on the amounts partitioned to the photosynthesising organs and roots respectively. For the immediate future then it is unlikely that any crop simulation model will be robust

enough to perform reliably in environments for which it was not calibrated. They should never be used in isolation from other information and expertise.

From our observations it appears that nitrogen has little or no effect on the proportions of carbon found in the various organs in the shoot (leaf, stem, ear). There is some suggestion from the instantaneous coefficients that there were possible differences between various treatments in the timing and degree of relocation of resources from the stem to the ear. However, to attribute this to a particular treatment could be misleading. In practise, it is more likely that the stem is acting as a buffering mechanism. If there is adequate supply of carbohydrate from assimilation during grain filling then the *net* exchange of resources between stem and ear is much less – the amount recycled between these organs may be similar or even greater!

5.2.2 Carbon assimilation and nitrogen content

There is a close link between the nitrogen content of a leaf (photosynthetic tissue in general) and its ability to assimilate carbon. Thus the distribution of nitrogen in the canopy in relation to assimilation is important. Looking at the approaches taken by crop modellers, similar criticisms of global control apply to the use of critical nitrogen concentrations. An average concentration of nitrogen is usually taken over the whole of the leaf tissue or even over the whole plant. This concentration is then used to decide what reductions if any should be made to processes such as assimilation, leaf expansion, tiller production etc. Again, like partitioning, global control is being invoked where local reactions should be considered. Field (1983), Field & Mooney (1983) and Hirose & Werger (1987 a, b) demonstrated that there was an optimal distribution for nitrogen down the canopy which would maximise canopy photosynthesis for a given amount of nitrogen. Pozo (1992) has observed such distributions in wheat canopies, particularly when nitrogen is limiting. Field (1983) was concerned that there was a cost of redistribution that needed to be subtracted in order to achieve the optimum distribution if it was not already optimised. However, this is falling into the same conceptual trap of global control. It assumes that the crop is able to sense where

optimality lies and move itself towards it! We will now show that such a result can be obtained using a local mechanism only i.e. without invoking such a teleonomic goal.

5.2.3 Model of nitrogen limited growth

Background

Greenwood (1982), Greenwood *et al.* (1985 a, b) have provided a simple, practical method for estimating the amount of nitrogen required to maintain the growth rate of a crop at its maximum. The optimum nitrogen content is that which is just sufficient to maintain the maximum. Any less nitrogen and growth rate is reduced, any more nitrogen has no effect. The excess is surplus to current photosynthetic and structural requirements and is sometimes referred to as "luxury" uptake. However, it may be required at some later date when uptake from the soil becomes restricted. The method derived by Greenwood *et al.* (1985b) was based on their observed relation between nitrogen concentration and weight of a plant which appears to be universal for annual C_3 crops (Figure 5.2.3F1). The decline in nitrogen concentration with increase in plant dry weight and hence time was interpreted as a change in the proportion of structural and storage tissues to the metabolically active tissues. Initially the plant has a high proportion of metabolically (photosynthetic) active tissue which has a high demand for nitrogen (approximately 0.07 g(N) gDW^{-1}). By maturity the plant is dominated by structural and storage materials which have much lower nitrogen requirements (0.001 to 0.02 g(N) gDW^{-1}). In order to make practical use of this relation a model of crop growth is required to predict the increase in plant dry weight with time. Once the target dry weight is known then it is simply a case of finding the corresponding nitrogen concentration and multiplying the two together to calculate the total amount of nitrogen required by the crop (Figure 5.2.3F1). The model of growth used by Greenwood *et al.*, (1985b) takes no account of the environment. It is simply a function of time and therefore its application is restricted to the local conditions under which it was developed and represents an approximation to the average response.

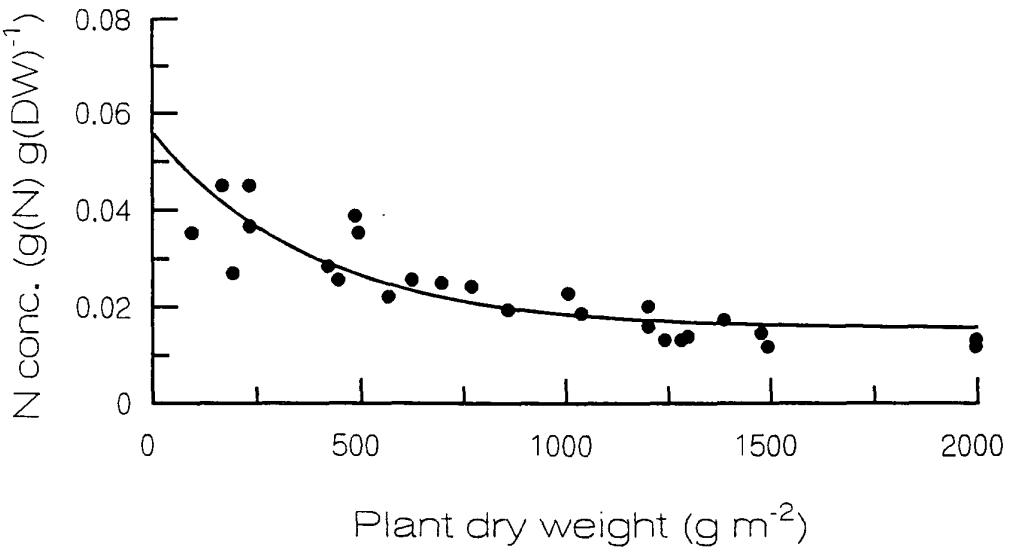


Figure 5.2.3F1 The observed relation between the average nitrogen concentration of plants, grown with optimal levels of fertiliser, and the total dry weight (excluding roots) at harvest of 22 different species (after Greenwood, 1982, and Greenwood et al., 1985a).

During the 1970's Monteith (1978), Biscoe & Gallagher (1977, 1978) and others demonstrated the general principle of solar radiation as a determinant of crop growth rate. They showed that the total plant dry weight attained by a crop was proportional to the amount of radiation intercepted (Figure 5.2.3F2). Further, when growth was not limited by nitrogen, water or disease the slope of this relation, the light conversion coefficient, ε, was found to be conservative for C_3 crops with a value of approximately 1.8 g MJ(total solar radiation)$^{-1}$. A little later, Ingestadt (1982) and colleagues were looking at the early growth of slow growing plants under carefully controlled conditions of nutrient supply. They found that for a given set of environmental conditions (temperature, radiation etc) that the relative growth rate (RGR, growth rate per unit dry weight) was a linear function of nitrogen concentration of the whole plant (Figure 5.2.3F3). Marshall & Porter (1991) took these two concepts, the former determining *absolute* growth rate and the later *relative* growth rate and combined them. While plants are small, every investment in organs which capture resources, such as leaf surfaces which intercept sunlight and assimilate carbon and roots which take up nutrients, will tend to increase the growth rate of the plant *pro rata* i.e. doubling a small leaf area doubles the growth rate. This results in rapidly increasing or exponential growth rates. This is when a constant, high value of RGR is achievable. However, it is not long before leaves start to overlap, first within the plant and then across neighbouring plants. Ultimately the canopy completely covers the ground and further increase in leaf area does not increase the amount of sunlight intercepted. Absolute growth rate has now reached a maximum and remains constant until the canopy senesces. During this time, since absolute growth rate is constant and plant weight steadily increases then the growth per unit dry weight (RGR) declines, and thus from the observations of Ingestadt et al., (1982) (Figure 5.2.3F3) the desired nitrogen concentration also declines. The equation

$$N_{c,opt} = (\varepsilon S_o/\beta')\ (1 - e^{-K\phi W})/W + N_{c,min} \qquad (5E2)$$

derived by Marshall & Porter (1991) provides an accurate description of the observations of Greenwood *et al.* (1985b). $N_{c,opt}$ and W are the nitrogen concentration and dry weight of the whole plant respectively. $N_{c,min}$ is the average nitrogen concentration of the

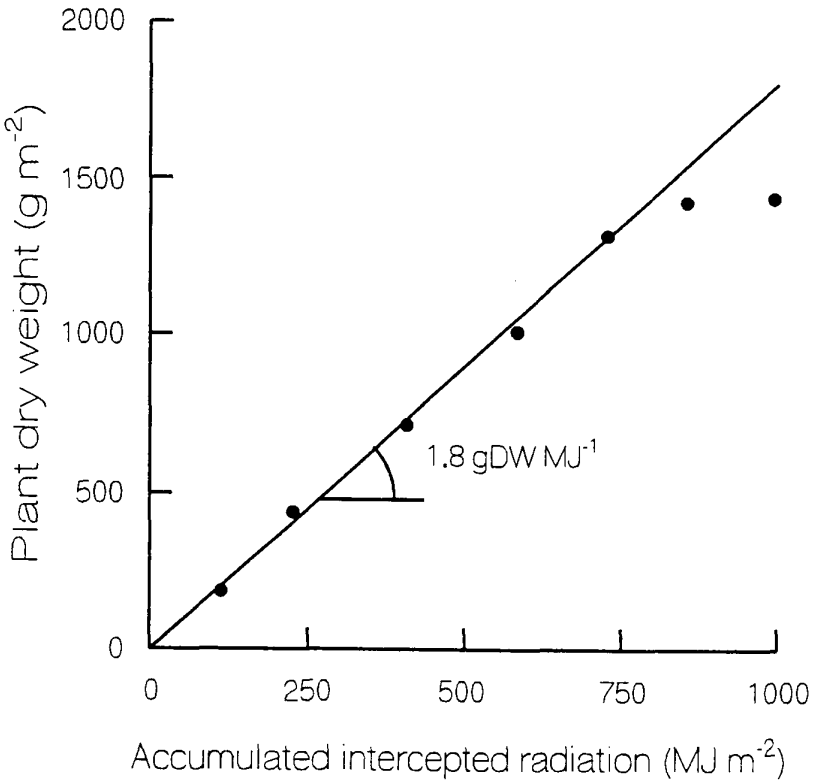


Figure 5.2.3F2 Typical relation between the amount of radiation intercepted by a C_3 crop and the amount of total dry matter produced.

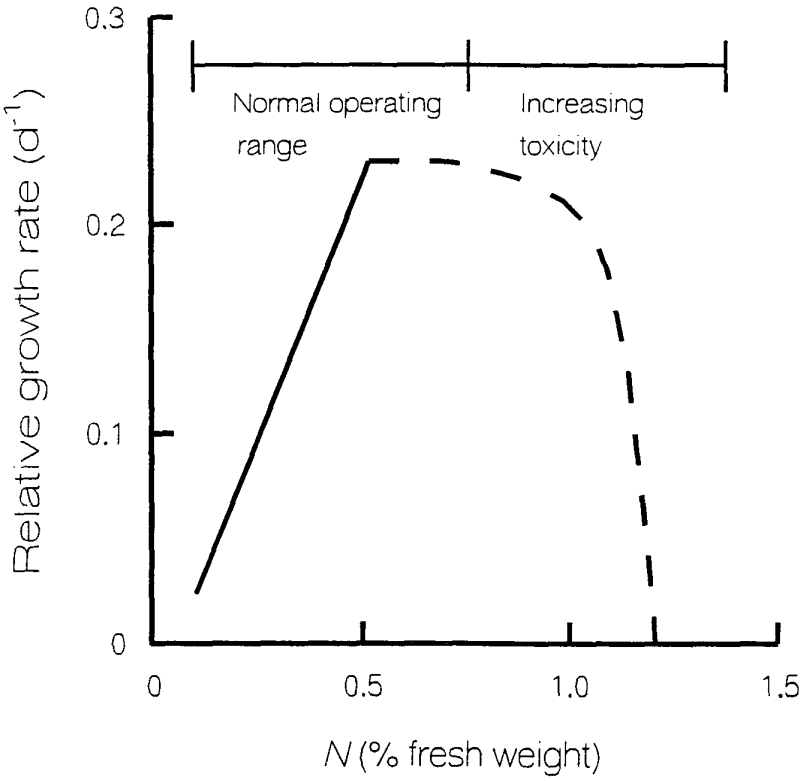


Figure 5.2.3F3 Relation between the relative growth rate and nitrogen concentration of an entire plant (N, fresh weight; after Ingestadt, 1982).

structural plus storage material. This is the nitrogen concentration that the plant tends towards as it matures. ε is the light conversion coefficient; S_o, the quantity of solar radiation incident each day; K, is the light extinction coefficient and ϕ, the specific leaf area. The term $(1 - e^{-K\phi W})$ is the proportion of light intercepted by a plant of weight W. Hence the quantity $\varepsilon S_o/(1 - e^{-K\phi W})$ is the daily growth rate and when divided by plant weight gives the relative growth rate. β' is the linear part of the slope of the relation (converted to a dry weight basis) in Figure 5.2.3F3 and converts relative growth rate into the equivalent nitrogen concentration of the metabolic tissue.

Problem

The curve derived by Greenwood et al. (1985b) and the similar result of Marshall & Porter (1991) provide a good estimate of the optimum nitrogen requirements to just achieve maximum yield. But what happens if nitrogen is limiting growth i.e. below the optimum? If a crop is deficient in nitrogen what are the prospects for such a crop getting back to optimum nitrogen status?

To ensure the crop is not nitrogen limited a considerable safety margin above the optimum could be used. However the bigger the margin the greater the risk of polluting the environment and compromising the malting quality of the grain. A new model, consistent with the above observations, is required which in addition takes account of nitrogen limitations on crop growth.

Definition

Such a model is described in detail in Appendix A1. The relations used in this new model are based on actual observations. They are:-

1 - ***photosynthesis-light response of a single leaf is assumed to be represented by two straight-lines,***

2 – *the maximum or light saturated rate of photosynthesis of an individual leaf (P_{max}) is directly proportional to the concentration of nitrogen in the photosynthetic pool,*

3 – *solar radiation is attenuated exponentially down the canopy which is characterised by the extinction coefficient, K.*

These relations are summarised in Figure 5.2.3F4. In practice the photosynthesis–light response is rounded at the point of intersection and can be better described by a non–rectangular hyperbola, NRH, with parameters: P_{max}, the light saturated rate of photosynthesis; α, the initial slope and Θ, the degree of curvature at the shoulder (See Figure A.1F1 in Appendix A1). In the 1960's a rectangular hyperbola (a special case of NRH with $\theta = 0$) had been used to describe this response (Figure 5.2.3F4A). But it's approach to light saturation proved to be too gradual. Marshall & Biscoe (1980 a,b) found the value of θ for winter wheat to be close to unity, two straight lines. The important features are the initial slope at low light (α) and the plateau region in bright light (P_{max}). The precise details of the shoulder are not important and do not influence the conclusions of the model.

There is one critical assumption,

the nitrogen concentration of the photosynthetic system is proportional to the light intensity incident on the tissue.

Thus leaves at the top of the canopy, which are in bright light, have higher nitrogen concentrations than leaves lower in the canopy with darker environments. This is an example of a local mechanism. It does not invoke the need for a "brain" – a failing of current crop models. However, it can be shown to have global consequences. If this assumption is correct then the distribution of nitrogen down the canopy will mirror that of the light profile and canopy photosynthesis is maximised. Furthermore, if nitrogen content of the uppermost leaf is just sufficient to ensure that the leaf is on the point of light saturation – the intersection of the lines in Figure 5.2.3F4A – then all leaves down the profile will also be at their respective, local saturation points, canopy photosynthesis is maximal and nitrogen content of the canopy optimal.

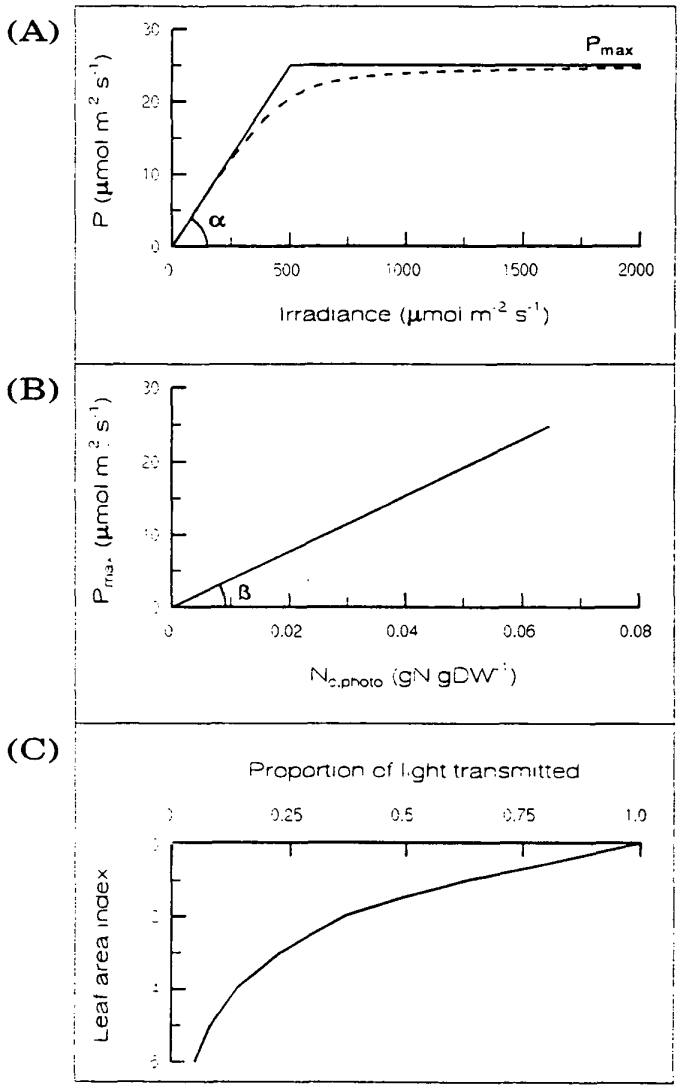


Figure 5.2.3F4 Canopy growth model: (a) the leaf photosynthesis(P)-light response (b) relation between light saturated rate of photosynthesis (P_{max}) and the concentration of nitrogen in the photosynthetic pool ($N_{c,photo}$), and (c) the attenuation of light down the leaf canopy.

There is one driving variable,

nitrogen content of the non-reproductive biomass.

This is significantly different from the previous models of Greenwood *et al.* (1985) and Marshall & Porter (1991) where the nitrogen content of the whole plant was considered. The reason for restricting it to the non-reproductive biomass (NRB, leaf plus stem) is because this is where the bulk of the photosynthetic tissue resides. Organelles in the ear are also capable of photosynthesis, however the bulk of the nitrogen in the ear is associated with storage proteins in the developing grains and does not contribute to photosynthesis. The consequences are clearly demonstrated when Ingestadt plots (RGR v % N) of first, nitrogen concentration of the *whole* plant (ear included) and then of the *NRB* only (Figures 5.2.3F5 and 5.2.3F6 respectively). When the whole plant is used the RGR after anthesis declines to zero while whole plant nitrogen concentration remains constant. This is particularly noticeable in the Low N treatment (arrows in Figure 5.2.3F5). This is because nitrogen is being relocated from the photosynthetic tissues to the ear during this period. By considering only the NRB the effect of relocation on photosynthesis now becomes evident - both RGR and nitrogen concentration decline together (Figure 5.2.3F6).

Other environmental variables (temperature and solar radiation) are assumed to be constant and water non-limiting.

Finally there are three nitrogen pools in the model which are shown in Figure 5.2.3F7. They are the photosynthetic pool (N_{photo}), the structural pool (N_{struc}) and the storage pool (N_{store}). The storage pool simply refers to nitrogen that is currently neither required for photosynthesis nor for structural components. Nitrogen enters and leaves the non-reproductive biomass via this notional storage pool. Any nitrogen remaining in the storage pool is equivalent to the luxury uptake referred to earlier. In times of high demand elsewhere in the plant there can be a net-removal of nitrogen from the photosynthetic pool, thus reducing future rates of photosynthesis. No such removal is possible from the structural pool.

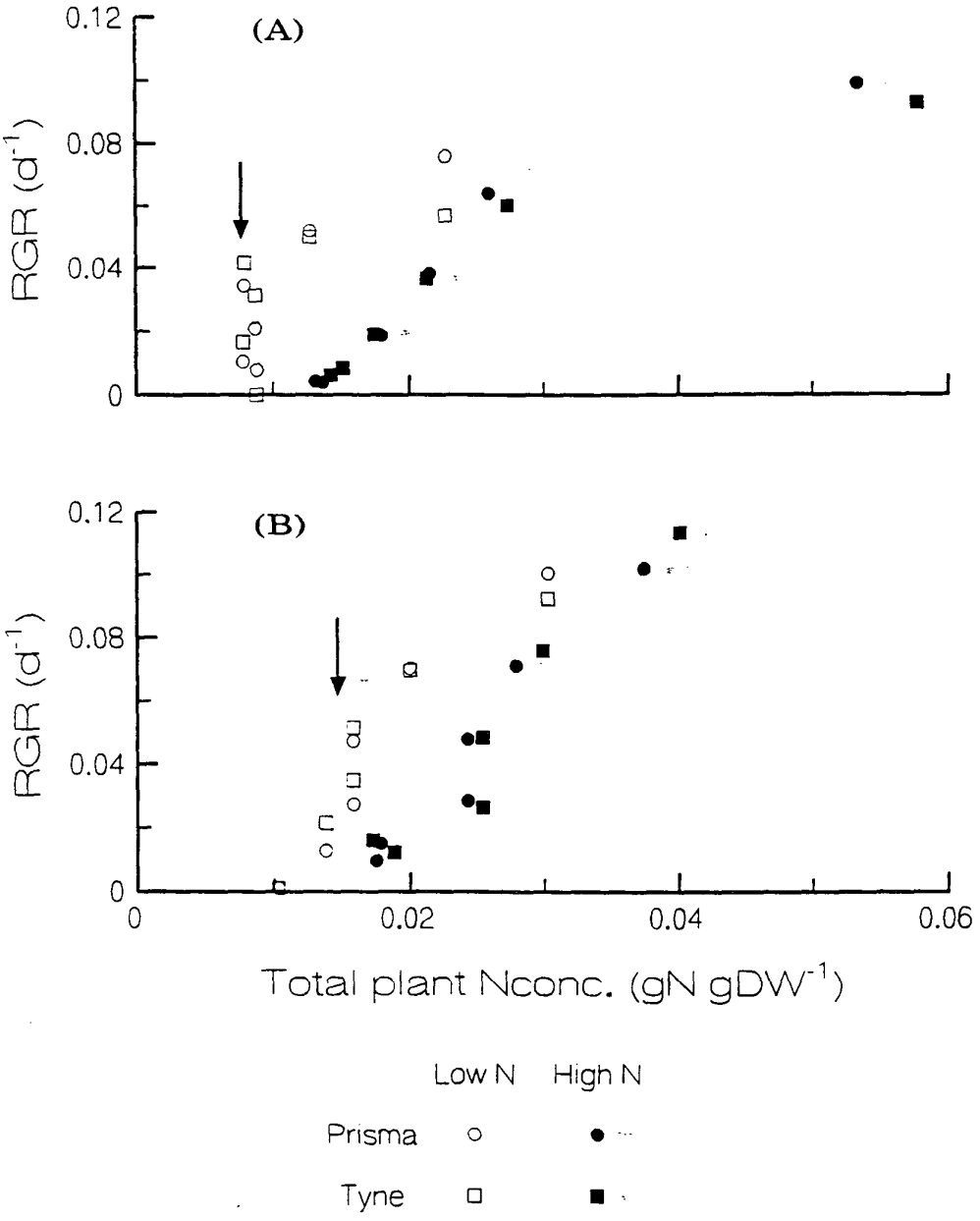
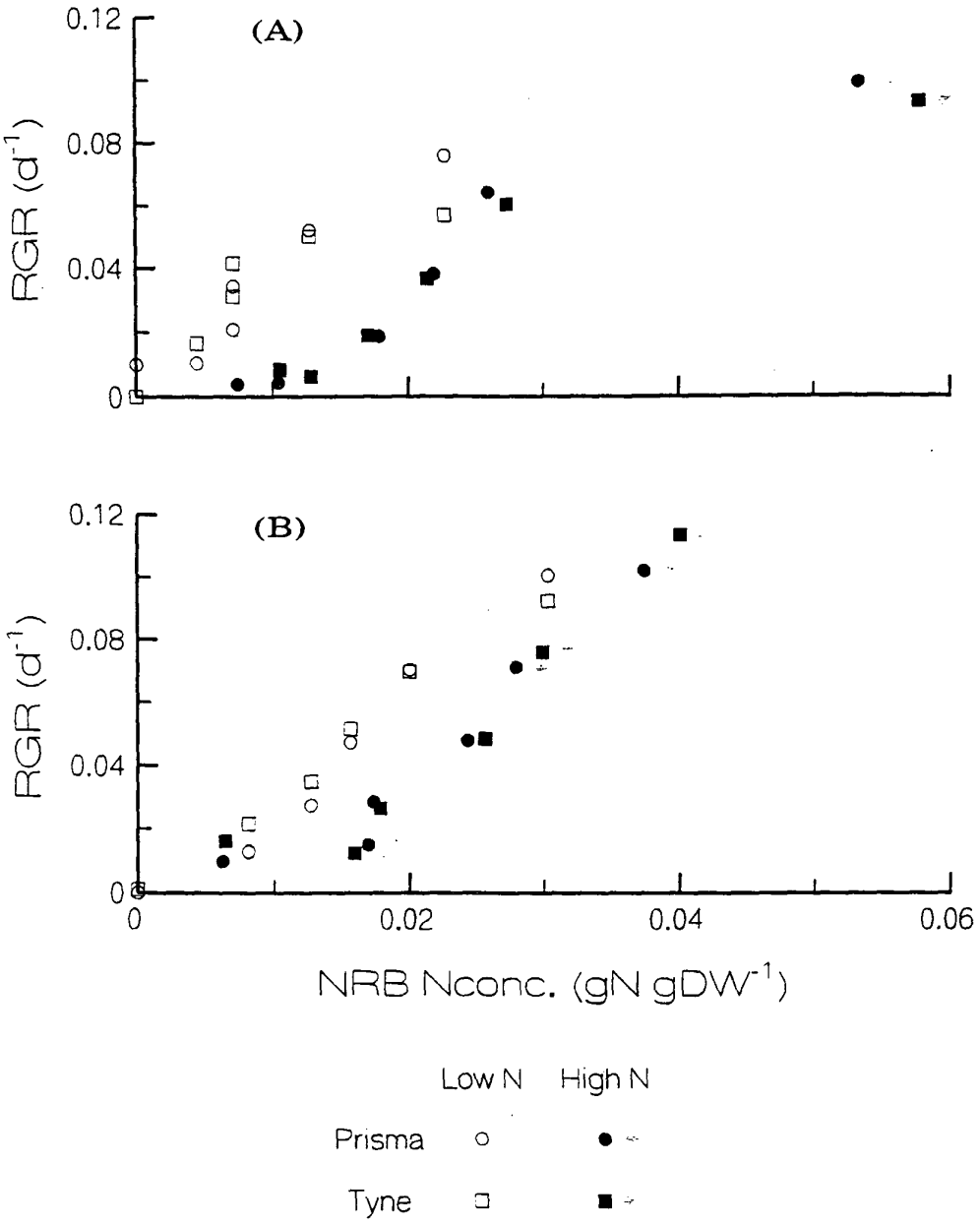


Figure 5.2.3F5 The relation between the relative growth rate of the plant (RGR) and the nitrogen concentration of the whole plant in (a) 1989 and (b) 1990.



Figue 5.2.3F6 The relation between relative growth rate of the plant (RGR) and the nitrogen concentration of the non-reproductive biomass (NRB) in (a) 1989 and (b) 1990.

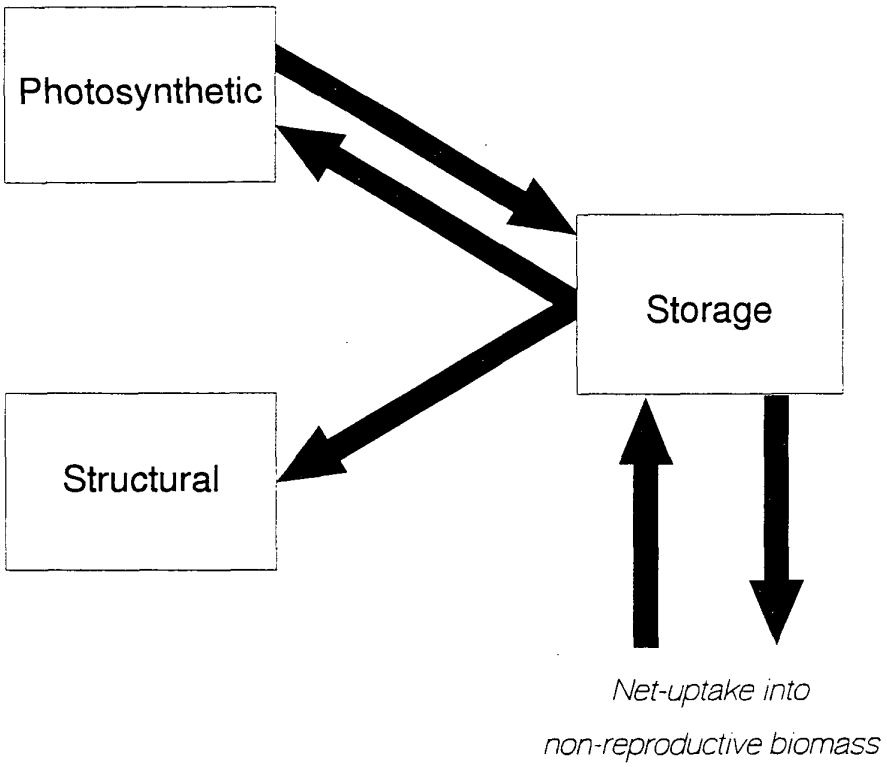


Figure 5.2.3F7 The three notional nitrogen pools used in the model of nitrogen determined canopy growth rate. The pools reside in the non-reproductive biomass. Nitrogen in the ear is excluded.

Evaluation

The model as described in Appendix A1 was implemented in Fortran and executed with a one day time step. The parameter values are as defined in Appendix A1, Table A.1T1. The radiative environment is assumed constant throughout the season (14 MJ (total solar) m^{-2} d^{-1}), and temperature is assumed not to limit growth. The maximum growth rate of the crop, achieved when the canopy intercepts all the incident light, is 25.2 g(DW) m^{-2} d^{-1}. The time course of nitrogen uptake and the value of $N_{c,struc}$ are the only factors which may change in the following numerical simulations.

Optimal nitrogen conditions

Under optimal nitrogen conditions it is possible to find an analytical solution (see Appendix A1 equation F15), equivalent to equation 5E2 above,

$$N_{c,total} = (N_{c,max}/\phi k)\ (1 - e^{-k\phi W})/W + N_{c,struc} \qquad (5E3)$$

Equations 5E2 and 5E3 are identical in form. $N_{c,total}$ and $N_{c,opt}$ are equivalent, namely the average concentration of nitrogen in the whole plant. $N_{c,struc}$ and $N_{c,min}$ are also equivalent, except that their interpretation differs. $N_{c,min}$ includes storage tissues, such as grain or tubers, as well structural tissue, whereas $N_{c,struc}$ only includes the latter. The only apparent differences are the terms $(N_{c,max}/\phi k)$ and $(\varepsilon S_o/\beta')$. This reflects the different background from which the models are developed. The earlier model is based on processes at the crop level whereas the current model is based upon individual leaf photosynthesis. In fact both terms have the same dimensions and, with parameter values in Appendix A1, Table A1.T1 for the current model inserted into 5E3 and those of Marshall & Porter (1991) (see Table 2) inserted into 5E2, the terms also have equal magnitude, 8 g(N) m^{-2}. Thus at the crop level the two models are equivalent.

To test that the numerical implementation of the model was consistent with the analytical solution, the nitrogen uptake was defined as that required to maintain

$$N_{photo} = N_{opt} \qquad (5E4)$$

and meet the structural requirements for growth. The optimum nitrogen content of the photosynthetic pool is that which is just sufficient to avoid restricting the rate of photosynthesis (see Appendix A1 equation 15). Thus the daily uptake of nitrogen,

$$\Delta N = N_{opt}[W + \Delta W] - N_{opt}[W] + \Delta W\, N_{c,struc} \qquad (5E5)$$

i.e. the increase over the day in the optimal nitrogen content of the canopy due to the increase in canopy weight (ΔW) plus the associated increase in structural nitrogen. The square brackets indicate that the optimum nitrogen content changes with the weight of the plant. From equations 8 and 14 in Appendix A1,

$$N_{opt}[W] = N_{c,max}\,(1 - e^{-k\phi W})$$

and

$$N_{opt}[W+\Delta W] = N_{c,max}\,(1 - e^{-k\phi(W+\Delta W)}) \qquad (5E6)$$

The value of $N_{c,struc}$ does not affect the behaviour of the model significantly, when run under optimal conditions. It simply defines the additional nitrogen required for structural growth. For consistency with the value $N_{c,min}$ as used by Marshall & Porter (1991) the same value, 0.0076 g(N) g(DW)$^{-1}$, has been used for $N_{c,struc}$ in this simulation. The predicted relation between nitrogen concentration of the canopy (sum of photosynthetic and structural nitrogen pools divided by plant weight; the storage pool being empty) and plant weight is shown in Figure 5.2.3F8 along with the original relation of Marshall & Porter (1991) (dashed line). The agreement between the two is perfect. Thus the assumption that nitrogen profile down the canopy mirrors the light profile is valid.

For comparison, the original relation proposed by Greenwood *loc cit.* (1985a),

$$N_{c,plant} = 0.0133 + 0.0405\, e^{-0.0026W} \qquad (5E7)$$

is also shown (solid line). There is good agreement between this relation and that of Marshall & Porter (1991), and hence the current model, for plant weight in the range 250 to 2000 g m^{-2}. For plant weights below 250 g m^{-2} there is a divergence between the two relations; likewise above 2000 g m^{-2}. The relation of Greenwood *et al.* has a

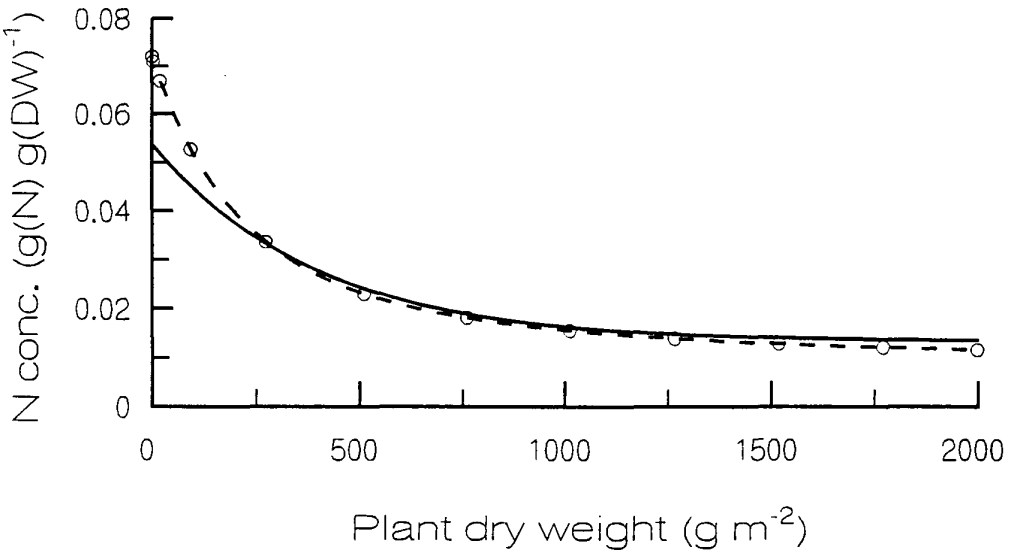


Figure 5.2.3F8 Canopy growth model: predicted relation between the nitrogen concentration of the plant and its dry weight (open circle, plotted at 10 day intervals). The Marshall and Porter (1991) relation (dashed line), to which it should be identical, and the Greenwood et al. (1985b) relation (solid line), are shown for comparison.

maximum value of 0.0538 g(N) $g(DW)^{-1}$ when W = 0, and falls to 0.0133 g(N) $g(DW)^{-1}$ as W becomes very heavy. The corresponding value for the relation of Marshall & Porter, and the current simulation, 0.0076 g(N) $g(DW)^{-1}$. The difference between the upper limits of nitrogen concentration are well within the bounds of the data originally used by Greenwood and coworkers (e.g. see Figure 11, Marshall & Porter, 1991). In terms of absolute amounts of nitrogen required this difference is small. The differences in the lower limit on the other hand appear small but in terms of absolute amounts of nitrogen can be significant since dry weight is now considerably heavier. Greenwood and colleagues were considering the whole plant (excluding fibrous roots) which includes the storage organ – in their case a potato tuber. Thus the lower limit is dominated by the nitrogen concentration of this tissue which is greater than the minimum nitrogen concentrations observed in stem and leaf tissues. The current model is only concerned with the nitrogen content of NRB i.e. the storage organ is excluded.

From the same simulation, the desired time course of nitrogen uptake can be deduced (Figure 5.2.3F9). This was implicit in the cumulative nitrogen uptake for optimal growth implied by the relation of Greenwood *et al.* (1985b), shown earlier in Figure 5.2.3F1. The most striking feature is the need for fast rates of uptake, approaching a peak of 5 kg(N) ha^{-1} d^{-1}, when the crop is still very young, circa 30 days after emergence. At this stage, crop dry weight is only around 1000 kg ha^{-1} and optimal nitrogen concentration around 0.05 g(N) $g(DW)^{-1}$. Lower temperatures may reduce this demand a little in spring sown crops, and more so in winter sown crops. In both crops the peak demand will occur in the spring when the leaf area is rapidly expanding (approximately LAI 1 to 2). Nevertheless this reinforces the importance of adequate nitrogen early in the life of a crop.

Constant nitrogen concentration

The assumption that the relative growth rate (RGR) of a plant is linearly dependent on the average concentration of nitrogen in the plant (Ingestadt, 1982) is generally applicable – not just to slow growing isolated plants – is crucial to the validity of the

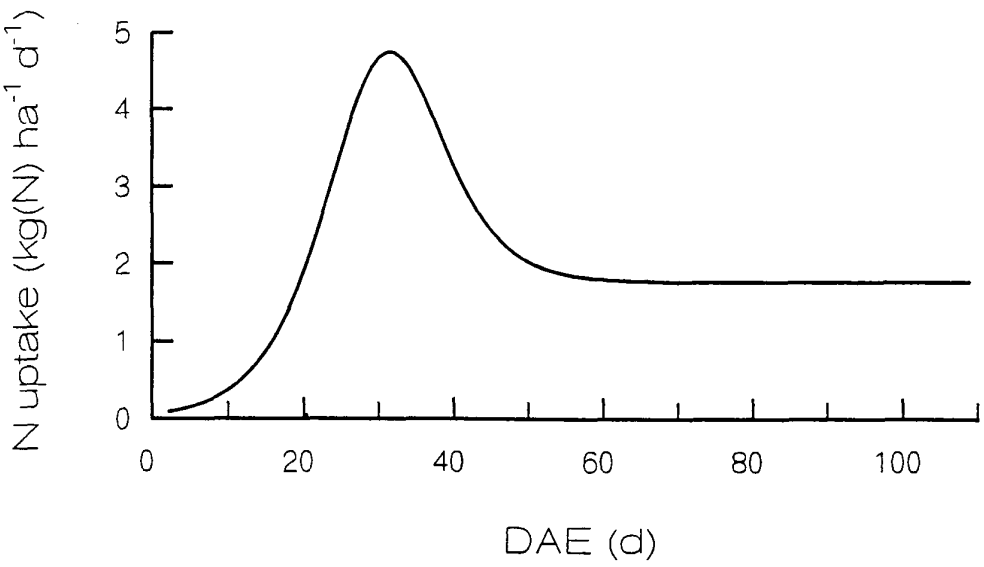


Figure 5.2.3F9 Canopy growth model: predicted rate of nitrogen uptake to maintain maximum growth rate (optimal nitrogen) with days after emergence (DAE).

relation proposed by Marshall & Porter (1991). Ingestadt & coworkers were able to maintain a constant nitrogen concentration in the plant by careful control and adjustment of the rates at which nutrients were supplied. The plants studied were either young or slow growing plant and in their exponential phase of growth. Thus nutrients were supplied at an exponentially increasing rate, a *relative addition rate*. Marshall and Porter had to assume that the same relation between relative growth rate and plant nitrogen concentration held when the plants were older, growing faster and no longer in exponential phase of growth. The current model, which is not based on this assumption, can be used to test the assumption.

The only modification from the previous simulation for optimal growth is to the time course of nitrogen uptake. In order to maintain constant nitrogen concentration, N_{conc}, the daily uptake of nitrogen is simply defined as

$$\Delta N = N_{conc}\, \Delta W \qquad (5E8)$$

and the concentration is defined at the beginning of each simulation. A typical simulation is shown in Figure 5.2.3F10. The target concentration for the plant in this simulation was 0.0476 g(N) $g(DW)^{-1}$ i.e. structural nitrogen concentration at 0.0076 g(N) $g(DW)^{-1}$ plus a target concentration for the photosynthetic pool of 0.0400 g(N) $g(DW)^{-1}$. After a small, initial variation about the target concentration, which is probably an initial numerical instability that dies away, both the concentration and RGR remain constant (Figure 5.2.3F10A). However, as the plant increases in size so the optimal nitrogen concentration in the plant falls (dashed line, Figure 5.2.3F10A). When this falls below the target concentration, 46 days after emergence, the plant is no longer able to maintain exponential growth. Growth rate is now limited by the quantity of light intercepted and can only increase with the continued expansion of the canopy. Thus RGR declines steadily with time.

Up to the point when light limits growth, nitrogen has built up in the photosynthetic and structural pools alone: the storage pool remaining empty. After this point, the size of

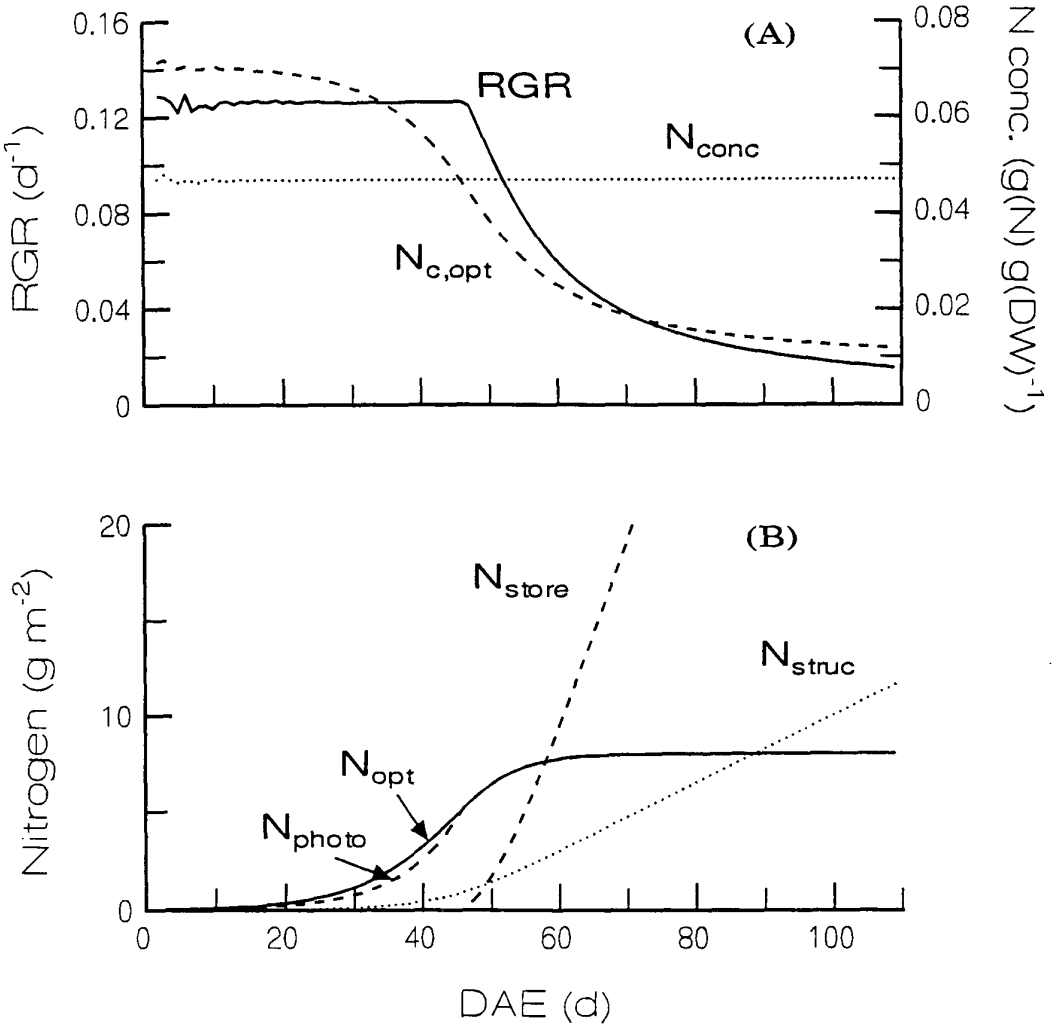


Figure 5.2.3F10 Canopy growth model: showing the time courses of (a) relative growth rate (RGR) and optimal nitrogen concentration ($N_{c,opt}$) when plant nitrogen concentration (N_{conc}) is held constant, and (b) the nitrogen contents of the photosynthetic pool (N_{photo}), structural pool (N_{struc}) and storage pool (N_{store}). The optimal size of the photosynthetic pool (N_{opt}) is also shown.

photosynthetic pool is restricted to that which is sufficient for optimising growth; the structural pool having initially increased exponentially now tends towards a linear rate of increase as canopy growth rate shifts from exponential to linear growth; and the excess nitrogen goes to a rapidly increasing storage pool. The size of the storage pool will eventually become unrealistic. In reality, uptake would be reduced by feedback effects. The main interest of this simulation is the equilibrium value of RGR that is achieved while the nitrogen concentration is below optimal.

This simulation was repeated for a series of target nitrogen concentrations and the equilibrium values of RGR calculated. The results are shown in Figure 5.2.3F11. The relation is indeed as found by Ingestadt (1982): a linear relation of intercept $N_{c,struc}$ (set to 0.0076 g(N) $g(DW)^{-1}$ in this case), slope 3.156 d^{-1} (Ingestadt expressed nitrogen concentration on a fresh weight basis, see Marshall & Porter (1991) for dry weight basis), and upper limit $N_{c,max}$ + $N_{c,struc}$ (0.0716 g(N) $g(DW)^{-1}$). When the nitrogen concentration in the plant is held at the upper limit, the maximum RGR defined by the radiative environment (0.2 d^{-1}) is achieved momentarily and declines immediately. Thus with the single assumption that the nitrogen concentration induced in a leaf is proportional to the incident light intensity with the consequence that nitrogen concentration down the canopy profile is optimised for growth when nitrogen is limiting, the relation observed by Ingestadt has been shown to hold for older and faster growing plants.

Observed nitrogen uptakes in barley canopies

In the simulations so far, the nitrogen content of the canopy has been increasing with time. The only restriction on canopy expansion has been mediated through restrictions on canopy photosynthesis alone. In practice, the changing partitioning of nitrogen and growing demand for nitrogen in the ear results in an eventual decline in nitrogen content of the NRB (Figure 4.2.F1). Thus the photosynthetic capacity of the NRB will also decline.

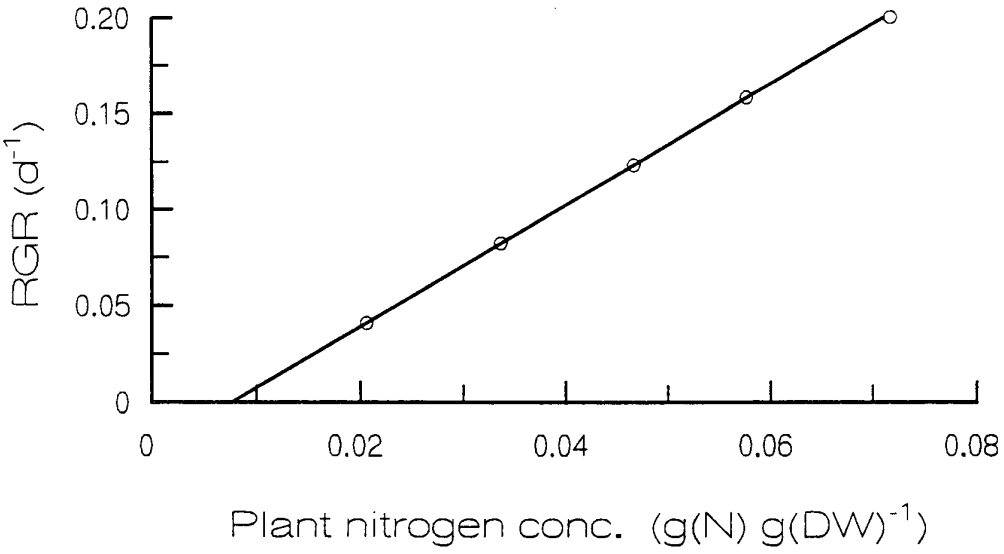


Figure 5.2.3F11 Canopy growth model: The equlibrium value of relative growth rate (RGR) when the plant nitrogen concentration is held constant.

The nitrogen contents of the NRB of the barley in the PTX were used to derive the time course of nitrogen uptake into the NRB. The change in nitrogen content between successive harvests divided by the time interval was used as a rough approximation to the pattern of uptake. This introduces discontinuities in the uptake rate at each harvest point and it is sensitive to sample variations. Alternative methods of approximating the time course of nitrogen content were tried (e.g. a polynomial time series) but they were subject to similar uncertainties. It was decided that a linear interpolation between harvest dates was the simplest, most robust method and adequate for the purpose of comparing nitrogen treatments.

Eight simulations, one for each combination of cultivar and nitrogen treatment in both years, were carried out. The first harvest was used as the starting point in each case; defining the initial dry weight and nitrogen content of the NRB. At the start of a simulation the initial nitrogen was allocated according to the rules in the model (structural requirement of the starting dry weight taking first priority and then photosynthetic requirements and the excess, if any, placed in the storage pool). The simulations were then run to the last harvest date.

It was found that growth was underestimated in all eight simulations and was particularly restricted in the Low N treatments. The only parameter value that could be modified, without losing consistency with the models of Greenwood *et al.* (1985a,b) and Marshall & Porter (1991) (maximum growth rates, daily radiation receipts, curvature of the relation between nitrogen concentration and plant dry weight must remain unchanged), was that for $N_{c,struc}$. As pointed out earlier, this was originally considered as an average value for the *whole* plant, and set at 0.0076 g(N) $g(DW)^{-1}$. However, in this case only NRB is being considered. Nitrogen concentrations at crop maturity in the leaf tissues of either main-stem or tillers were down in the range 0.005 to 0.01 g(N) $g(DW)^{-1}$ (see section 4.2.5). Similar minimum values were observed in potato leaf tissues (0.007 g(N) $g(DW)^{-1}$) with low nitrogen supply (Marshall & Vos, 1991). In winter wheat the values were at the higher end of the range, around 0.01 g(N) $g(DW)^{-1}$ (Gregory *et al.*, 1981). NRB also includes stem tissue and the nitrogen concentrations

in this tissue were lower, in the range 0.002 to 0.004 g(N) g(DW)$^{-1}$ (see section 4.2.5). Stem nitrogen is the major component of the nitrogen in the NRB by final harvest (see Figure 4.2.4F3). Thus the value of 0.0076 g(N) g(DW)$^{-1}$ for $N_{c,struc}$ which was derived for whole plant tissue is an overestimate for NRB tissue.

A manual optimisation of the fit between observed and predicted plant dry weight over harvest 2 through to 6 was conducted. A value of 0.035 g(N) g(DW)$^{-1}$ for $N_{c,struc}$ was found to give the best fit over the eight simulations (Figure 5.2.3F12).

There is good agreement between model and observation, particularly so when the only environmental variable that is changing with time and between simulations is the nitrogen content of NRB. There is little difference between the two cultivars either in the observed or predicted values. The model has no cultivar specific parameters. The only possible differences between cultivars would be fed in via observed differences in the nitrogen contents of the canopies.

There are two areas of discrepancy between observation and prediction

- the Low N treatments in 1989, where the model underestimates growth (overestimates the severity of the nitrogen limitation) in the later part of the season, and
- the growth between the penultimate and final harvest in High N treatments in 1989 is overestimated (the two final points are above the 1:1 relation).

The later discrepancy simply reflects the fact that recirculation of water through the beds was stopped during the second half of grain filling to aid maturation. There is no water limitation included in the model. The reason for the former discrepancy is not simply explained. With the observed nitrogen contents of the canopy it is not clear how so much growth could have been achieved. One possibility is that ear photosynthesis has made a significant contribution to crop growth, especially around ear emergence. The contribution from the ear to the net carbon balance of the plant is very important. The bulk of ear photosynthesis serves to largely offset the considerable respiration of the

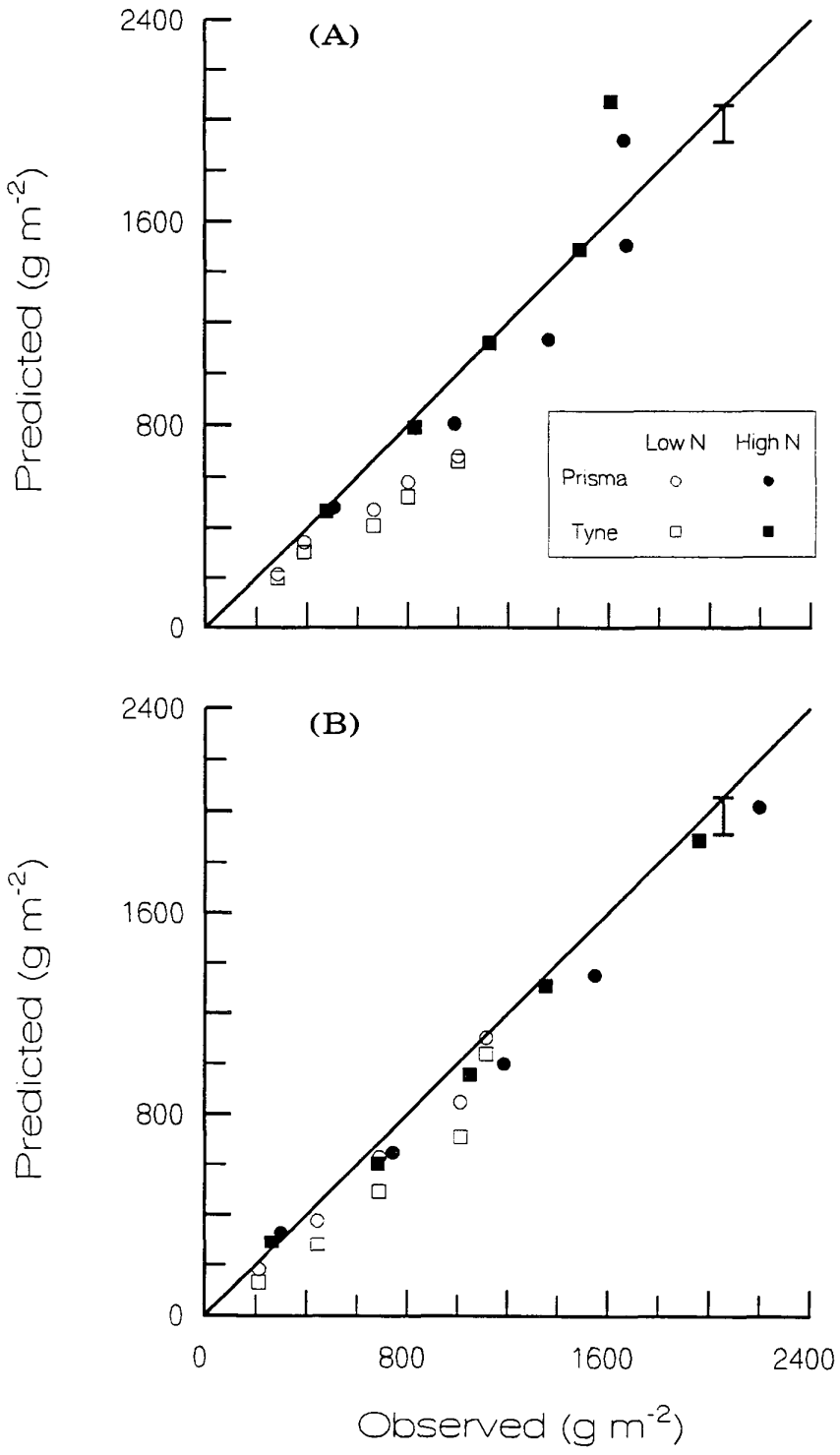


Figure 5.2.3F12 Comparison of predicted and observed total biomass production in the PTX experiments in (a) 1989 and (b) 1990. The predictions are based on the observed nitrogen content of the NRB. The 1:1 lines are shown (vertical bars see text).

filling grain. Biscoe *et al.* (1975) estimated the contribution of ear net-photosynthesis to grain filling to be around 13% by final harvest. Since the ear weight is about 0.6 of the total plant weight by final harvest (Figure 4.2.3F3) then total plant weight could be underestimated by around 8% (13 x 0.6) by ignoring ear photosynthesis in the model. Biscoe *et al.* (1975) estimated this percentage contribution on a fertilised field of spring barley. Although the percentage contribution by the ear is probably greater in the Low N treatments the absolute amount will be the same or less, as the ears are smaller. This effect will only be present from around anthesis onwards (the last three data points in each treatment, Figure 5.2.3F12). An 8% underestimate for a final plant weight of 2000 g m^{-2} would translate into a absolute underestimate of 160 g m^{-2}. This potential discrepancy is shown as vertical bar in Figure 5.2.3F12. Another possibility is that the necessarily crude approximations to the time courses of nitrogen uptake into (or out of) the NRB may play a part in this discrepancy.

Since the behaviour of the cultivars is similar the contrasts between years and nitrogen treatments is best illustrated by focusing on one cultivar. The plant and canopy growth rates and nitrogen contents of the canopy (canopy refers to NRB i.e. excludes the ear) for cv. Tyne in the Low N 1989 and 1990, and High N 1990 are shown in Figures 5.2.3F13, 5.2.3F14 and 5.2.3F15 respectively. The canopy growth rate (ΔW_{canopy}) is indicated as a vertical hatching to distinguish it from plant growth rate (ΔW_{plant}), since the two often have the same value. They only differ when nitrogen limits canopy growth. In this case the carbon assimilated is assumed to go elsewhere in the plant – in this case the ear. The simulations start at the first harvest, 37 and 43 days after sowing (DAS), and continue through to final harvest, 126 and 137 DAS in 1989 and 1990 respectively.

In both years the nitrogen content of the photosynthetic pool in the Low N treatments is always below optimal and the storage pool empty (Figure 5.2.3F13 and 5.2.3F14). Canopy growth rate mirrors the nitrogen content of the photosynthetic pools, which peaks and then declines to near zero by final harvest. By final harvest the bulk of the nitrogen remaining in the canopy is associated with the structure of the canopy. In

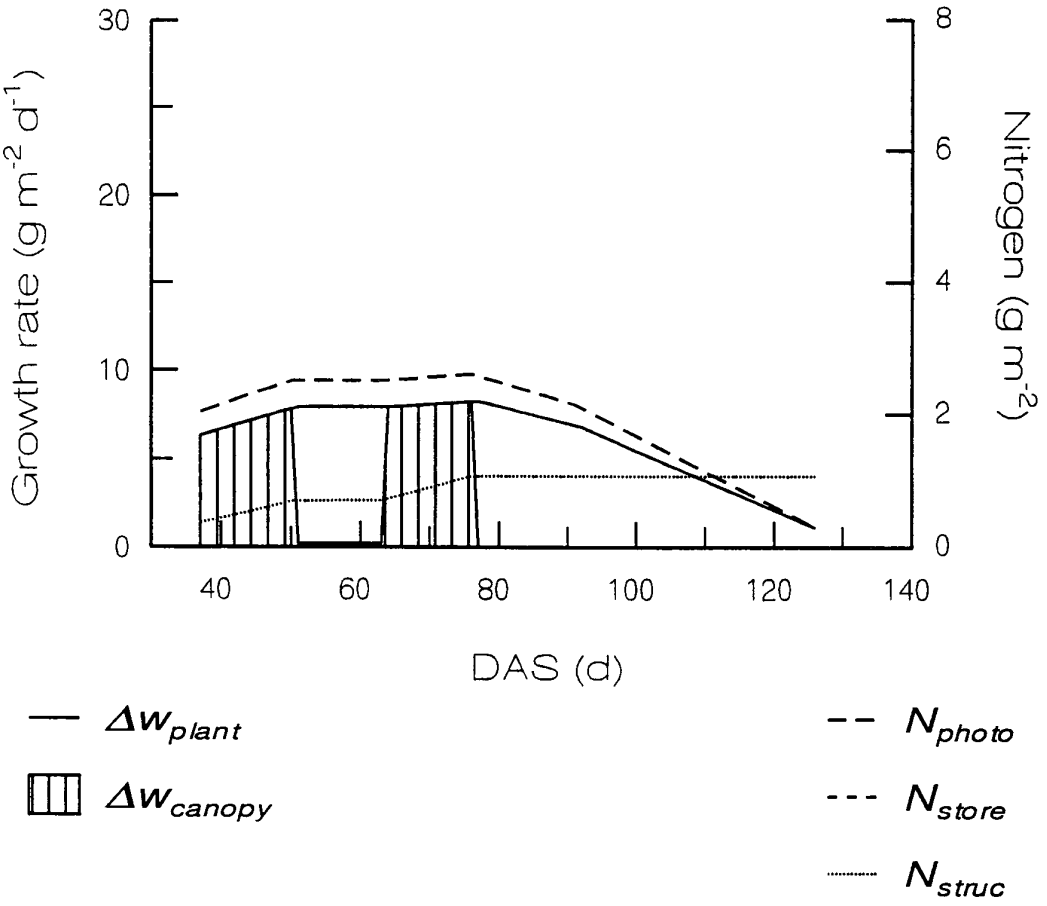


Figure 5.2.3F13 Canopy growth model: simulation run using the observed nitrogen content of the non-reproductive biomass in cv. Tyne with Low N in 1989. The change with time (days after sowing, DAS) of the growth rate of the plant (Δw_{plant}) and the and the canopy ($\Delta w_{canopy} <= \Delta w_{plant}$), and the nitrogen contents of the photosynhtetic (N_{photo}), storage (N_{store}) and structural (N_{struc}) pools are shown.

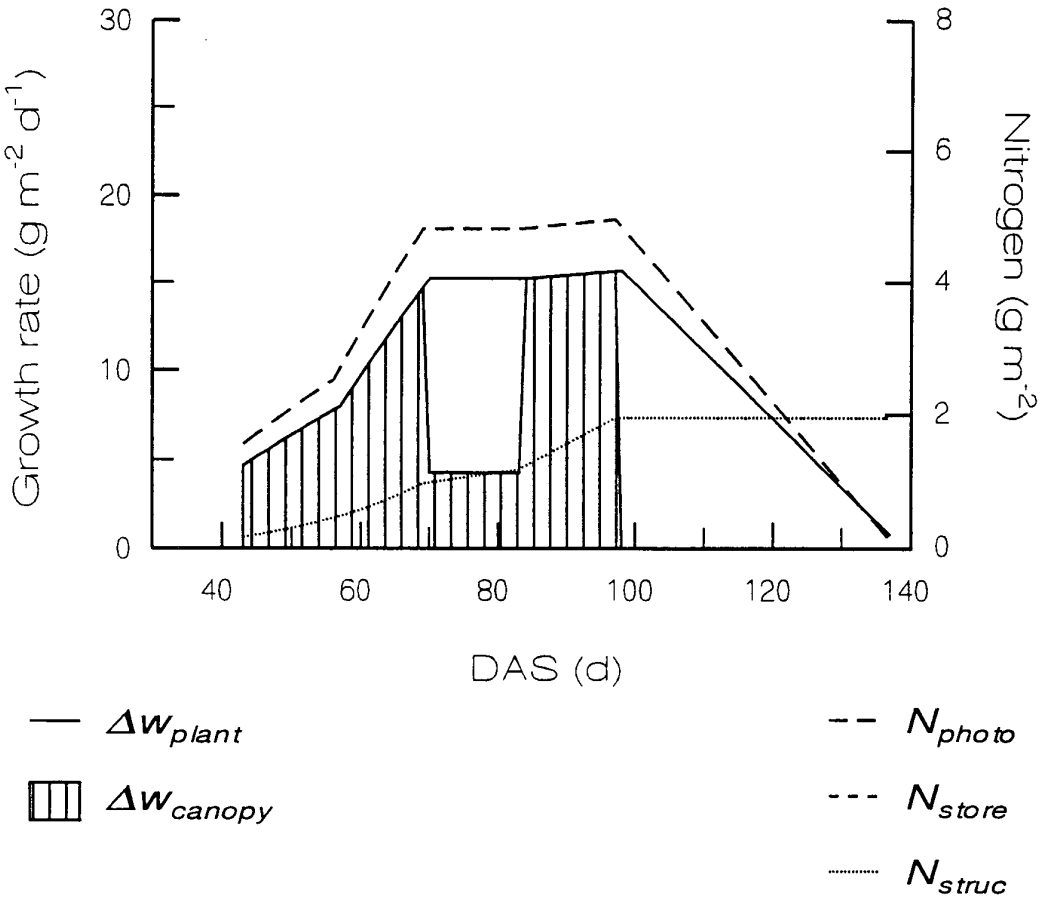


Figure 5.2.3F14 Canopy growth model: simulation run using the observed nitrogen content of the non-reproductive biomass in cv. Tyne with Low N in 1990. The change with time (days after sowing, DAS) of the growth rate of the plant (Δw_{plant}) and the canopy ($\Delta w_{canopy} <= \Delta w_{plant}$), and the nitrogen contents of the photosynthetic (N_{photo}), storage (N_{store}) and structural (N_{struc}) pools are shown.

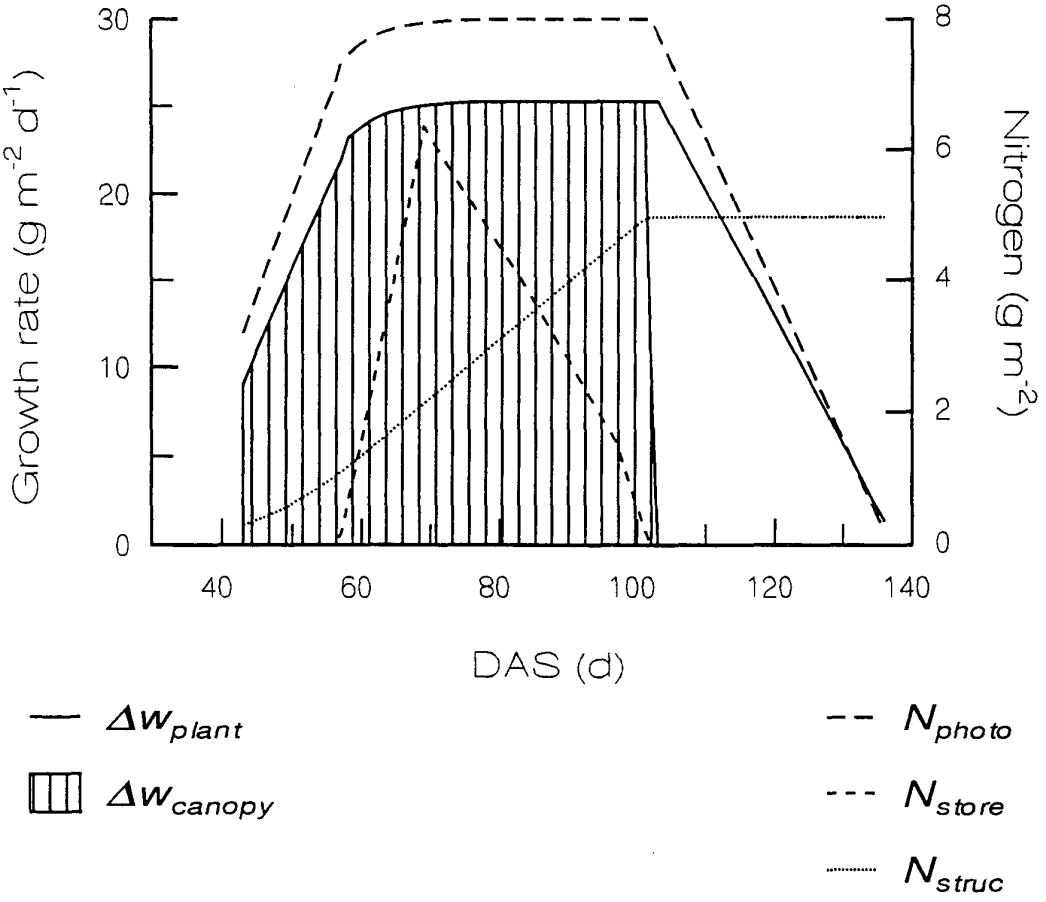


Figure 5.2.3F15 Canopy growth model: simulation run using the observed nitrogen content of the non-reproductive biomass in cv. Tyne with High N in 1990. The change change with time (days after sowing, DAS) of the growth rate of the plant (Δw_{plant}) and the canopy ($\Delta w_{canopy} <= \Delta w_{plant}$), and the nitrogen contents of the photosynthetic (N_{photo}), storage (N_{store}) and structural (N_{struc}) pools are shown.

1989, around 51 DAS, there is insufficient nitrogen to meet the structural requirements for canopy growth (Figure 5.2.3F13); ΔW_{canopy} drops to zero and the excess carbohydrate is assumed to either be exported from the canopy to the ear or remain as sucrose. A little later, around 63 DAS, the nitrogen uptake has increased sufficiently for canopy growth to briefly resume before stopping permanently. The same picture evolves in 1990 (Figure 5.2.3F14). The main contrast is that more nitrogen was taken up initially. There is still a reduction in canopy growth, but this occurs later and does not fall to zero. The final cessation of canopy growth is also later. These patterns and contrasts in timings between years are visible in the observed changes in NRB shown in an earlier section (Figure 4.2.3F1).

In High N treatments in 1990, the nitrogen content of the canopy was initially below optimal and this feature also shows up in the simulation (Figure 5.2.3F15). The storage pool at the start of the simulation period is empty. It is not until around 58 DAS that excess nitrogen starts to accumulate in the storage pool. Again plant growth rate mirrors the nitrogen content of the photosynthetic pool. This is a feature of the model since excess nitrogen is not allowed to accumulate in this pool. The storage pool reaches a peak around 65 DAS and then falls as total nitrogen in the canopy starts to decline (70 DAS). The shift out of the storage pool maintains canopy growth and an optimal nitrogen in the photosynthetic pool, but is emptied around 103 DAS. At this point, canopy growth stops and nitrogen starts to be withdrawn from the photosynthetic pool. By the final harvest, this pool is also close to empty. The corresponding treatment in 1989 (not shown) showed similar features. The main difference being the presence of nitrogen in the storage pool at the start of the simulations.

Limitations and future development

The model is consistent with the observations of Ingestadt (1982), Monteith (1978), Greenwood (1982), Greenwood *et al.* (1985 a, b) and Marshall & Porter (1991); is based only on local mechanisms (no global "brain") and explains most of the variation in the observed data of the PTX experiments. Redistribution of resources is not an intermittent

process, switched on when a particular organ is deficient in a resource, it takes place continuously irrespective of relative deficiencies. The associated energy cost is the cost of "communication" within and between cells and between organs. The benefit is the ability of the plant to achieve self-organisation in a variable environment. In addition, unlike the earlier models, it is able to predict the consequences of a less than optimal supply of nitrogen. In further simulations (not shown in this report) nitrogen productivity of a crop (dry weight produced unit of nitrogen taken up) is shown to be dependent on the history of nitrogen uptake. A constant proportional limitation in nitrogen uptake (e.g. 70% of optimal requirement) throughout the season has no effect on nitrogen productivity, whereas an increasing proportional limitation results in increased nitrogen productivity.

Despite the assumption that all other environmental factors (solar radiation and temperature) were assumed constant and the crude approximations to nitrogen uptakes used in each treatment, the model predictions were close to that observed. This suggests that the effects of variation in solar radiation and temperature were largely reflected in the observed nitrogen uptake. Thus nitrogen uptake is a useful driving variable. It would be relatively straight forward to include solar radiation and temperature as modifying factors in the model. Duller radiation levels and cool temperatures would reduce the potential growth rates and hence the optimal requirements for nitrogen. Similarly the primary effects of water restriction would be to reduce growth rate and hence nitrogen requirement. The preferential restriction on leaf expansion due to adverse plant water relations may have to be included, particularly during rapid canopy expansion.

In its present form the model has three nitrogen pools: photosynthetic, structural and storage pools (Figure 5.2.3F7). The term "storage" in this context simply means not yet allocated to either photosynthetic and structural components. The distinction between the photosynthetic and storage pools occurred because the photosynthetic-light response was assumed to be two straight lines. Thus any nitrogen that raised the maximum rate of photosynthesis above that which was possible with the available light was assumed

to be luxury and resided in the storage pool. In practice there is always some degree of curvature between the light limited and light saturated regions of the response. Thus the distinction between the two pools is blurred. In either case the behaviour is the same, and the approximation valid. There is no constraint on the size of the storage pool (luxury uptake) in the present model. In plant tissues osmotic considerations will provide a constraint. Observed luxury uptakes are typically limited to around 10% over optimal nitrogen contents.

To integrate this canopy growth model into a whole plant model requires an understanding of the mechanisms determining the distribution of carbon and nitrogen resources around the plant. As stated earlier, Cheeseman (1993) offers a new conceptual way forward in this area, especially for distributing resources between shoot and root. The deliberately simplistic model of shoot growth used by Cheeseman would be replaced by the model presented here which is more appropriate for the field. The outstanding difficulty is our lack of understanding of factors determining root distribution and activity. Cheeseman assumes that a doubling of root length results in a doubling of the uptake rate. This is not the case in reality.

5.2.4 Soil nitrogen, root growth and activity

As noted earlier, nitrogen had little or no effect on the partitioning of resources between tissue types in the shoot. The effect on root growth was not studied although potentially this is the largest effect of nitrogen on partitioning. The proportion of carbon in a plant which resides in the roots can increase when the plant is deficient in nitrogen. This is interpreted as a compensatory strategy that has developed in some species, through natural selection. When a plant experiences a deficiency its growth rate is reduced and it is possible by changes in root:shoot ratio to recover some of this loss in growth rate (Robinson, 1991). The local mechanisms proposed by Cheeseman (1993) produce just this effect. In the PTX experiments such changes in partitioning were unlikely to influence the quantity of nitrogen taken up, since by design uptake in the nitrogen limited plants was determined by supply rather than root length and activity.

Equally important if not more so than weight of the root system is the rate at and extent to which roots explore the soil volume. This is poorly understood and likely to remain so for some time yet. Despite many attempts to relate root development to internal factors they have not yet been successful (Robinson *et al.*, 1994). To date therefore models have generally attempted to predict the time course of maximum rooting depth, and either assumed all soil in a layer once penetrated is fully accessible or assumed an exponential distribution of root length down the profile. The distribution of roots in the soil is affected by localised compaction (Garcia *et al.*, 1988) and the feedback between water extraction by roots and increase in soil impedance can reduced root growth to as much as one half (Sharpe & Davies, 1985; Bengough, *pers. comm.*).

Modellers, with no information available to the contrary or otherwise, assume that all parts of the root system are equally active or at least have the capacity to be so. Based on this assumption critical soil N concentrations have been calculated, above which uptake should not be limited by soil supply (Barraclough, 1986, 1989). However, Robinson *et al.* (1994) have shown this not to be the case. At soil solution concentrations of N higher than the critical level plant growth was shown to be still limited by N uptake. There are several possible reasons (physical and biological) which are being investigated.

In addition to the uncertainties about the root system and its activity there exist similar, equally important uncertainties about the soil supply of nitrogen. Much if not all the nitrogen that is applied as fertiliser passes through microorganisms before it is finally taken up by the root or lost through leaching and gaseous emission, or carried over in organic form into the following seasons. The speed with which it is cycled through, size and quality of these microbial communities will influence the rate and timing at which nitrogen becomes available to the plant. To date, attempts to provide a quantitative understanding of these processes in real soils has not been successful. Only, relatively recently has the significance of soil structure and its inherent heterogeneity or variability been fully appreciated. It first became evident in the failure of mass flow models, developed at laboratory scale levels, to translate to predicting water flow in the

field. To circumvent this discrepancy the dual scales of by-pass flow models were developed. In reality there exists a continuum of structural scales. For the first time quantitative measures based on fractal geometries are being developed which predict the behaviour of soil properties from direct measurement of structure e.g. gas diffusion and water flow, movement of microorganisms and refuge sites. This work is crucial for the advancement of our understanding and informed management of soils. In the meantime a measure of the time course of nitrogen uptake would provide a quantitative insight into the effectiveness of management strategies and the interpretation of field experiments.

5.3 Grain Quality

5.3.1. Nitrogen requirements in relation to growth

The interaction of nitrogen/ irradiance/ temperature/ water is dynamic and the *history* of this interaction is critical. Thus final observation alone is insufficient to determine why a particular nitrogen concentration and yield has been achieved.

Our proposition is that the temperature principally determines how quickly the canopy develops and expands. In turn this sets the time window in which the spikelets and grain must be produced. The latest version of the AFRC wheat model no longer incorporates the effect of the rate of change of daylength. Previous estimates of the temperature of the meristem were incorrect and it is now no longer necessary to include changes in daylength to explain differences in the rate of differentiation from spring and autumn sowings (Porter personal communication).

After the effect of temperature, radiation and/or water set the maximum growth rate. This, through photosynthetic requirements for nitrogen, determines the optimum nitrogen content for the canopy at any point in time. Greenwood's curve is generalised and is no longer a 2-dimensional plot but has extra dimensions for temperature/radiation and water i.e. it becomes a surface with nitrogen concentration on the vertical axis, below which nitrogen is limiting. The average UK yields for barley are considerably below potential growth defined by temperature and radiation because of water limitations.

Therefore Greenwood's curve is an inappropriate optimum. We need to consider a lower optimum. Because water supply is variable from year to year both in quantity and pattern then many runs need to be done in order to ascertain the optimum strategy.

5.3.2 Grain size and crop quality

Before malting grain is cleaned, i.e. dust, chaff and broken grain is removed, and screened over a 2.2 mm or 2.5 mm sieve. The relationship between grain weight and screening losses depends on grain shape, particularly breadth. For a given cultivar it can usually be assumed that heavier grain will give samples with smaller screening losses. In PTX 1990 grain weight thresholds of 30 mg to 45 mg would result the following number of grains per ear contributing to harvest yield:-

Cultivar	Nitrogen Level	Stem	Grain weight threshold 30 mg	40 mg	45mg
Prisma	High	MS	24 (100%)	24 (100%)	23 (96%)
		T3	16 (100%)	16 (100%)	15 (94%)
	Low	MS	22 (100%)	22 (100%)	21 (95%)
		T3	9 (100%)	9 (100%)	7 (78%)
Tyne	High	MS	23 (100%)	22 (96%)	20 (87%)
		T3	18 (100%)	12 (67%)	6 (33%)
	Low	MS	23 (100%)	22 (96%)	19 (96%)
		T3	14 (100%)	7 (50%)	6 (43%)

Grain weight thresholds that are appropriate for field performance do not apply to the PTX because of the almost complete lack of moisture stress. These figures clearly illustrate the difference in performance between cvs Tyne and Prisma. The potential screening losses, which range from 4–77% per ear, are most severe because of the small grain size on tiller 3 of cv. Tyne. Screening losses can be high in erectoid cultivars (Thomas *et al.*, 1990) or where grain filling is disrupted by disease epidemics (Jenkyn,

1984; Jenkyn & Anilkumar, 1990; Carver & Griffiths, 1981). However, the potentially high screening losses for the maltster are, in practice, borne by the farmer as combining losses. Thus small grain, which a maltings would sell as animal feedstuff, is spread over the field and complicates the farming system by persisting in following crops. If ploughing, an energy demanding process, is not practised and stubble burning not permitted, as in England and Wales, the use of a close rotation would necessitate the use of herbicides pre- and post-sowing. It is not certain that herbicides will be available to all farmers in the future for *ad lib* usage, particularly in areas with problematic drainage systems.

It might be that plant breeding programmes could obviate the problem of high grain losses by selection for uniform grain size. However, similar comments would apply to breeding and farming systems. Losses from combines are common to both systems as breeders would usually evaluate grain quality in combine harvested samples after screening over a 2.2 mm or 2.5 mm sieve. Selection for high yield would be less effective than selection for parallel ear types, particularly in winter barley. An alternative strategy would be to practise selection for uniform grain size in hand harvested plots, which is a labour intensive and costly exercise.

The maximum weight of a grain is affected by the choice of cultivar and by the husbandry employed during crop growth (Table 4.2.6T1). Nitrogen application and stem position both show highly significant effects; the latter indicating the importance of plant spacing. Similar effects, reflecting the size of an ear, are seen for grain number per ear (Table 4.2.6T2). In contrast, grain nitrogen by ear position did not show differing and variable effects (Table 4.2.6T5). In particular the analysis of variance showed no genetic effect. This does not mean that there is no effect of cultivar, simply that the experimental design and analysis did not partition the within plant component separately from environmental effects (Giles, 1990). The significant items for stem by grain position and nitrogen by cultivar and stem interactions support this hypothesis. The rate of germination (Table 4.2.6F6/7) showed even fewer effects with only grain position achieving significance.

It is not clear why grain position on the ear should affect germination rate in the absence of dormancy. Post-harvest dormancy may be attributable to changes in growth hormone levels or "after ripening". Other effects on germination rate can be presumed to reflect the consequences of ear development. The primordia at the base of the ear are formed first and the cells grow and differentiate into spikelet under the conditions of least nutrient stress. When the maximum number of spikelet primordia have formed, just before anthesis at the time stem extension starts, the apical dome dies. It is not clear exactly what causes the apex to die but it has been attributed to nutrient stress. The upper most spikelet primordia, which form the grain at the tip of the ear, are formed and differentiate at the period of greatest stress within the stem apex. In addition to the greater or lesser levels of nutrient stress primordia at the base of the ear differentiate over a longer period. It is possible that there is a gradient of these processes which affect embryo function differentially depending on ear position.

A striking comparison can be made between the results of the PTX and field experiments in the pattern of variation in nitrogen levels in main-stem and tillers. The lower order tillers of field grown, adapted cultivars had higher grain nitrogen content than the main-stem. This pattern is seen in all the PTX results except those for Prisma in 1990 i.e. all these situations represent the reactions of adapted cultivars. This with visual inspection of plant growth in the PTX confirm the relevance of this protected environment experiment to field conditions.

The effect of grain position on nitrogen and germination rate conflict with the requirements of good quality. The best combination is rapid germination with low nitrogen and this is to be found in grain from the base of the ear. Selection for quality should emphasise grain size because the effect of stress is to decrease grain size and so increase grain nitrogen content.

6.0 CONCLUSIONS

The results of this project can be summarised under the following headings:-

General

- in this project, and in others which aimed to simulate yield, simulation modelling failed to further understanding of complex crop processes
- in contrast the model described in this report provides insight into nitrogen metabolism and consequent effects on yield
- the single, locally applied rule "the nitrogen concentration of the photosynthetic system is proportional to the light intensity incident on the tissue" is able to explain both optimal and nitrogen limited productivity of the crop
- N content of NRB determines RGR rather than total plant nitrogen
- N distribution within the NRB, as predicted by the model, is consistent with other observations and predicts crop growth rates accurately
- for a given environment there exists a unique relationship between growth and %N when growth rate is optimal
- the optimal growth rate is determined primarily by the available soil water, radiation and, for winter cereals, temperature
- timing of N supply is critical if optimal growth is to be achieved
- the levels of early nitrogen are important to establish a photosynthetically active canopy and a high proportion of the nitrogen in the ear is taken up in the first few weeks of plant growth
- the history of nitrogen limitation determines the nitrogen productivity (biomass produced/unit nitrogen uptake)

- N productivity increases with N limitation which increases throughout the growing season
- sources of variability are manifest in the tillers rather than main-stems
- variation in partitioning of dry weight between tissue types over the whole plant (leaf, stem and ear) are small in relation to effects on the ratio of tiller versus main-stem material
- the partitioning of N to the ear are still to be addressed conceptually and limits on luxury N uptake identified
- ear differentiation sets up differences in embryo competence but the mechanism is not known.

Considerations for the farmer

- the N uptake target is linked to environment and largely influenced by factors that cannot be economically controlled
- nitrogen concentration by itself is not a good indicator of the growth of the plant. Its location and absolute quantities need to be known
- management can add to or decrease variability inherent in cereal crops (the target crop structure including tiller hierarchy and grain size still needs to be understood)
- the use of appropriate inputs is complicated by seasonal differences, similarly these are also the biggest problems for breeders and agronomists
- the greatest risk of moving to low input farming systems is that disease epidemics could become a significant factor and lower yield and quality
- economic cereal production which uses appropriate inputs will also tend to be favourable to the general environment
- soil type can often be limiting because of the interactions between water and nitrogen on the timing of field operations

- performance of spring crops depends on winter rainfall and this gives some potential for forward yield prediction
- autumn sown crops have their yield potential determined by early development and a model for optimum levels of spring top-dressing is possible
- given the best conceptual models it must be recognised that there are limited opportunities for correcting the balance between nitrogen uptake and carbon fixation
- mathematical models deal with precise and certain values. In practice knowledge is imprecise, uncertain and sometimes in a form unsuitable for formal mathematical expression
- uncertainty derives from several sources: variability of observations about the fitted relations, future market prices and weather
- in reaching decisions a measure of uncertainty or risk is important
- recent developments in Artificial Intelligence provide the possibility of incorporating these different qualities of knowledge with associated uncertainties in decision support systems using a combination of rule-based and causal modelling. These approaches are being developed at the Scottish Crop Research Institute.

Considerations for maltster

- the specification of barley cultivar, nitrogen and grain moisture will still remain the basic trading tools
- it is well known in the trade that the performance of established cultivars can be optimised by appropriate handling (storage temperature, grain cleaning and sieving etc.)
- germination rate and grain size are related within a cultivar
- germination rate changes systematically with grain position on the ear
- the change in germination rate with ear position is similar to that with grain size
- the degree of change in germination rate with ear position depends on cultivar

- grain size is determined by rate of crop growth which in turn depends on cultivar, nitrogen application and seed spacing.

Considerations for the breeder

- performance of contrasting cultivars was similar in the PTX with the main difference being in the number of tillers, leaf partitioning and spread of germination rates
- cv. Tyne contrasted in several respects to cv. Prisma and was less responsive to environmental effects
- high environmental response may be associated with high yield potential but also higher grain nitrogen and poorer quality
- the manipulation of internal nutrient pools offers a further yield component to be manipulated by the breeder but current physiological knowledge is lacking
- no attempt has been made to observe responses to temperature in crop growth rate
- an obvious way forward is to use random inbred lines which have been characterized for yield
- our small solution experiment shows a major difference between cultivars in the amount of nitrogen in the ear, this indicates a possible difference in storage protein deposition which requires further examination
- the PTX system offers a viable method to examine cultivar characteristics in the absence of water stress
- nutrient culture is a simple system which allows the identification of genotypes with the ability to produce grain with low N content and its findings are relevant to mechanisms operating in the field.

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A1 MODEL OF NITROGEN AND RADIATION LIMITED CANOPY GROWTH

A1.1 Model description

This model describes the influence of nitrogen in the non-reproductive biomass (NRB) on the rate of crop growth. It assumes that

- there are three nitrogen pools (see below); nitrogen associated with photosynthesis, nitrogen associated with structure and a mobile pool which can act as a temporary store for nitrogen not immediately required for either building new supporting structures or building photosynthetic apparatus.
- all contributions to increase in plant dry weight (roots are excluded) come from leaf and stem tissue alone,
- the concentration of nitrogen in a leaf which is directly associated with photosynthetic apparatus is proportional to the irradiance incident upon it,

Time step – The model uses a daily (24 h) time step.

Nitrogen pools – The size of each nitrogen pool is expressed as weight of nitrogen per unit area of ground. The three nitrogen pools are

N_{photo}, photosynthetic nitrogen pool (g(N) m^{-2})

N_{store}, temporary storage pool (g(N) m^{-2})

N_{struc}, structural nitrogen (g(N) m^{-2})

The nitrogen concentration of these pools is expressed per unit dry weight of the NRB (g(N) $g(DW)^{-1}$) and they are $N_{c,photo}$, $N_{c,store}$, and $N_{c,struc}$ respectively.

Individual leaf photosynthesis – The relation between the rate of gross photosynthesis and irradiance incident on a leaf is best described by a non–rectangular hyperbola which is defined by three parameters, α, P_{max} and θ (Marshall & Biscoe, 1980a, see Figure A.1F1). The parameter θ defines the degree of curvature as the photosynthetic system changes from light limited to light saturated conditions. Its value is in the range 0 (a rectangular hyperbola) to 1 (two straight lines). In field grown cereals the value is close to unity e.g. Marshall & Biscoe (1980b) found that the value was typically around 0.95 and independent of leaf age. In this model the ***two straight line*** response is used and is defined as

$$\begin{aligned} P(L) &= \alpha\, I(L) && \alpha\, I(L) \le P_{max}(L) \\ &= P_{max}(L) && > P_{max}(L) \end{aligned} \qquad [1]$$

where P(L), $P_{max}(L)$ and I(L) are the actual and maximum gross photosynthetic rates of and mean irradiance incident on leaf tissue below cumulative leaf area index, L, respectively.

Similar effects of nitrogen on leaf photosynthesis have been found in both mono– and di–cotyledons. Hirose & Werger (1987) examined the influence of leaf nitrogen concentration on α, P_{max} and θ in a perennial herb *Solidago altissima* L (Compositae). They found the strongest correlation ($r^2 = 0.83$) was with P_{max}. Although there were significant correlations with the other two parameters, they were much weaker ($r^2 = 0.36$ and 0.22 for α and θ respectively). The weak correlation of θ was in fact negative. Field & Mooney (1983) found little effect of leaf age or P_{max} on the value of α, which was in agreement with Marshall & Biscoe (1980b). Since differences in P_{max} and leaf age are associated with differences in leaf nitrogen concentration in the experiments by Marshall & Biscoe (1980b), they are contrary to the findings of Hirose & Werger (1987). There is a lack of sensitivity in the estimation of both α and θ when the nitrogen concentration in the leaf and P_{max} decline to low values. This can lead to spurious correlations. All observations show a strong link between P_{max} and nitrogen concentration. Marshall & Vos (1991) found a similar strong correlation in potato. In

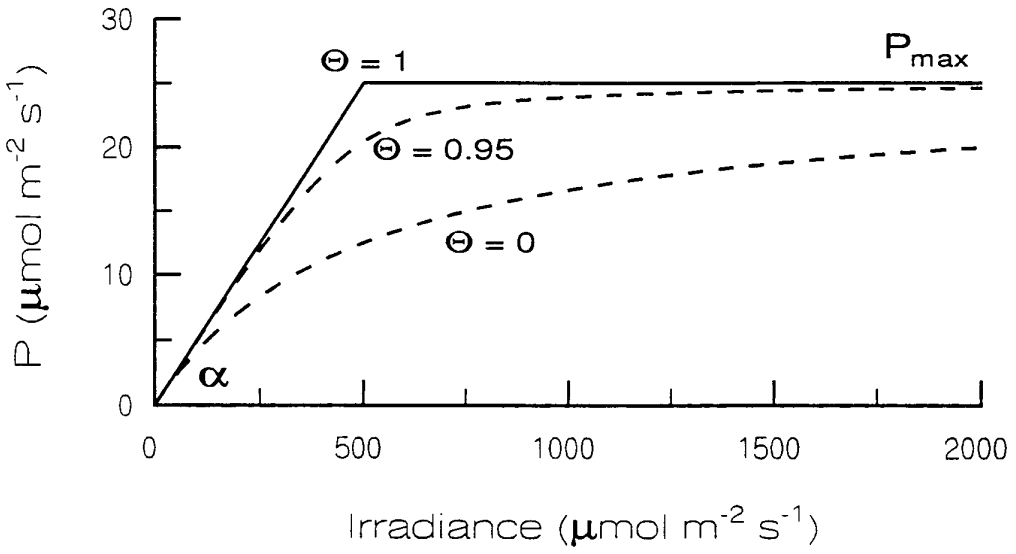

Figure A.1F1 Canopy growth model: the leaf photosynthesis (P) - light response The dashed lines are non-rectangular hyperpobolae ($\Theta P^2-(\alpha I P_{max})P+\alpha I P_{max}=0$) with $\Theta = 0$, rectangular hyperbola, and $\Theta = 0.95$, typical value for cereals. When Θ is close to unity the relation (solid line) approximates to two straight lines.

a range of nitrogen treatments the slope of the regression was found to be constant but the intercept systematically declined with reducing nitrogen uptake, when a fixed leaf position in the canopy was observed over time.

The relation between P_{max} and nitrogen concentration used in this model is shown in Fig. A1.F2 and is defined as,

$$\begin{aligned} P_{max}(L) &= \beta\, N_{c,photo}(L) && N_{c,photo}(L) \le N_{c,max} \\ &= \beta\, N_{c,max} && > N_{c,max} \end{aligned} \qquad [2]$$

where $N_{c,max}$ is the maximum nitrogen concentration of the photosynthetic pool allowable in any part of the canopy.

Canopy radiation – The attenuation of radiation down the canopy is assumed to be exponential (Szeicz, 1974). The irradiance on a *horizontal* surface below leaf area index, L,

$$I_h(L) = I_h(0)\, e^{-k\,L} \qquad [3]$$

where $I_h(0)$ is the irradiance incident on top of the canopy and k is the light extinction coefficient.

However, the leaves in a canopy are not orientated horizontally. The mean irradiance incident on a leaf is equal to the amount of light it intercepts divided by its leaf area i.e.

$$I(L) = -dI_h/dL = k\, I_h(0)\, e^{-k\,L} \qquad [4]$$

Maximising canopy photosynthesis – The model assumes that the concentration of nitrogen in a tissue that is associated with the photosynthetic system is proportional to irradiance falling upon it. This is precisely the condition that maximises photosythesis. Marshall & Porter (1991) showed that in order to maximise the rate of canopy

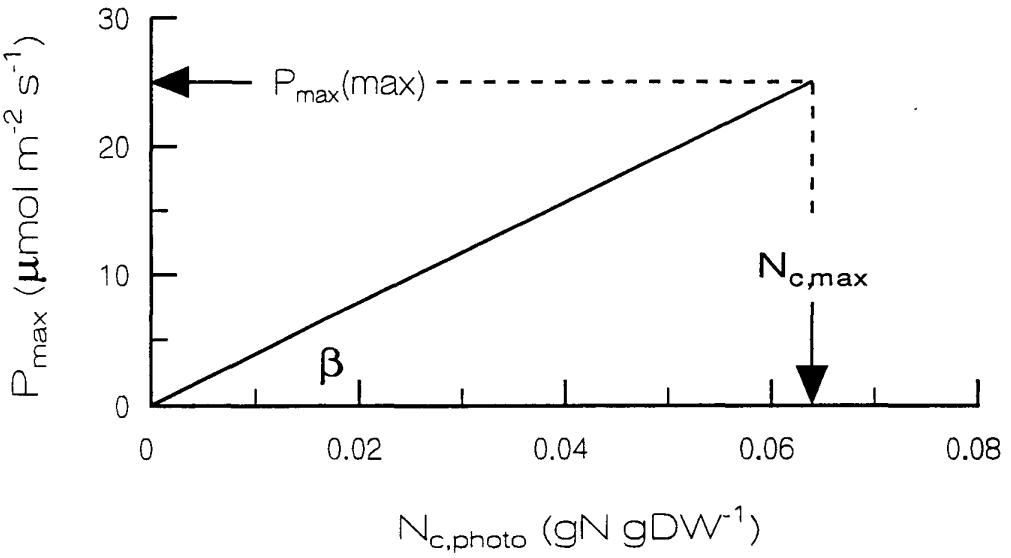

Figure A.1F2 Canopy growth model: the dependency of the light saturated rate of leaf photosynthesis (P_{max}) on the concentration of nitrogen in the photosynthetic pool ($N_{c,photo}$). The upper limit of P_{max} (P_{max}(max)) and $N_{c,photo}$ ($N_{c,max}$) is defined by the light environment at the top of the canopy.

photosynthesis, when nitrogen was a constraint, $P_{max}(L)$ had to mirror the profile of irradiance in the canopy,

$$P_{max}(L) = P_{max}(0)\ I(L)/I(0)$$

$$P_{max}(L) = P_{max}(0)\ e^{-k\,L} \qquad [5]$$

where $P_{max}(0)$ is the light–saturated rate of photosynthesis of the leaves at the top of the canopy. Since the maximum rate of photosynthesis is linearly related to the nitrogen concentration (equation 2) then nitrogen concentration must also mirror the profile of irradiance.

Critical nitrogen concentration – The critical nitrogen concentration, $N_{c,max}$, is defined as the concentration of nitrogen in the photosynthetic pool that is just sufficient to avoid light saturation at the top of the canopy. Under these conditions

$$P_{max}(0) = \alpha\ I(0)$$

and $P_{max}(0) = \beta\ N_{c,max}$

thus

$$N_{c,max} = (\alpha\ I(0)) / \beta \qquad [6]$$

Since the relation between P_{max} and nitrogen concentration is linear (equation 2) it follows that the profile of nitrogen concentration of the photosynthetic pool must also mirror that for irradiance. Hence

$$N_{c,photo}(L) = N_{c,max}\ e^{-k\,L} \qquad [7]$$

and the optimal nitrogen content of the canopy is then the integral of the nitrogen concentration over the whole canopy,

$$N_{opt} = \int_0^L (N_{c,photo}(L)/\phi)\ dL = N_{c,max}\ (1-e^{-k\,L})/(\phi k) \qquad [8]$$

Since nitrogen concentration is expressed per unit *weight* of canopy, it is necessary to convert it to unit *area* basis by dividing by ϕ, the specific leaf area (m^2 $g(DW)^{-1}$), before integrating it over the leaf area of the canopy.

Canopy photosynthesis – The instantaneous rate of canopy gross photosynthesis is the sum of contributions from all parts of the canopy and is defined as

$$P_c = \int_0^L P(L)\ dL = \int_0^L \alpha\ I(L)\ dL \qquad [9]$$

Substituting I(L) from equation 4 and integrating gives

$$P_c = \alpha\ I_h(0)\ (1 - e^{-k\,L}) \qquad [10]$$

By definition, the maximum rate of canopy photosynthesis, $P_{c,max}$, occurs when the nitrogen content is optimal. From equation 6 this is when

$$\alpha\ I(0) = \beta\ N_{c,max}$$

and $I(0) = k\ I_h(0)$ from equation 4, thus

$$P_{c,max} = (\beta\ N_{c,max}/k)\ (1 - e^{-k\,L}) \qquad [11]$$

When the nitrogen content of the photosynthetic pool in the canopy is less than N_{opt} then the nitrogen concentration profile down the canopy, $N_{c,photo}(L)$, and hence the corresponding photosynthetic capacities, $P_{max}(L)$, are reduced by the factor N_{photo} / N_{opt} i.e. photosynthesis is now nitrogen limited.

$$P_c = (N_{photo}\ /\ N_{opt})\ P_{c,max} \qquad [12]$$

Daily growth and leaf area – The light environment is assumed constant over the season with daylength, H h, and incident photon irradiance, $I_h(0)$ μmol m^{-2} s^{-1}. A fixed

proportion of the daily gross photosynthesis of the canopy is assumed to be respired, R_{coef}.

Thus the daily increment in crop dry weight (g(DW) m^{-2} d^{-1}),

$$\Delta W = P_c (1 - R_{coef}) H 3600 \Gamma \quad [13]$$

where P_c is in μmol m^{-2} s^{-1} and Γ is the conversion factor for μmol into g CH_2O (dry weight). This is then added to the previous canopy weight, W, and the corresponding new leaf area is

$$L = \phi W \quad [14]$$

Uptake and allocation of nitrogen – The daily uptake of nitrogen into the canopy (NRB), ΔN, is pre-defined. Each day can be set to a different value. It is important to note that it is only the nitrogen in the non-reproductive biomass that is being considered, not the whole of the nitrogen taken up by the crop. This model is not species specific. In the case of potato it refers to the whole of the shoot but excludes the nitrogen in the tubers and roots. In cereals it refers to leaf plus stem tissues but excludes the ear and roots. The daily values can either be read in from a table (input file) or calculated within the program according to a preset criterion e.g. to maintain a constant nitrogen concentration in the photosynthetic pool.

The daily procedure in the model is

First the increment in crop growth, ΔW, is calculated based on the nitrogen status pertaining at the end of the previous day.

Then the allocation of nitrogen is carried out. The daily uptake of nitrogen is initially placed in the storage pool. From this storage pool nitrogen is first withdrawn to meet the structural requirements of growth of the canopy,

$$= N_{c,struc} \Delta W$$

where $N_{c,struc}$ is the nitrogen concentration of structural material in the canopy, which is assumed constant.

Sufficient nitrogen is then withdrawn to achieve the new optimal nitrogen content of the photosynthetic pool (N_{opt}, equation 8). Note that as the canopy grows in weight so does its maximum rate of photsynthesis and hence its optimal nitrogen content.

Any nitrogen remaining is left in the storage pool for later use, if required. The only nitrogen that is no longer available for photosynthesis is that in the structural pool.

If there is insufficient material to achieve N_{opt} then all the nitrogen remaining in the storage pool (that required for structural growth having been removed first) is placed in the photosynthetic pool. In this circumstance canopy photosynthesis is now nitrogen rather than light limited.

If at the first withdrawal, there is insufficient nitrogen in the storage pool to meet the structural growth of the canopy then ΔW is reduced to that possible with the nitrogen left in the storage pool. Under this circumstance there can be no increase in the photosynthetic nitrogen pool. Again canopy photosynthesis is nitrogen limited and canopy growth is further restricted by nitrogen. When $\Delta N \leq 0$ and there is no nitrogen in the storage pool structural growth of the canopy stops. Although structural growth of the canopy may stop, its photosynthetic ability is not immediately lost. The declining nitrogen content of the canopy, as defined by continuing daily negative values of ΔN, will steadily deplete the nitrogen in the photosynthetic pool and hence reduce canopy photosynthesis. Only when this pool is empty does photosynthesis cease. The carbohydrate produced by canopy photosynthesis that is not used up in structural growth of the canopy i.e. when nitrogen becomes limiting, is exported. Thus it contributes to crop dry weight but not canopy dry weight. The model keeps separate accounts of the increases in canopy and crop dry weights.

A1.2 Analytical solution for optimal nitrogen

When nitrogen supply is just sufficient to achieve maximum growth rate then by definition the nitrogen content of the photosynthetic pool from equation 8 is

$$N_{photo} = N_{opt} = N_{c,max} (1-e^{-k L})/(\phi k),$$

and the storage pool is empty. Thus the total nitrogen of the canopy is the sum of the photosynthetic and structural pools,

$$N_{total} = N_{photo} + N_{struc}$$
$$= N_{c,max} (1-e^{-k L})/(\phi k) + N_{c,struc} W$$

where W is the total canopy weight. Substituting $L=\phi W$ and dividing through by W gives the average concentration in the canopy,

$$N_{c,total} = (N_{c,max}/(\phi k)) (1-e^{-k \phi W})/W + N_{c,struc} \quad [15]$$

This equation is identical in form to that found earlier by Marshall & Porter (1991). Their equivalent relation is

$$N_{c,total} = (\varepsilon S_0/\beta) (1-e^{-k \phi W})/W + N_{MIN} \quad [16]$$

Their model is based on the concept that the production of dry matter by a plant or crop is determined by the amount of light intercepted and the light conversion coefficient, ε (Monteith, 1977). More importantly that the value of ε is conservative within C_3 and C_4 species (Monteith, 1978). They used a value of 1.8 g(DW) MJ^{-1} *total solar radiation* for ε. They ran their model with a daily receipt of of total solar radiation, S_0, of 14 MJ m^{-2} d^{-1} (equivalent to 31.8 mol m_{-2} d_{-1} *photosynthetically active radiation*). The second concept they used was the observation by Ingestadt (1982) that the relative growth rate was a linear function of $N_{c,total}$, providing nitrogen was limiting growth. The slope of this relation, β, was 3.15 d^{-1}. Thus the value of the term ($\varepsilon S_0/\beta$) was 8 g(DW) m^{-2}. With this value and that for N_{MIN} of 0.0076 gN $g(DW)^{-1}$ they showed that their relation was consistent with that observed for optimal growth by Greenwood (1982) and Greenwood et al. (1985a,b).

Comparison of equations 15 and 16 shows that the term ($N_{c,max}/(\phi k)$) must equal 8 g(DW) m^{-2} for equivalence between them. Marshall and Porter used values of 0.016 m^2 $g(DW)^{-1}$ and 0.5 for ϕ and k respectively. Thus $N_{c,max}$ must equal 0.064 gN $g(DW)^{-1}$ for consistency between models, and hence with the observations of Greenwood and colleagues on 22 C_3 species.

The photsynthesis–light response of many species has been studied, on winter wheat Marshall & Biscoe (1980b) found values of around 10 $g(CO)_2$ MJ^{-1} (0.05 mol mol^{-1}) and approaching 4 $g(CO)_2$ m^{-2} h^{-1} (25 μmol m^{-2} s^{-1}) for α and P_{max} respectively. The critical irradiance, $I_h(0)$, is thus defined (equations 4 and 6, = $P_{max}/k\alpha$) as 1000 μmol m^{-2} s^{-1}, and to be consistent with the 14 MJ m^{-2} d^{-1} total solar radiation receipt used by Marshall & Porter (1991) constrains the daylentgh to 8.85 h.

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The parameter β is constrained by equation 6 (= $P_{max}/N_{c,max}$) to 391 μmol m^{-2} s^{-1}.

A summary of the parameters and the values used for the simulations are given in Table A.1T1. The only parameter value not defined at this stage is $N_{c,struc}$.

Table A.1T1. Parameters used in the nitrogen limited model of canopy growth

Process/Parameter	Symbol	Value Units
Photosynthesis–light response		
– initial slope	α	0.05 mol mol^{-1}
– light saturated rate	P_{max}	25 μmol m^{-2} s^{-1}
Photosynthesis–nitrogen response		
– slope	β	391 μmol m^{-2} s^{-1}
– max. conc. photosyn. pool	$N_{c,max}$	0.064 gN $g(DW)^{-1}$
Light attenuation		
– light extinction coef.	k	0.5
Crop growth**[1]		
– initial plant weight	W(1)	0.625 g
– specific leaf area	ϕ	0.016 m^2 g^{-1}
– conversion, μmol > gCH2O	Γ	0.00003 g μmol^{-1}
– respiration coefficient	R_{coef}	0.473
Nitrogen		
Environment**[2]		
– incident irradiance	$I_h(0)$	1000 μmol m^{-2} s^{-1}
– daylength	H	8.85 h

[1] Maximum rate of crop growth constrained to 25.2 g m^{-2} d^{-1}

[2] Radiative environment is constrained to 31.97 mol m^{-2} d^{-1} i.e. equivalent to a daily receipt of 14 MJ m^{-2} d^{-1}.

A2 TABLES

Table 4.1T1. Grain nitrogen concentration of sieving fractions from spring barley (VNT)

(a) Low N (top dressing 80 kg (N) ha^{-1})

	Nitrogen (%DM)			
Grain Fraction	<2.25	2.25–2.5	2.5–2.75	>2.75
Cultivar				
Doublet	1.70	1.71	1.76	1.71
Klaxon	1.81	1.76	1.81	1.77
Regatta	1.76	1.76	1.78	1.78
Natasha	1.85	1.84	1.87	1.91
Vista	1.72	1.76	1.77	1.79
Heriot	1.76	1.76	1.78	1.78
Tyne	1.76	1.78	1.76	1.70
SCRI240	1.77	1.77	1.82	1.78
Mean	1.76	1.77	1.79	1.78
se	0.05	0.04	0.05	0.05

(b) High N (top dressing 120 kg (N) ha^{-1})

	Nitrogen (%DM)			
Grain Fraction	<2.25	2.25–2.5	2.5–2.75	>2.75
Cultivar				
Doublet	1.76	1.76	1.85	1.81
Klaxon	1.86	1.87	1.90	1.86
Regatta	1.87	1.86	1.88	1.85
Natasha	1.89	1.92	1.93	1.92
Vista	1.79	1.82	1.82	1.81
Heriot	1.87	1.86	1.88	1.85
Tyne	1.90	1.89	1.86	1.83
SCRI240	1.91	1.85	1.89	1.88
Mean	1.86	1.85	1.88	1.85
se	0.05	0.04	0.05	0.05

Table 4.1T2. Effects of nitrogen treatment on spring barley cultivars in the VNT. Yield (kg ha^{-1}), grain nitrogen (% DM), TCW (g), HWE (°L/kg), yield% and % recovery of applied nitrogen.

(a) Analysis of variance (MS)

Source	df	Yield	Nitrogen	TCW	HWE
Genotype	7	11.3***	0.026***	61.60***	404***
Nitrogen	2	0.4*	0.065***	5.00***	180***
G x N	14	0.1NS	0.004NS	5.00NS	170NS

(b) Mean effect of nitrogen

Level	Yield	Nitrogen	TCW	HWE	Yield %	Recovery %
N1[f]	5.42	1.76	38.2	307.0	95.4	119
N2	5.54	1.78	37.8	305.0	98.6	99
N3	5.64	1.84	37.4	302.7	103.8	86
se	0.079	0.04	0.96	2.5		

[f]N1, N2 and N3 are 80, 100 and 120 kg (N) ha^{-1} respectively.
* = P<0.05, ** = P .01-0.001, *** = P<0.001).

Table 4.1T3. Nitrogen concentration of grain from the main-stem and tillers of plants from a trial sown at different seed rates

Cultivar	Nitrogen (%DM)	
	Main-stem	Tillers
Igri	1.85	1.79
Halcyon	1.57	1.65
Marinka	1.70	1.67
Plaisant	1.73	1.76
Mean	1.71	1.72
se	0.052	0.044

Table 4.2.1T1 Significance levels for the variation in total nitrogen uptake by individual harvest for 1989 and 1990.

Harvest		1	2	3	4	5	6
Source							
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	***	**	**	**	***	***
Cultivar	1989	NS	NS	NS	NS	NS	NS
Cultivar	1990	NS	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

Table 4.2.1T2 The mean over three replicates and – and + one standard error (s.e.) of the nitrogen in the plant (g(N) m^{-2}, excluding roots) at anthesis (harvest 4) and final harvest (harvest 6) in (a) 1989 and (b) 1990. The standard errors are asymmetrical because they have been detransformed from the logarithmic values upon which the analysis of variance was carried out.

(a)

	Harvest 4			Harvest 6		
	mean	– s.e	+ s.e.	mean	– s.e	+ s.e.
Low N						
Prisma	5.6	5.1	6.3	8.7	7.7	9.8
Tyne	5.2	4.6	5.7	6.9	6.1	7.8
High N						
Prisma	23.8	21.4	26.5	22.2	19.7	25.0
Tyne	19.1	17.1	21.2	23.7	21.0	26.7

(b)

	Harvest 4			Harvest 6		
	mean	– s.e	+ s.e.	mean	– s.e	+ s.e.
Low N						
Prisma	9.4	8.3	10.7	10.3	9.0	11.8
Tyne	8.3	7.3	9.4	9.7	8.5	11.1
High N						
Prisma	20.3	17.9	23.0	31.1	27.2	35.6
Tyne	19.7	17.4	22.3	26.9	23.5	30.7

Table 4.2.1T3 Significance levels for the variation in total plant dry weight by individual harvest for 1989 and 1990.

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	**
Nitrogen	1990	***	**	**	**	***	***
Cultivar	1989	NS	NS	NS	*	NS	NS
Cultivar	1990	*	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

Table 4.2.1T4 The mean over three replicates and – and + one standard error (s.e.) of the plant dry weight (kg m^{-2}, excluding roots) at anthesis (harvest 4) and final harvest (harvest 6) in (a) 1989 and (b) 1990. The standard errors are asymmetrical because they have been detransformed from the logarithmic values upon which the analysis of variance was carried out.

(a)

	Harvest 4			Harvest 6		
	mean	– s.e	+ s.e.	mean	– s.e	+ s.e.
Low N						
Prisma	0.66	0.63	0.70 1.00	0.91	1.10	
Tyne	0.55	0.52	0.58 0.76	0.69	0.84	
High N						
Prisma	1.36	1.29	1.44 1.66	1.51	1.83	
Tyne	1.12	1.07	1.19 1.61	1.46	1.77	

(b)

	Harvest 4			Harvest 6		
	mean	– s.e	+ s.e.	mean	– s.e	+ s.e.
Low N						
Prisma	0.69	0.63	0.75 1.11	1.01	1.22	
Tyne	0.51	0.47	0.56 1.11	1.01	1.22	
High N						
Prisma	1.19	1.09	1.29 2.20	2.00	2.41	
Tyne	1.05	0.96	1.14 1.96	1.78	2.15	

Table 4.2.1T5 Significance levels for the variation in total plant nitrogen concentration by individual harvest for 1989 and 1990.

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	**
Nitrogen	1990	**	*	**	NS	**	*
Cultivar	1989	NS	NS	NS	NS	*	NS
Cultivar	1990	**	*	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

Table 4.2.1T6 Significance levels for the variation in (a) main-stem and (b) total leaf area by individual harvest for 1989 and 1990.

(a)

Source	Harvest	1	2	3	4	5
Nitrogen	1989	NS	*	**	**	***
Nitrogen	1990	**	*	**	**	**
Cultivar	1989	NS	NS	NS	NS	NS
Cultivar	1990	NS	NS	*	*	NS
Nit*Cult	1989	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS

(b)

Source	Harvest	1	2	3	4	5
Nitrogen	1989	*	*	***	**	**
Nitrogen	1990	*	***	**	***	***
Cultivar	1989	NS	NS	NS	NS	NS
Cultivar	1990	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS

Table 4.2.1T7 Significance levels for the variation in the proportion of dead leaf lamina in the plant by individual harvest for 1989 and 1990.

Source	Harvest	1	2	3	4	5
Nitrogen	1989	***	**	***	***	***
Nitrogen	1990	NS	NS	NS	NS	*
Cultivar	1989	*	NS	NS	NS	NS
Cultivar	1990	***	***	NS	NS	**
Nit*Cult	1989	NS	NS	*	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	**

Table 4.2.2T1 The number of stems per plant found by plant dissection.

Probability

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	NS	***
Nitrogen	1990	***	***	***	**	***	***
Cultivar	1989	**	NS	NS	NS	NS	NS
Cultivar	1990	NS	NS	**	NS	*	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

Means

	Harvest	1	2	3	4	5	6
Low Nitrogen							
Prisma	1989	2.2	2.5	2.1	2.7	3.2	3.6
Prisma	1990	1.4	1.6	1.5	2.4	2.8	3.0
Tyne	1989	2.9	2.4	2.3	2.3	3.1	2.4
Tyne	1990	1.4	1.8	2.3	3.9	4.6	4.2
High Nitrogen							
Prisma	1989	3.5	3.6	4.1	4.4	4.0	4.1
Prisma	1990	2.3	2.6	2.6	4.9	5.9	5.8
Tyne	1989	4.4	4.0	4.2	5.4	4.5	4.8
Tyne	1990	2.4	2.7	3.3	4.4	6.2	5.7

Table 4.2.2T2 Significance levels for the variation in leaf number on the main-stem and tillers obtained by plant dissection.

a) Main-stem leaf number

		Probability			
	Source	Harvest 2	Harvest 3	Harvest 4	Harvest 5
Nitrogen	1989	***	NS	NS	NS
Nitrogen	1990	NS	NS	NS	
Cultivar	1989	***	*	NS	NS
Cultivar	1990	NS	NS	NS	
Nit*Cult	1989	*	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	

b) Coleoptile Tiller leaf number

		Probability			
	Source	Harvest 2	Harvest 3	Harvest 4	Harvest 5
Nitrogen	1989	NS	*	*	***
Nitrogen	1990	*	NS	NS	
Cultivar	1989	**	NS	NS	NS
Cultivar	1990	NS	NS	***	
Nit*Cult	1989	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	*	

c) Tiller 1 leaf number

		Probability			
	Source	Harvest 2	Harvest 3	Harvest 4	Harvest 5
Nitrogen	1989	**	NS	*	***
Nitrogen	1990	*	NS	NS	
Cultivar	1989	NS	NS	NS	NS
Cultivar	1990	NS	NS	NS	
Nit*Cult	1989	**	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	

Table 4.2.2T2 Continued

d) Tiller 2 leaf number

		Probability			
	Source	Harvest 2	Harvest 3	Harvest 4	Harvest 5
Nitrogen	1989	**	**	**	**
Nitrogen	1990	**	NS	NS	
Cultivar	1989	NS	NS	NS	NS
Cultivar	1990	NS	NS	NS	
Nit*Cult	1989	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	

e) Tiller 3 leaf number

		Probability			
	Source	Harvest 2	Harvest 3	Harvest 4	Harvest 5
Nitrogen	1989	*	NS	*	NS
Nitrogen	1990				
Cultivar	1989	NS	NS	NS	NS
Cultivar	1990				
Nit*Cult	1989	NS	NS	NS	NS
Nit*Cult	1990				

Table 4.2.2T3 Significance levels and means of number of ears per plant determined by plant dissection at harvests 3–6.

(a) Analysis of variance

		Harvest			
	Source	3	4	5	6
Nitrogen	1989	***	***	***	***
Nitrogen	1990	NS	***	***	**
Cultivar	1989	NS	*	NS	NS
Cultivar	1990	NS	*	NS	*
Nit*Cult	1989	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS

(b) Means

		Harvest			
		3	4	5	6
Low Nitrogen					
Prisma	1989	0.3	0.7	1.2	1.7
Prisma	1990	0.0	0.7	1.8	2.8
Tyne	1989	0.9	1.3	2.0	1.8
Tyne	1990	0.1	1.6	2.9	4.2
High Nitrogen					
Prisma	1989	2.5	3.0	3.2	3.1
Prisma	1990	0.2	2.1	3.7	5.1
Tyne	1989	2.9	3.6	3.9	4.2
Tyne	1990	0.4	2.8	4.3	5.9

Table 4.2.3T1. Significance levels for the variation in cumulative dry weight of non-reproductive biomass (NRB, stem and leaf tissues) and ears separated into main and tiller stems and analyzed by individual harvest for 1989 and 1990.

a) NRB, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	*	*	NS	**	**
Nitrogen	1990	**	*	NS	*	NS	NS
Cultivar	1989	*	**	***	**	***	***
Cultivar	1990	*	*	*	***	***	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

b) NRB, Tillers

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	***	*	**	***	***	***
Cultivar	1989	NS	NS	NS	NS	NS	NS
Cultivar	1990	*	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ears, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	-	-	NS	NS	NS	NS
Nitrogen	1990	-	-	NS	NS	NS	NS
Cultivar	1989	-	-	NS	NS	*	*
Cultivar	1990	-	-	NS	NS	*	NS
Nit*Cult	1989	-	-	NS	NS	NS	NS
Nit*Cult	1990	-	-	NS	NS	NS	NS

d) Ears, Tiller

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	-	-	***	***	***	*
Nitrogen	1990	-	-	NS	***	***	***
Cultivar	1989	-	-	NS	NS	NS	NS
Cultivar	1990	-	-	NS	NS	NS	NS
Nit*Cult	1989	-	-	NS	NS	NS	NS
Nit*Cult	1990	-	-	NS	NS	NS	NS

Table 4.2.3T2. Significance levels for the variation in the proportion of total plant weight that is main-stem, analyzed by individual harvest for 1989 and 1990. The significance levels are identical whether the proportion refers to main-stem or tiller.

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	***	*	***	***	***	***
Cultivar	1989	***	NS	NS	*	***	NS
Cultivar	1990	NS	NS	NS	*	**	*
Nit*Cult	1989	***	NS	NS	NS	***	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

Table 4.2.3T3. Significance levels for the variation in the proportions of total plant weight that are stem, leaf and ear tissues, analyzed by individual harvest for 1989 and 1990.

a) Stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	NS	***	NS	NS	NS
Nitrogen	1990	NS	NS	NS	**	*	NS
Cultivar	1989	*	***	*	NS	***	NS
Cultivar	1990	**	NS	NS	***	**	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	***	NS	NS

b) Leaf

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	NS	**	*	***	*
Nitrogen	1990	NS	NS	NS	NS	NS	NS
Cultivar	1989	*	***	*	NS	NS	NS
Cultivar	1990	*	NS	NS	NS	NS	*
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ear

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	–	–	NS	*	*	NS
Nitrogen	1990	–	–	NS	NS	NS	NS
Cultivar	1989	–	–	NS	NS	***	NS
Cultivar	1990	–	–	NS	*	*	NS
Nit*Cult	1989	–	–	*	*	*	NS
Nit*Cult	1990	–	–	NS	NS	NS	NS

Table 4.2.3T4. Significance levels for the variation in the proportions of tissue that are stem, leaf and ear within the main-stem, analyzed by individual harvest for 1989 and 1990.

a) Stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	**	**	NS	NS	NS
Nitrogen	1990	NS	NS	NS	*	NS	NS
Cultivar	1989	*	**	NS	NS	**	NS
Cultivar	1990	**	**	NS	**	**	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NSNS	

b) Leaf

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	**	***	**	***	***
Nitrogen	1990	S	NS	NS	NS	*	NS
Cultivar	1989	*	**	NS	NS	NS	NS
Cultivar	1990	**	**	NS	NS	NS	*
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ear

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	**	**	NS	NS	NS
Nitrogen	1990	NS	NS	NS	*	NS	NS
Cultivar	1989	*	**	NS	NS	**	NS
Cultivar	1990	**	**	NS	**	**	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

Table 4.2.3T5. Significance levels for the variation in the proportions of tissue that are stem, leaf and ear within the tillers, analyzed by individual harvest for 1989 and 1990.

a) Stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	NS	NS	NS	*	NS
Nitrogen	1990	NS	NS	NS	**	***	NS
Cultivar	1989	NS	***	NS	NS	***	NS
Cultivar	1990	NS	NS	NS	**	**	NS
Nit*Cult	1989	NS	NS	NS	NS	*	NS
Nit*Cult	1990	NS	NS	NS	**	NS	NS

b) Leaf

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	NS	NS	NS	NS	NS
Nitrogen	1990	NS	NS	NS	NS	NS	NS
Cultivar	1989	NS	***	NS	NS	*	NS
Cultivar	1990	NS	NS	NS	*	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	*	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ear

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	–	–	NS	NS	NS	NS
Nitrogen	1990	–	–	NS	NS	NS	NS
Cultivar	1989	–	–	NS	NS	*	NS
Cultivar	1990	–	–	NS	**	*	NS
Nit*Cult	1989	–	–	*	*	***	NS
Nit*Cult	1990	–	–	NS	NS	NS	NS

Table 4.2.4T1. Significance levels for the variation in cumulative weight of nitrogen in the non-reproductive biomass (NRB, stem and leaf tissues) and ears separated into main and tiller stems and analyzed by individual harvest for 1989 and 1990.

a) NRB, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	*	*	NS	**	**
Nitrogen	1990	**	*	NS	*	NS	NS
Cultivar	1989	NS	**	***	**	***	***
Cultivar	1990	*	*	*	***	***	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

b) NRB, Tillers

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	***	*	**	***	***	***
Cultivar	1989	NS	NS	NS	NS	NS	NS
Cultivar	1990	*	NS	NS	NS	NS	NS
Nit*Cult	1989	*	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ears, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	-	-	NS	NS	NS	NS
Nitrogen	1990	-	-	NS	NS	NS	NS
Cultivar	1989	-	-	NS	NS	*	*
Cultivar	1990	-	-	NS	NS	*	NS
Nit*Cult	1989	-	-	NS	NS	NS	NS
Nit*Cult	1990	-	-	NS	NS	NS	NS

d) Ears, Tiller

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	-	-	***	***	***	*
Nitrogen	1990	-	-	NS	***	***	***
Cultivar	1989	-	-	NS	NS	NS	NS
Cultivar	1990	-	-	NS	NS	NS	NS
Nit*Cult	1989	-	-	NS	NS	NS	NS
Nit*Cult	1990	-	-	NS	NS	NS	NS

Table 4.2.4T2. The absolute and relative reductions by final harvest in the nitrogen content of the non-reproductive biomass (NRB) from the observed maximum contents in main-stem and tillers.

Reduction Average over	Maximum	Absolute	Relative
1989 & 1990	g(N) m^{-2}	g(N) m^{-2}	(%)
Main-stem (NRB)			
Low N - 1989	2.06	1.46	72
- 1990	3.31	2.58	78
High N - 1989	5.33	3.43	65
- 1990	5.94	4.66	78
Tillers (NRB)			
Low N - 1989	1.88	1.05	57
- 1990	4.00	2.88	72
High N - 1989	13.76	8.12	60
- 1990	11.87	7.98	67

Table 4.2.4T3. Significance levels for the variation in the proportion of total plant nitrogen that is main-stem, analyzed by individual harvest for 1989 and 1990. The significance levels are identical whether the proportion refers to main-stem or tiller.

	Harvest	1	2	3	4	5	6
Source							
Nitrogen	1989	***	***	***	***	***	**
Nitrogen	1990	***	**	**	**	***	NS
Cultivar	1989	***	NS	NS	NS	**	NS
Cultivar	1990	NS	NS	NS	NS	*	NS
Nit*Cult	1989	***	NS	NS	NS	*	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

Table 4.2.4T4. Significance levels for the variation in the proportions of total plant nitrogen that are stem, leaf and ear tissues, analyzed by individual harvest for 1989 and 1990.

a) Stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	**	NS	**	***	*
Nitrogen	1990	NS	NS	NS	NS	NS	NS
Cultivar	1989	NS	NS	**	NS	NS	NS
Cultivar	1990	**	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	*	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

b) Leaf

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	***	***	***	***	**
Nitrogen	1990	NS	NS	NS	NS	*	NS
Cultivar	1989	NS	**	***	*	NS	NS
Cultivar	1990	**	NS	NS	*	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ear

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	–	–	***	***	***	**
Nitrogen	1990	–	–	NS	NS	*	NS
Cultivar	1989	–	–	NS	NS	NS	NS
Cultivar	1990	–	–	NS	NS	NS	NS
Nit*Cult	1989	–	–	NS	NS	NS	NS
Nit*Cult	1990	–	–	NS	NS	NS	NS

Table 4.2.4T5. Significance levels for the variation in the proportions of nitrogen that reside in the stem, leaf and ear tissues within the main-stem, analyzed by individual harvest for 1989 and 1990.

a) Stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	***	NS	*	***	*
Nitrogen	1990	NS	NS	NS	NS	NS	NS
Cultivar	1989	NS	NS	*	NS	*	NS
Cultivar	1990	*	NS	NS	NS	NS	*
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

b) Leaf

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	*	***	***	***	***	***
Nitrogen	1990	NS	NS	NS	NS	**	NS
Cultivar	1989	NS	NS	***	NS	NS	NS
Cultivar	1990	*	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ear

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	-	-	***	***	***	**
Nitrogen	1990	-	-	NS	NS	*	NS
Cultivar	1989	-	-	NS	NS	**	NS
Cultivar	1990	-	-	NS	NS	NS	NS
Nit*Cult	1989	-	-	NS	NS	NS	NS
Nit*Cult	1990	-	-	NS	NS	NS	NS

Table 4.2.4T6. Significance levels for the variation in the proportions of nitrogen that reside in the stem, leaf and ear tissues within the tillers, analyzed by individual harvest for 1989 and 1990.

a) Stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	*	NS	NS	NS	NS
Nitrogen	1990	NS	NS	NS	NS	NS	NS
Cultivar	1989	NS	***	*	NS	***	NS
Cultivar	1990	NS	NS	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	***	NS
Nit*Cult	1990	NS	NS	NS	NS	**	NS

b) Leaf

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	NS	*	NS	***	**	NS
Nitrogen	1990	NS	NS	NS	NS	NS	NS
Cultivar	1989	NS	***	*	*	NS	NS
Cultivar	1990	NS	NS	NS	*	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ear

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	–	–	NS	*	**	NS
Nitrogen	1990	–	–	NS	NS	NS	NS
Cultivar	1989	–	–	NS	NS	**	NS
Cultivar	1990	–	–	NS	NS	NS	NS
Nit*Cult	1989	–	–	NS	NS	***	NS
Nit*Cult	1990	–	–	NS	NS	NS	NS

Table 4.2.5T1. Significance levels for the variation in nitrogen concentration in the three tissue types (leaf, stem and ear) separated into main and tiller stems and analyzed by individual harvest for 1989 and 1990.

a) Leaf, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	*	NS	**	*	**	***
Cultivar	1989	NS	NS	NS	NS	*	NS
Cultivar	1990	*	**	NS	NS	*	**
Nit*Cult	1989	NS	NS	*	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	**	NS

b) Stem, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	**
Nitrogen	1990	NS	*	**	NS	*	**
Cultivar	1989	NS	NS	NS	NS	***	NS
Cultivar	1990	*	NS	NS	NS	*	**
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

c) Ears, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	-	-	***	*	***	***
Nitrogen	1990	-	-	NS	NS	*	***
Cultivar	1989	-	-	**	NS	NS	NS
Cultivar	1990	-	-	*	*	NS	NS
Nit*Cult	1989	-	-	NS	NS	NS	NS
Nit*Cult	1990	-	-	NS	NS	NS	*

Table 4.2.5T1. (continued)

d) Leaf, Tillers

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	**	NS	***	NS	**	***
Cultivar	1989	NS	NS	NS	NS	NS	NS
Cultivar	1990	*	**	*	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	NS	NS

e) Stem, Tillers

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	*
Nitrogen	1990	NS	*	*	NS	*	**
Cultivar	1989	NS	NS	NS	NS	NS	NS
Cultivar	1990	**	NS	NS	NS	NS	*
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

f) Ears, Tiller

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	–	–	*	*	***	***
Nitrogen	1990	–	–	NS	NS	NS	*
Cultivar	1989	–	–	NS	NS	NS	NS
Cultivar	1990	–	–	NS	**	NS	NS
Nit*Cult	1989	–	–	NS	NS	NS	NS
Nit*Cult	1990	–	–	***	NS	NS	NS

Table 4.2.5T2. Observed differences in ear nitrogen concentrations between cultivars (cv. Prisma – cv. Tyne, mg(N)/g(DW)) at final harvest in main-stem and tillers.

	Main-stem		Tiller	
	1989	1990	1989	1990
Low N	+0.7	−0.8	+0.4	+1.8
High N	+1.9	+2.1	+0.6	+0.3

Table 4.2.5T3. Significance levels for the variation in nitrogen concentration of the non-reproductive biomass (NRB, stem and leaf tissues) separated into main and tiller stems and analyzed by individual harvest for 1989 and 1990.

a) NRB, Main-stem

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	***
Nitrogen	1990	*	*	**	NS	**	***
Cultivar	1989	NS	NS	NS	NS	***	NS
Cultivar	1990	*	*	NS	NS	*	**
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

b) NRB, Tillers

Source	Harvest	1	2	3	4	5	6
Nitrogen	1989	***	***	***	***	***	**
Nitrogen	1990	NS	NS	**	NS	*	**
Cultivar	1989	NS	NS	NS	NS	NS	NS
Cultivar	1990	*	*	NS	NS	NS	NS
Nit*Cult	1989	NS	NS	NS	NS	NS	NS
Nit*Cult	1990	NS	NS	NS	NS	*	NS

Table 4.2.6T1 Significance levels for variations in maximum grain weight, W_{max}.

	MS, T1 & T2		MS & T3	MS, T3 & T4[1]
	1989	1990	1989	1990
Nitrogen	***	***		
Cultivar	***	***	NS	*
Nit*Cult	NS	NS		
Stem	***	***	***	***
Nit*Stem	**	**		
Cult*Stem	*	***	***	**
Nit*Cult*Stem	NS	NS		

[1] The abbreviations (MS, main-stem; T1, tiller 1 etc) indicate which stem types were included in each analysis of variance.

Table 4.2.6T2 Significance levels for variations in the number of grain bearing positions, R.

	MS, T1 & T2		MS & T3	MS, T3 & T4[1]
	1989	1990	1989	1990
Nitrogen	***	***		
Cultivar	**	**	***	**
Nit*Cult	**	*		
Stem	***	***	**	***
Nit*Stem	NS	**		
Cult*Stem	***	NS	NS	NS
Nit*Cult*Stem	NS	NS		

[1] The abbreviations (MS, main-stem; T1, tiller 1 etc) indicate which stem types were included in each analysis of variance.

Table 4.2.6T3 The grand mean of the estimates of linear component of the increase in grain weight up to the heaviest grain (S_1) in the two sets of comparisons in each year. Note that values for the main-stem are common to both analyses within a year.

Year	Stem types	S_1 (mg/grain position)
1989	MS T1 T2	1.44
1990	MS T1 T2	1.57
1989	MS T3	1.35
1990	MS T3 T4	1.56

Table 4.2.6T4 Significance levels for variations in the number of grain bearing positions, S_2.

	MS, T1 & T2		MS & T3	MS, T3 & T4[1]
	1989	1990	1989	1990
Nitrogen	**	*		
Cultivar	***	***	*	NS
Nit*Cult	NS	NS		
Stem	NS	NS	NS	*
Nit*Stem	NS	NS		
Cult*Stem	*	NS	NS	NS
Nit*Cult*Stem	NS	NS		

[1] The abbreviations (MS, main-stem; T1, tiller 1 etc) indicate which stem types were included in each analysis of variance.

Table 4.2.6T5 Significance levels for variations in grain nitrogen concentration at three grain positions (single sites at the bottom, middle and top of the ear). The observations are based on sub-samples of 10 grains per grain position per replicate.

	MS, T1 & T2		MS & T3	MS, T3-4[1]
	1989	1990	1989	1990
Nitrogen	**	***		
Cultivar	NS	NS	NS	NS
Nit*Cult	NS	**		
Stem	***	NS	***	***
Grain Pos	*	***	NS	**
Nit*Stem	NS	***		
Cult*Stem	NS	***	NS	***
Nit*Grain Pos	NS	NS		
Cult*.Grain Pos	NS	**	NS	NS
Stem.GrainPos	*	***	*	NS
Nit*Cult*Stem	***	**		
Nit*Cult*GrainPos	NS	**		
Nit*Stem*GrainPos	NS	NS		
Cult*Stem*GrainPos	NS	NS	NS	NS
Nit*Cult*Stem*GrainPos	NS	NS		

[1] The abbreviations (MS, main-stem; T1, tiller 1 etc) indicate which stem types were included in each analysis of variance.

Table 4.2.6T6 Significance levels of the variation in time taken to germinate for individual grains taken from five grain positions (single sites at the bottom, lower quartile, middle, upper quartile and top of the ear) and three stem types (Main-stem, tiller 1 and tiller 2). Germination tests A were observed during day time only and tests B were also observed during night time (i.e. finer resolution of time scale).

	1989		1990	
	A	B	A	B
Within treatments				
Nitrogen	NS	NS	NS	NS
Cultivar	NS	NS	NS	*
Nit*Cult	NS	NS	NS	NS
Within plots				
Stem	*	NS	NS	NS
GrainPos	***	***	***	***
Nit*Stem	NS	NS	NS	NS
Cult*Stem	NS	NS	NS	NS
Nit*GrainPos	NS	NS	NS	NS
Cult*.GrainPos	NS	*	NS	*
Stem.GrainPos	NS	NS	NS	NS
Nit*Cult*Stem	NS	NS	NS	NS
Nit*Cult*GrainPos	NS	NS	**	NS
Nit*Stem*GrainPos	NS	NS	NS	NS
Cult*Stem*GrainPos	NS	NS	NS	NS
Nit*Cult*Stem*GrainPos	NS	NS	NS	NS

Table 4.2.6T7 Significance levels of the variation in time taken to germinate for the same individual grains as in Table 4.2.6F6 and including the weight of the individual grains as a covariate. Germination tests A were observed during day time only and tests B were also observed during night time (i.e. finer resolution of time scale).

	1989		1990	
	A	B	A	B
Within treatments				
Nitrogen	NS	NS	NS	NS
Cultivar	NS	NS	NS	NS
Nit*Cult	NS	NS	NS	NS
Covariate	NS	NS	NS	NS
Within plots				
Stem	***	NS	NS	NS
GrainPos	***	***	***	***
Nit*Stem	NS	NS	NS	NS
Cult*Stem	NS	NS	NS	NS
Nit*GrainPos	NS	NS	NS	NS
Cult*.GrainPos	NS	*	NS	**
Stem.GrainPos	NS	NS	NS	NS
Nit*Cult*Stem	NS	NS	NS	NS
Nit*Cult*GrainPos	NS	NS	**	NS
Nit*Stem*GrainPos	NS	NS	NS	NS
Cult*Stem*GrainPos	NS	NS	NS	NS
Nit*Cult*Stem*GrainPos	NS	NS	NS	NS
Covariate	***	***	***	***

Table 4.2.6T8 Significance levels of the variation in time taken to germinate for individual grains taken from three grain positions (single sites at the bottom, middle and top of the ear) and three stem types (Main-stem, tiller 3 and tiller 4) from the High N treatments only, and including the weight of the individual grains as a covariate. This test was carried out at the lower time resolution only.

	1989	1990
Cultivar	NS	NS
Covariate	NS	NS
Stem	NS	NS
GrainPos	***	*
Cult*Stem	NS	NS
Cult*GrainPos	*	*
Stem.GrainPos	NS	NS
Cult*Stem.GrainPos	NS	NS
Covariate	***	**

Table 4.3T1. Nitrogen concentration, nitrogen content, ^{15}N content, percentage contribution to final grain nitrogen from uptake during first week following transfer to ^{15}N labelled nutrient solution (Nc), and dry weight of ears 105 days after planting.

	cv. Klaxon		cv. Blenheim	
	Steady state	High low	Steady state	High low
Total N (%)	3.25 (0.369)[1]	2.35 (0.055)	2.14 (0.115)	2.11 (0.026)
Total N content (mg)[2]	20.6 (3.45)	27.0 (7.29)	10.8 (1.82)	18.1 (1.75)
Total ^{15}N content (mg)	4.97 (0.83)	7.48 (2.01)	3.17 (0.54)	5.72 (0.55)
N_c (%)	24.1	27.71	29.4	31.6
Dry weight (mg)	633 (106)	1151 (310)	503 (85)	859 (83)

[1] Values are means of five replicates (se in parenthesis).
[2] Weights are expressed on a per plant basis.