BARLEY MODELLING

TO IMPROVE THE EFFICIENCY OF FIELD TRIALS

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INDEX OF ABBREVIATIONS

ARC	Agricultural Research Council
CABO	Centre for Agrobiological Research, Wageningen
CVT	Co-ordinated Variety Trials
DANI	Department of Agriculture for Northern Ireland
DSSAT	Decision Support System for Agrotechnology Transfer
IERM	Institute of Ecology and Resource Management, Edinburgh
IFRC	International Fertiliser Research Centre, Alabama
IBSNAT	International Benchmark Sites Network for Agrotechnology Transfer
LARS	Long Ashton Research Station, Bristol
MAFF	Ministry of Agriculture, Fisheries and Food
NIAB	National Institute of Agricultural Botany, Cambridge
PBI	Plant Breeding Institute, Cambridge
RES	Rothamsted Experimental Station
SAC	Scottish Agricultural College, Edinburgh
SASS	Scottish Agricultural Statistics Service
SCRI	Scottish Crop Research Institute, Dundee

Phenological development stages

CI	Collar Initiation
DR	Double Ridge
MPN	Maximum Primordium Number
TS	Terminal Spikelet

Canopy development

AWR	Area to Weight Ratio	$m^2\ g^{-1}$
GAI	Green Area Index	$m^2\ m^{-2}$
I_0	Intercepted Photosynthetically Active Radiation	$MJ\ m^{-2}\ d^{-1}$
LAD	Leaf Area Duration	$m^2\ d^{-1}$
LAI	Leaf Area Index	$m^2\ m^{-2}$
PAR	Photosynthetically Active Radiation	$MJ\ m^{-2}\ d^{-1}$
SLA	Specific Leaf Area	$g\ m^{-2}$

Weather variables

CHGDL	Rate of change of daylength at emergence	hours
DAY	Daylength at emergence	hours
DTT	Daily thermal time	°Cdays
PHINT	Phyllochron	°Cdays
SUMDTT	Accumulated temperature	°Cdays

Other model variables

k	Light extinction coefficient	
P_b	Base photoperiod	hours
P_f	Photoperiod correction factor	°Cdays
P_{opt}	Optimum photoperiod	hours
R_l	Rate of leaf appearance	°Cdays
R_p	Rate of leaf primordia initiation	°Cdays
R_s	Rate of spikelet primordia initiation	°Cdays
T_b	Base temperature	°C

GLOSSARY OF MODELLING TERMS

analogue	one property is used to represent another
analytical	analysis of a process by conventional statistical methods
auxiliary variable	variable produced as an intermediate stage used to simplify the process
continuous time	the model is solved using differential or difference equations; the state variables are changing continuously
deterministic model	has no associated probability distribution for the results. The outcome will be the same each time the model is run with the same basic set of parameters.
discrete time	the model can be solved by recurrence equations and the state variables updated at regular intervals
driving variable	characterise the influence from outside the system but are not affected by changes within it, eg: temperature, solar radiation, time
dynamic model	uses time as the driving variable. Relationships are expressed as a set of equations, describing the process of change over time
empirical model	a descriptive model based on observation and experiment, with no theoretical foundation. For example the description of an extensive data set by regression equations. No attempt is made to explain the relationships in terms of the underlying mechanisms involved
forcing variable	*exogenous* or *driving variable*
iconic model	physical model in which only a transformation of scale is involved eg: field trial plot as a model of a farmers field
mechanistic model	analyses a system in terms of the behaviour of its components and their interactions, requiring knowledge of the mechanisms present
model	a simplification of reality as an aid to understanding; a description of a system, often in mathematical terms.
multivariate analysis	the simultaneous evaluation of many variables or attributes of a system using statistical techniques
phenomenological	describing a process at the level of organisation under study
rate variable	expressed as a function of state variables, for example, growth rate
sensitivity analysis	testing the sensitivity of the model to small changes in the basic parameters of the model to determine the relative importance of processes
simulation	a threefold process involving model-building, validation and experimentation
state variable	primary variable, sometimes called status variable
static model	model in which time is not used as a driving variable
statistical model	or *correlative model* using regression or other statistical technique to describe theoretical relationships between factors
stochastic model	contains random elements or probability distributions within it, and predicts the variance of the results
system	a limited part of reality surrounded by a conceptual boundary, containing a number of interdepemdent elements
systems analysis	holistic study of a system, its structure and behaviour
validation	quantitative comparison of model results with independent data, using statistical tests for 'goodness of fit'
variable	element within the system
verification	testing the model over a range of parameter values, to ensure that the model performs as a correct representation of the real system

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This thesis is also a tribute to my long-suffering family to whom it is lovingly dedicated.

To quote the three laws of simulation (Dillon, 1971):

Simulation, like statistics, cannot prove anything

Simulation, like statistics, can nearly prove anything

Once started, simulation of a system will continue until available funds are exhausted!

ABSTRACT

The application of crop growth models to the barley crop in Scotland was investigated. Three models, the ARCWHEAT winter wheat model (Weir *et al.*, 1982), the CERES barley model (Ritchie *et al.*, 1987, developed directly from the CERES wheat model, Ritchie *et al.*, 1984) and a spring wheat model (van Keulen & Seligman, 1987) were evaluated using data from a range of seasons, cultivars and sites in South-East Scotland. The chosen models used different methods to predict crop development, based on the principle that development rate is a function of temperature and photoperiod. Specification of cultivars was based on differences in vernalisation requirement and photoperiod sensitivity which were found hard to quantify precisely. Crop performance was not modelled reliably enough to allow these models to identify Genotype x Environment interactions in variety testing. Thorough model validation required more data than those collected in the normal course of field trials.

Agronomic and physiological data from field experiments from a broad range of environments and cultivars were compiled into a database to examine the mechanisms controlling barley growth and development. Cultivars were classified according to genotypic characters which could be easily recognised such as winter/spring type, semi-dwarf/tall habit and ear row number. Rules and relationships derived from these data were used to build the modular, deterministic DAFS BARLEY MODEL which contained a range of options for simulating crop development. The pathway through the model has a large effect on the outcome and an optimisation procedure to select the most appropriate route and improve model accurary is discussed. It is thus envisaged that the resulting barley model will be used as an adjunct to, rather than as alternative to the existing field trials program.

The model was constructed to:

a. systematize historical knowledge gained from field trials

b. enable data from existing field trials to be used as a guide to future research needs

c. enable the results from trials to be reliably extrapolated to other sites and seasons

d. aid in design of more cost-effective and efficient plans for field trial measurement, including the precise specification of data collection and recording methods for field trials.

1. INTRODUCTION

The list of recommended barley cultivars grown in Scotland is under constant review as new cultivars are developed by plant breeders and established ones are superseded. The development and testing of barley cultivars relies upon an extended programme of field trials over many years. Statistical analysis of trial results identifies cultivars with potential merit over a wide range of conditions, which qualify for recommendation to the farmer. These trials are limited by time and cost in terms of the range of sites and number of seasons that can be sampled. Simulation modelling could assist in reliable extrapolation of trial results to other possible genotype/environment combinations, since a model predicting crop yield and quality accurately will reduce the dependency on lengthy field trials to measure these characters directly.

Response to environmental variation, notably in temperature, light, nutrient and water availability, accounts for much of the difference in performance between cultivars. Cultivars vary in photoperiod sensitivity, vernalisation requirement and earliness of maturity, and thus timing of development stages, also in the rate and capacity of grain fill, dormancy and their resistance to disease, lodging, grain splitting and shedding. Fertilisation and irrigation regimes can remediate adverse nutrient and water status for the crop, and crop management decisions of site, sowing and harvest date, crop protection strategies can minimise the effects due to genotypic variation. However, interactions between environment and genotype form an important part of the overall variation which cannot be fully assessed during the trialling stages.

The objectives of the project reported in this thesis were:

a. To establish, by investigation and experiment, whether the growth and development of barley can be reliably simulated using mathematical modelling,

b. To assemble a body of data for model validation and testing,

c. To develop and test a working model using the results from field experiments.

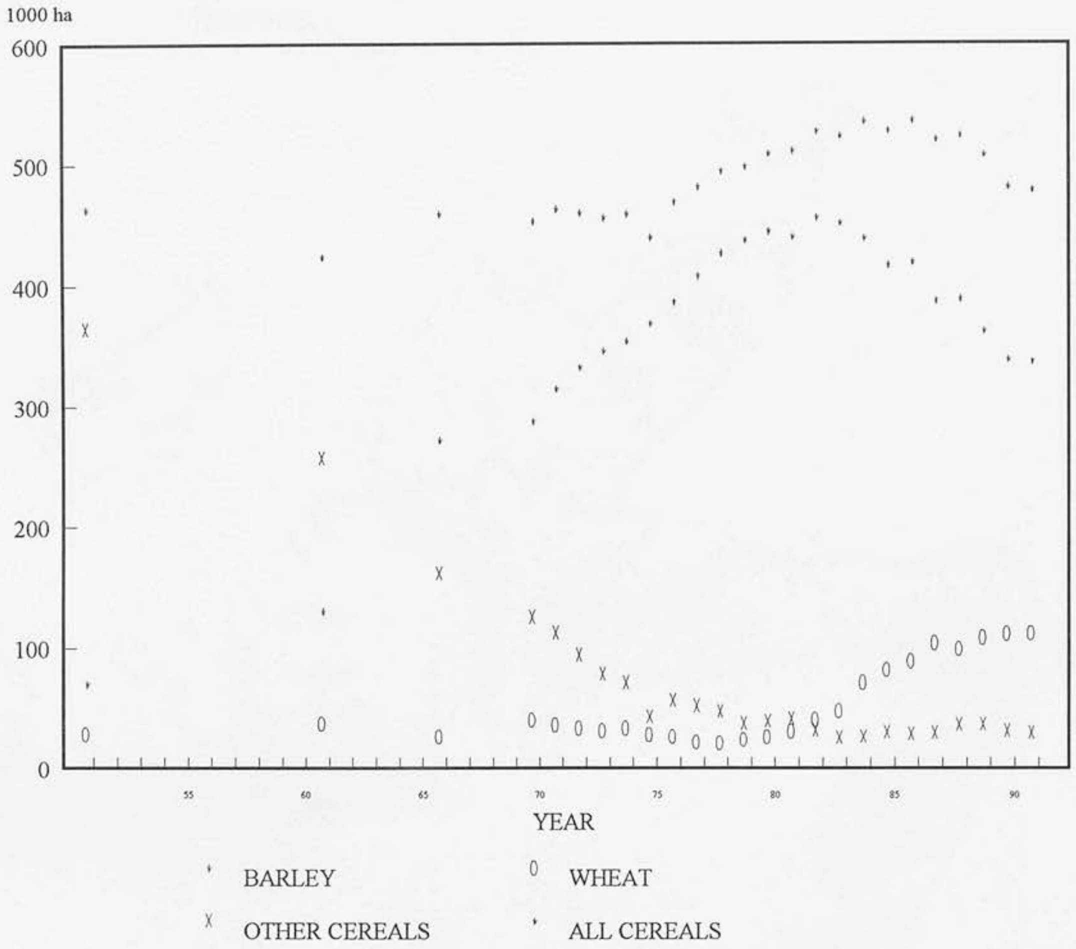
Barley is the principal cereal crop grown in Scotland. Its success can be partly attributed to the work of plant breeders and agronomists developing and testing new cultivars and optimum crop management strategies. Current testing and decision making schemes force a compromise between trial costs in both real and hidden terms (eg. delayed introduction of a new cultivar) and the precision of predicted yields. Any techniques to increase the reliabilty of extrapolation beyond the trial situation would find ready use as an adjunct to the field trials program.

1.1. DISTRIBUTION AND PRODUCTION OF BARLEY IN SCOTLAND

Barley ranks fourth in production of the world's cereal food crops, after wheat, maize and rice. It is grown over the widest range of environments in terms of latitude, altitude and rainfall - from altitudes of near sea level in the Netherlands to over 3000m in Zimbabwe, Ethiopia and Bolivia, and from the tropics to the arctic circle - although most of the area of production is in temperate climate zones between latitudes 30° and 60°N. Barley tends to be grown in preference to wheat wherever water availability limits wheat yields. The United Kingdom is the fifth largest barley producer in the world, after the USSR, Canada, USA and France, producing 6.4% of the world's barley in 1979-81, and 5.4% in 1985-1987 (FAO, 1988). Scotland accounts for over 22% of the United Kingdom total, with 1,708,597 kg from 336710 ha of barley grown in 1991. High yields are not always commensurate with high production, but UK barley yields are consistently amongst the highest in the world, with Belgium, France, Eire, Netherlands and Switzerland also regularly achieving mean yields of over 5 t ha^{-1}.

In Scotland, as in the rest of the UK, there was a relatively small increase in the total cereal area grown between 1951 and the late 1980's, but the balance of wheat, barley and oat production changed considerably (Figure 1.1). There was a dramatic switch from oats to barley during the period 1951-1980 due to a general reduction in the demand for oats with increasing mechanisation of agriculture. Since then, the area of wheat has increased, contrary to predictions in the early 1970's that the area was considered to be limited for climatic and husbandry reasons, partly due to difficult harvests in wet seasons. The increase can be ascribed largely to the introduction of new winter cultivars which showed considerable improvement over older ones in terms of yield, disease resistance, and winter hardiness. Scotland has an extended growing season in comparison to Southern England, due to cooler temperatures, longer summer days and lower probability of drought. Yields in Scotland are therefore potentially higher, despite the greater risk of weather damage before harvest (Ellis, 1986). However, Scottish cereal production is restricted by the natural limitations imposed by geography and climate. The principal barley growing areas in Scotland are lowlands, with freely or imperfectly drained soils, particularly around the East and South West coasts: highland Scotland provides too inhospitable an environment in terms of temperature, wetness, slopes and soil quality. Some 70% of farm land in the Highland region is upland (Figure 1.2), often remote, with steep slopes, thin soil or prolonged winter frost. Much of the West of Scotland has high rainfall, and is better suited to pasture for cattle and sheep.

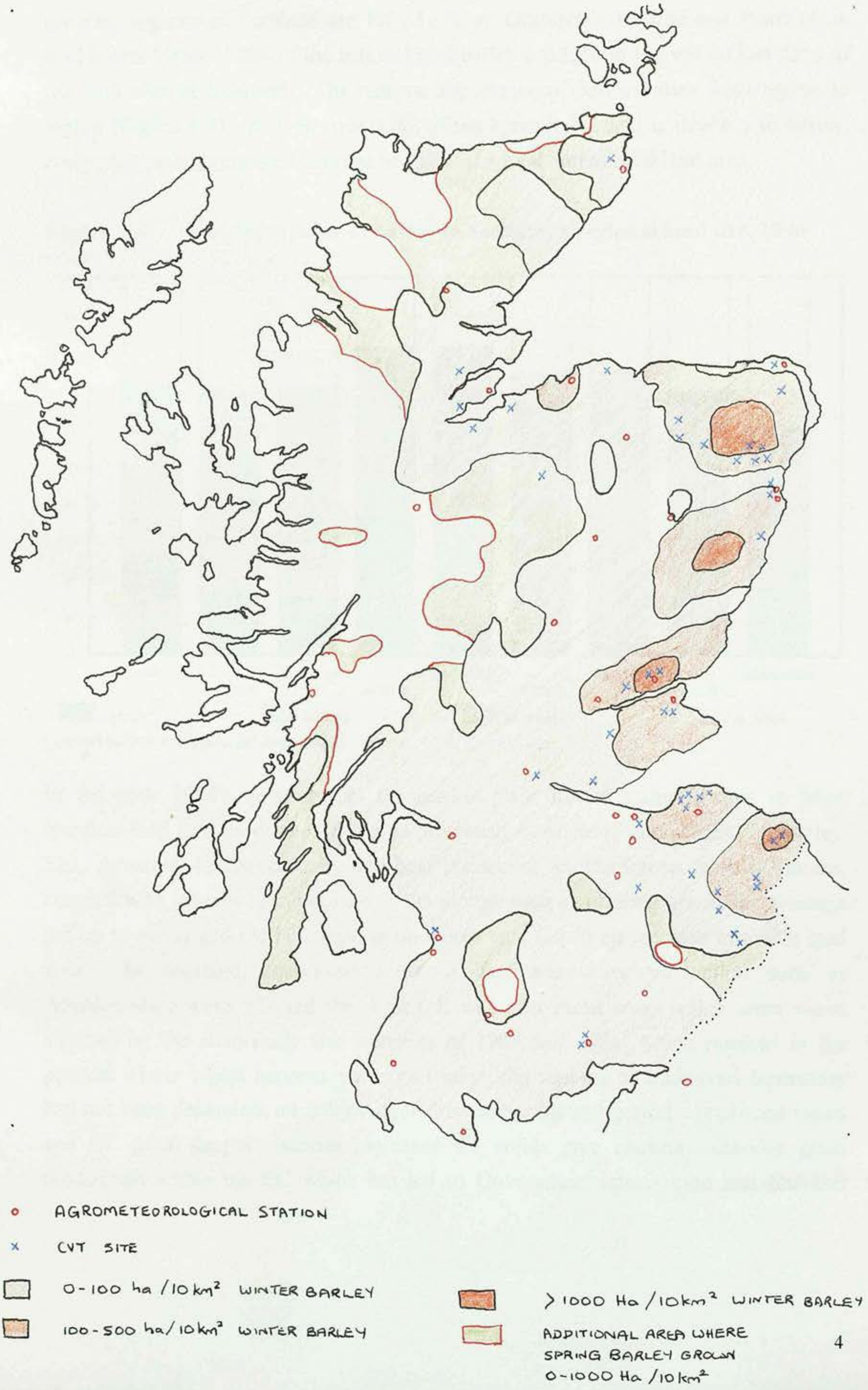
Figure 1.1. Cereal production in Scotland: Area grown: 1951 - 1991



Data: 1968 - 1984 Seed Sales Survey
1984 - 1991 June Census Results
'Other cereals' figures include Oats, Rye and Mixed Corn.

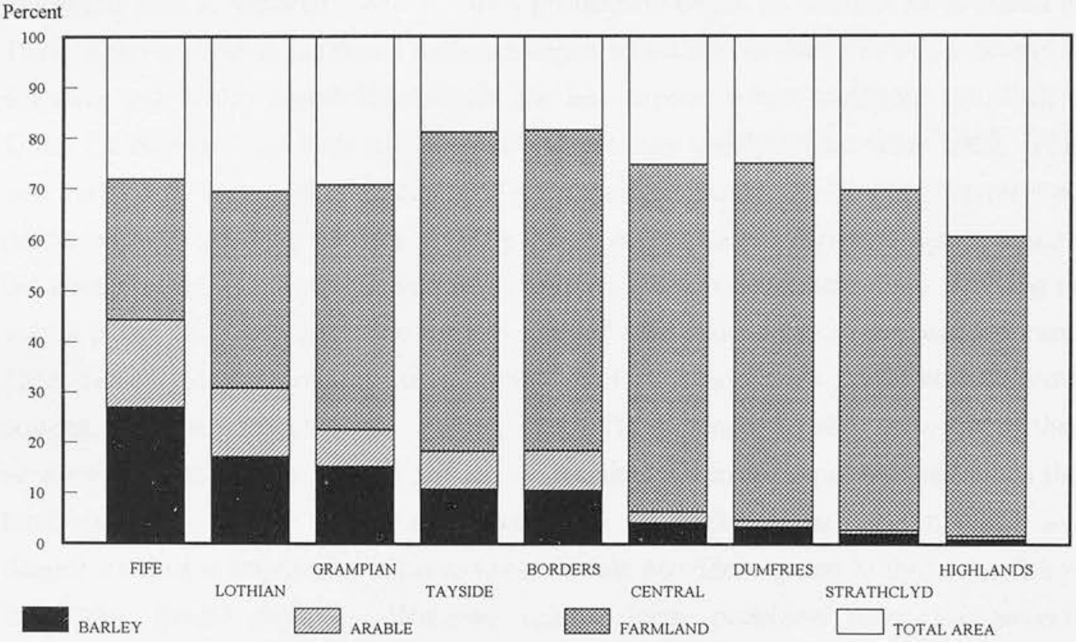
Barley distribution is closely related to the distribution of agricultural land (Figure 1.2; Appendix E), according to the Land Capability Classification for Agriculture (Bibby *et al.*, 1982). Grade 1 land is mostly well-drained, deep loam restricted to a few raised beach and alluvial deposits along the Eastern coast of Scotland, where high value horticultural crops can be grown. High yields can often be obtained from Grade 2 or 3 land in a favourable season but are less consistent due to wetness, drainage or workability problems. Grade 3 land may have added problems of restricted rooting depth, strongly sloping ground or erosion risk. Barley yields become increasingly unreliable on lower grade land due to interactions between climate, soil and management factors. Class 4 land is primarily used for grassland, with short arable breaks, but problems of soil, slope or climate bring yields well below the national average. Classes 5, 6 and 7 land is considered unsuitable for barley.

Figure 1.2. **Maps to show the distribution of spring and winter barley, agrometeorological stations and coordinated variety trial sites in Scotland.**



Ideal soils for barley are well drained and not prone to drought, such as raised beach deposits, partially sorted tills and clay tills. Soil acidity below pH 6.0 renders many of the upland, organic, peaty soils unsuitable for barley production. Thus the chief barley growing regions of Scotland are Fife, Lothian, Grampian, Tayside and Borders on land below 300m. 78% of the total area of barley production lies within just 31% of the land area of Scotland. The relative importance of barley varies from region to region (Figure 1.3). In Fife, over 37% of the agricultural land is devoted to barley, compared with the national average of 8% of the total agricultural land area.

Figure 1.3. The importance of barley to Scotland's regional land use, 1990



Farmland includes crops, grass and rough grazing

In the early 1970's, pressures of the market place forced many farmers to bring marginal land into production that was previously considered unprofitable for barley. EEC directives to reduce dairy and beef production by the introduction of quotas, coupled with incentives to put land to the plough such as offering grants for drainage (of up to 60%) and for buildings, grain stores etc., led to an increase in arable land area. In Scotland, traditional areas of beef and dairy production such as Aberdeenshire were affected the most. It was also these areas which were worst affected by the abnormally wet summers of 1985 and 1986, which resulted in the poorest winter wheat harvests yet experienced: the success of traditional husbandry had not been dependent on a dry August/September harvest period. Improved yields and EC price support policies increased the arable area causing excessive grain production within the EC which has led to Government intervention and financial incentives to reduce the area grown. Financial and environmental considerations are leading to a reappraisal of intensive arable farming methods, with its dependence on high fertiliser and chemical inputs. Methods to optimise inputs rather than concentrate on high yields may have the long-term effect of concentrating production on fewer, highly favourable areas. The Common Agricultural Policy of the EC may have far-reaching effects on the distribution of all the main crops within Europe as we see them today if this strategy is applied on a European scale.

Winter barley accounts for a small proportion of the total barley area, due to the higher variable costs in growing winter varieties (Table 1.1) and greater investment in machinery that is required. Winter barley production began to increase in Scotland in 1979, when seed from the first 3 cultivars appeared on the Scottish market, whereas in England and Wales where the winters are less severe, winter cultivars (cv. 'Maris Otter' for example) had been available and increasingly widely grown since 1965. This was partly due to the lack of cultivars of good malting quality. Cultivars are restricted to those which are cold tolerant: sowing should be completed early enough to ensure the development of a strong root system before the onset of winter. Frost heaving of young plants and waterlogging of poorly drained soils reduce the winter survival rate. Late harvest of the previous crop during cool, wet summers may delay autumn sowing, thus increasing the risk of winter-kill. The potential sowing period is further shortened by restrictions imposed by heavy machinery, which cannot be used when the land becomes too wet. Crop protection costs are higher since autumn weed and disease control is important: autumn-sown cereals provide a green bridge for mildew and other fungal disease. Weighed against these problems there are several advantages. Autumn sown cultivars can utilise warm days in early spring and establish complete canopy cover earlier than spring sown cultivars. Harvest is often complete by mid-August, before the weather deteriorates, allowing the land to be prepared for the next crop. Timing is particularly important when the rotation includes oil seed rape, which has drastically reduced survival and establishment when sown after the beginning of September. Yields may be up to 20% higher than those of the more traditionally grown spring varieties due in part to the longer growing season that can be exploited and the lower risk of drought during the early part of the growing season. However, winter cultivars intended for malting tend to have lower yields than crops intended for feed but prices can be £5 to £30 per tonne higher (UK average forward prices for January 1993 £149.20 t^{-1} malting barley, £132.40 t^{-1} feed barley, Farmers Weekly, 11 December, 1992), depending on the quality and supply position, particularly in Europe. Current commerical estimates make winter malting barley the best crop for the future.

Continuous barley yields also tend to be lower than yields from classic rotational systems and involve higher fertiliser costs (£13 ha^{-1} in 1992). Winter crops also provide continuous ground cover which reduces the leaching of excess nitrates during the wettest months. Winter barley production is especially important in the coastal areas of East Lothian, Fife, Aberdeenshire and Morayshire (Figure 1.2).

Spring cultivars are sown after the danger of severe frost has passed, and harvested during late August and September, often restricting the following crop in the rotation to spring-sown crops. There are also difficulties in harvesting some crops in a wet year when heavy autumn rainfall precedes crop maturity. Conversely, in a dry season spring-sown crops are more drought-prone. Later maturing crops are especially affected, so the emphasis in Scotland has traditionally been on early-maturing cultivars. The biggest problem for spring crops is variable yield, because they are more likely to be affected by weather and soil conditions due to the shorter growing period.

Table 1.1. Variable costs per hectare of the major cereal crops in 1992

	WINTER BARLEY (feed)			**SPRING BARLEY (malt)**			**WINTER WHEAT (feed)**		
	low	med	high	low	med	high	low	med	high
YIELD t ha^{-1}	4.32	5.56	6.79	3.70	4.94	6.17	4.94	6.79	8.64
GROSS OUTPUT (£)	459	590	721	481	642	802	533	733	933
VARIABLE COSTS (£)									
seed[1]	40	40	40	40	40	40	40	40	40
fertiliser	67	81	94	54	54	54	59	81	106
sprays[2]	89	104	119	54	69	81	106	121	136
miscellaneous	7	7	7	7	7	7	7	7	7
GROSS MARGIN (£)	**257**	**358**	**462**	**326**	**472**	**620**	**321**	**484**	**644**

From: Royal Bank of Scotland, 1992

Mid season sale prices - prices rise by £1.50 per month after October. Prices off the combine up to £20 per tonne lower

Straw prices excluded: 3 t ha^{-1} Spring barley; 3.7 t ha^{-1} Winter barley

[1] could be higher in the North of Scotland

[2] could be lower in the North of Scotland

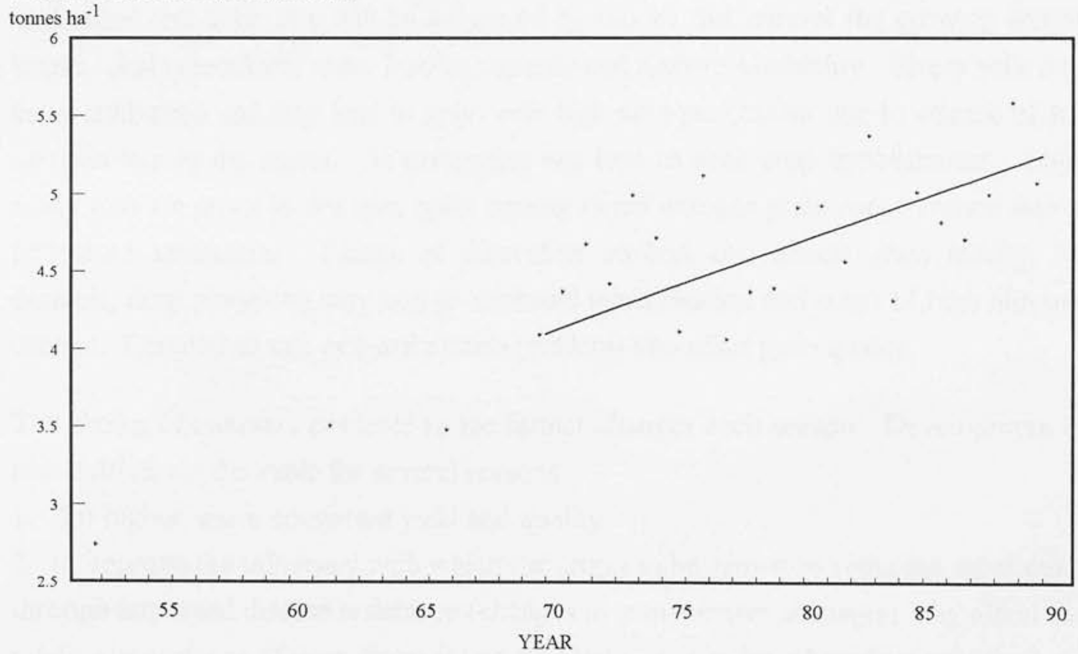
In Scotland, barley is grown primarily for animal feed products. A significant amount is not sold, but used on the farm. The proportion of the crop which is used for malting fluctuates between 16 and 25% according to the season. Custom and practice has led to certain areas being known as 'good malting areas' - areas of medium textured soils, reasonable moisture supply and no extremes of temperature or disease pressure. The export market has potential for considerable expansion, particularly to Belgium and West Germany, where the requirement for malting barley exceeds domestic production. Some 80% of barley straw is baled for use on-farm as livestock feed and bedding in preference to wheat straw, since the higher leaf:stem ratio makes the straw more digestible.

1.2. STATEMENT OF THE PROBLEM

Falling grain prices (EC Common Agricultural Policy target price £79 per tonne - 35% reduction from 1992 prices) place a pressure on farmers to increase the profitability of barley production, either by increasing grain yield or reducing input costs. A record yield of 11.5 t ha^{-1} (cv. 'Manitou', 1990) has been recorded in trials, but average yields fall far short of this level. UK yields have increased on average by 2% per year as new cultivars have been introduced (Silvey, 1986): average yields measured in Scotland over the last 40 years (Figure 1.4) have increased, but further increase becomes harder to attain.

Figure 1.4. Average yield of barley in Scotland, 1951 - 1991

Line shows regression of yield against year



Crop yield depends on the combination of genotype and environment and the interaction between the two, as modified by crop management. The farmer has a number of decisions to make regarding choice of crop, cultivar and husbandry to obtain the highest profits from his arable land. He has to judge the economic optimum level at which improved yield or quality achieved through additional inputs of fertiliser, herbicide, pesticide, fungicide or growth regulator is justified by their extra cost. Decisions are based on tradition and experience rather than theory (Sylvester-Bradley, 1991), together with recommendations from national and local advisers. Local variation in soil type and condition, aspect and drainage, mean that each field must be considered separately. Differences in potential arise through differences in soil, climate or topography over which he has little control. Profitability can be increased most in fields that fall furthest short of their potential, so prediction of potential yield has a direct bearing on farm management decisions.

Yield level	limited by
Attainable	evolution, cultivar
Achievable	land quality and climate
Affordable	input levels
Actual	pests, diseases etc

Malting barley is traditionally regarded as a low input crop with high potential profits, but greater risk of failing to reach the maltsters stringent quality specifications (e.g. Fenwick, 1990). Potential quality is under genetic control, but choice of a 'malting' cultivar will not guarantee malting quality because soil, health and husbandry all affect grain quality. Grain nitrogen concentration can be manipulated by careful timing and control of fertiliser application and grain size will be influenced by factors that control the growing season length. Soil type affects water holding capacity and nutrient availability. Heavy soils may delay cultivation and may lead to grain with high nitrogen content due to release of soil nitrogen late in the season. Waterlogging can lead to poor crop establishment. Light sandy soils are prone to drought, again causing raised nitrogen grain concentration due to premature senescence. Choice of cultivation method also affects grain quality, for example, deep ploughing may lead to increased mineralisation and crops of high nitrogen content. Compacted soil, pest and disease problems also affect grain quality.

The choice of cultivars available to the farmer changes each season. Development of new cultivars is desirable for several reasons:

1. for higher, more consistent yield and quality
2. to improve the efficiency with which the crop can be grown by reducing input costs through improved disease resistance (changes in management strategies may affect the relative importance of crop diseases and thus the priorities for a breeding program).
3. extensive planting of a few cultivars for long periods may highlight their weaknesses and allow certain pathogens to reach epidemic proportions, or the chance occurrence of freak weather events to cause widespread failure in susceptible cultivars; this places considerable pressure on the farmer to rotate and mix his cultivars.

In practical terms, increasing yield must involve a combination of

a) more grains per ear
b) more ears per unit area
c) larger grains
d) greater harvest efficiency

Modern varieties show an increase in photosynthetic efficiency providing both more assimilate for grain fill and a higher harvest index (Silvey, 1986). However, the barley breeder has to balance quantity with quality and fitness for purpose. Other genetic improvements include:

1. Improved seasonal adaptation - extending the growing season by, for example, increasing cold tolerance to allow earlier sowing of spring cultivars,
2. Tolerance of environmental stresses such as drought, wetness, wind, and temperature extremes,
3. Resistance to pest and disease attack.

Barley breeding involves a costly and time-consuming program of experimentation and trialling. 12 to 15 years elapse between the initial cross and the marketing of a certified cultivar with a success rate of only about 1 in 10000. The plant breeder has to aim for a market 12 to 20 years hence, in which time methods and management may change, so works with an ideotype in mind for a widely or locally adapted cultivar (Donald, 1968; Ellis, 1986). The desirable features for Scotland include uniformity, vigorous seedling growth, resistance to foliar disease, herbicide tolerance, stiff straw, strong neck resistance to grain splitting and sprouting and low grain loss. High yield, low post-harvest dormancy and good malting potential are desirable. There is a rapid turnover of new cultivars on the annual Recommended Lists of varieties (e.g. NIAB, 1992; SAC, 1992). Cultivars remain on the list for an average of only 3 or 4 years before they are superseded: those preferred by the Institute of Malting tend to be recommended for longer than feed barleys. The figures are distorted by a few very successful cultivars which remained on the market for a long time. For example, the early maturing, semi-dwarf spring barley cv. 'Golden Promise' was recommended in Scotland for 21 years due to its suitability for the Scottish climate and good malting quality, despite its extreme susceptibility to mildew attack.

Selection for stability across environments is unlikely to be efficient (Simmonds, 1979) because of seasonal variation and choice of site. For example, periods of drought or of excessive rainfall will have different effects on sandy or heavy clay soils; frost tolerance will only become apparent during severe winters; disease resistance if the weather favours the spread of the disease; brackling or lodging when the summer months are windy. These are often factors beyond the control of the triallist and can result in errors of two types (Talbot & England, 1984):

Type I. Rejection of lines which would show the desired character in a different season

Type II. Selection of inconsistent lines which show the desired character by chance alone.

Confidence in the performance of new cultivars across a wide range of environments can be raised by a) increasing the number, size or replication of field trials, or b) reducing the level of significance specified. Intensive breeding for high performance tends to increase the uniformity of cultivars and produce a crop with a narrow genetic base. Methods such as induction of mutations and wide hybridization may be used to counteract this effect. Since variation in yield becomes progressively smaller as cultivars improve (MAFF, 1982), small differences in performance assume high significance. The solution cannot lie simply in increasing the number of field trials due to the high costs involved (currently approx £5-6 per plot to the breeder). Constraints of cost, space and man-power limit the possibilities of increasing sample number by conventional methods. Estimates of yield stability can then only be related to a narrow range of environments. Extrapolation of results obtained in trials testing the effects of fertiliser and crop protection chemicals is complicated because of the lack of a suitable means to predict what those results would have been at other sites and seasons. Similar problems arise with the SCRI barley breeding programme because selections can only be assessed on a limited scale (Ellis & Brown, 1986). Interactions between genotype and environment cannot be assessed over the long periods desired, as lines have to be selected within a given season, and existing methods for relating results to other seasons are not reliable. Selection pressure could be adjusted appropriately if the factors limiting performance at the given site were identified and related to environmental variation in the area where the new cultivar is to be grown.

SAC has 16-30 Co-ordinated Variety Trial farm and college sites across Scotland (Figure 1.2) the number used varying from year to year, depending on availability and economic necessity. The location of trial sites in the main areas of barley cultivation cannot fully represent the range of environments under which barley is grown. Generally, sites are large enough for conventional farming techniques to be applied, with the effects of underlying gradients of slope, soil texture, fertility and drainage minimised by a replicated, randomised block trial design. 'Background variation' due to seed size, seed-bed condition and seed placement will always occur.

Patterson *et al.* (1977) showed that the probability of rejecting a cultivar with yield 5% above the control mean (Type I error) was reduced significantly by extending the trial to a third year (0.08 to 0.05), but not by increasing the number of trial centres from 10 to 15. Extending the trial programme to further sites is most effective when there are only a few sites overall (Talbot, 1984): increasing the number of replicates at each site only having a significant effect on precision when the variation between plots is high. However, increasing the number of sites in the final stages of cultivar testing does not compensate for using few sites in earlier years (Talbot & Robinson, 1988). The potential gain (mean of all cvs under trial - mean of cvs selected) to the plant breeder is not significantly reduced by changing the trial system to one with fewer sites. Increasing plot size decreases experiment variability up to a point, but may increase variability within the block when it causes an expanded block area. Larger plots tend to give more accurate estimates of yield, since edge effects are lessened and the effects of inter-plot competition are reduced, but they are also more expensive and reduce the replication possible. Smaller plot yields have a higher variance (Lin & Binns, 1984; Talbot & England, 1984) and give apparent advantage to taller cultivars which compete successfully for light with neighbouring plots of shorter cultivars (Austin, Morgan *et al.*, 1980). Plants at the edges of cereal plots are usually higher yielding due mainly to higher ear numbers, and are less likely to lodge than plants in the centre, so inclusion of edge rows in yield calculations will artificially boost yields. Edge-effects are reduced by separating plots with 'guard-rows' of the same or another cultivar, but this may not entirely prevent interference of different plot treatments. Long, narrow plots reduce trial error but have greater edge effects than square plots of the same area. A balance between plot size and level of replication must be reached.

The evaluation of results from CVT is a key part of the selection process. The data is frequently incomplete since the set of genotypes under test varies each year and between trials within any one year (Patterson & Silvey, 1980). Variation between cultivar yields can be attributed to several components:-

Between seasons within sites

Between sites within seasons

Between genotypes

Genotype x Environment interaction (G x E)

Gales (1983) reports on a survey of cereal variety trials in which coefficients of variation were 16% between sites within seasons and 11% between seasons within sites. The largest component (up to 59%) being the interaction of sites with seasons. Main effects and other interactions accounting for up to 14%. Talbot (1984) also showed that the Site x Season interaction factor accounted for the greatest variation in yield measurements (Table 1.2). While the effects of season can be large, this is dependent on the area chosen, for example, in Europe as a whole, site becomes a more important component of variance than season.

Table 1.2. Components of variance in variety trial results

	SPRING BARLEY	WINTER BARLEY
Years	1968 - 1978	1976 - 1980
Sites	26	9
Cultivars	75	52
Components of variance	t ha^{-1}	t ha^{-1}
Cultivar	0.021	0.13
Site	0.121	0.297
Season	0.132	0.057
Site x Season	0.531	0.508
Genotype x Environment	t ha^{-1}	t ha^{-1}
Site x Cultivar	0.013	0.024
Season x Cultivar	0.027	0.036
Site x Season x Cultivar	0.061	0.102
Error Term	0.1	0.098

Data from Talbot, 1984

Genotype x Site interactions can be handled by increasing the number of trial locations or the number of cultivars under test and by dividing a region into areas in which the interaction is minimal. Genotype x Season effects could similarly be handled by runnning the trial over a long period of years. The Site x Season x Cultivar term generally forms the largest part of the interaction.

Genotype x Environment interaction effects are much smaller than the site or season effects which account for a large part of the overall variation, both alone and in terms of their interaction and affect yield rather than quality. At its simplest, the interaction can be seen when considering two cultivars, one of which performs best in the first envionment, but worst in the second. Four main sources of G x E can be identified:

disease resistance, frost resistance, drought resistance and the timing of the life cycle to avoid stress. The small G x E interaction in barley (Fenwick, 1988) could be partly due to the wide adaptability of barley genotypes, although evidence has been found of genotype interaction with region, previous crop, soil type and fertility level. Trials to identify G x E effects would thus require very diverse sites to show up the interaction. Apportioning some of these interactions to factors such as region, soil type and rotational position is a long process since the number of field trials and physiological experiments involved escalates as each new factor is introduced into the investigation.

Traditionally, statistical modelling has been used to understand and explain the natural variation in crop performance but this does not lead to an understanding of the basic processes involved. The presence of a significant G x E interaction may be shown by Analysis of Variance (ANOVA) (Snedecor and Cochran, 1967). The ANOVA model divides the total squared deviations of trial means (SS) from the overall mean into main effects of Genotype and Environment (incorporating site and season), a G x E interaction, and, for replicates, an error term:

$$Y_{ge} = u + A_g + B_e + R_{ge} + E_{ger}$$

Y_{ge}	Mean yield of a genotype tested over a range of environments
u	Grand mean
A_g	Genotype mean deviation
B_e	Environment mean deviation
R_{ge}	Residual
E_{ger}	Error

The main effects in this model are additive by definition, but the interaction (residual from the additive model) is non-additive. The cause of the interaction is therefore not shown. The problem arises because the interaction contains a large number of degrees of freedom ((G-1)(E-1)), so that even if the interaction SS exceeds the main effects SS, the interaction Mean Square (MS) may be little more than the error MS and thus be declared insignificant (Zobel, Wright & Gauch, 1988).

Alternative statistical methods for trial result analysis have their own associated problems (Freeman, 1988). Principal Components Analysis (PCA) is a multiplicative model that does not adequately describe the main effects. Consequently the interaction factor, which is residual from the additive model, is not considered. Linear Regression (Finlay & Wilkinson, 1963) combines the additive and multiplicative models, but confounds the G x E with main effects as it considers multiplicative relationships between the genotype yields and the environment means, and vice-versa. When cultivars are regressed against environment, those which are relatively stable across environments will have a low slope ($b < 1$): those contributing more to the

G x E interaction will have a higher slope (b > 1), so this method does go some way towards investigating the cause of the interaction, provided extensive site and season results are available. A more effective and meaningful analysis would use an Additive Main effects and Multiplicative Interaction (AMMI), using ANOVA to examine the main effects, but then breaking down the interaction by PCA (Gauch, 1985; Zobel et. al., 1988). The addition of extra main effects into the model would reduce the G x E interaction term but add to the computation. Biplot graphical displays (Kempton, 1984; Campbell, 1988) can be used to illustrate the deviations from the mean, and identify genotypes with similar response to environmental factors.

An alternative to the statistical modelling solution lies in the prediction of crop performance using mathematical modelling techniques and expression of crop yield and performance in terms of a series of related mathematical equations. Simulation modelling can be used to interpret and predict the effect of different combinations of genotype and environment on crop performance and assess associated risks.

A model can catalogue experiences and pin-point reasons why a particular crop may fail to achieve its potential to enable optimum agricultural management strategies to be planned. It is often relative rather than absolute yield values which are of interest and the costs and benefits of multiple competing options can be studied. A model can be used to identify the particular processes of yield elaboration affected by a particular treatment. Its application will be restricted at first to situations with weeds, pests and diseases controlled. If successful, the study could extend to simulate the results from a broader range of agronomic field trials.

Modelling can be of great value as part of a carefully planned research programme in cases where it may be impossible or impractical to study the real world; measurement may disturb the real system, or field or laboratory experiments may be too costly or time-consuming (Dent & Anderson, 1971). However, this value must be measured against both cost of construction and ease of use.

The testing systems currently operated by the NIAB, SAC and DANI are very effective in identifying and providing information on cultivars which perform well over a wide range of seasons and sites, however, additional farmer-funded trials and National List trials under license have been required to provide information on the suitability of cultivars for particular locations and management situations such as soil type and position in the rotation. The co-ordinated system still falls short of the detailed requirements of individual farmers whose increased expertise in farm and environmental management demand an increased understanding of how cultivars respond to climatic and husbandry factors for the individual farm field. The erratic occurrence of disease, water and nutrient stress on the crop largely precludes their routine assessment during field trials, but these factors make an important contribution to field performance.

Increased communication is required between triallists and physiologists to determine both the extent to which the physiological knowledge acquired from a few cultivars can be applied to all cultivars, and also to consider the implications of physiological differences between cultivars for regional and specific cultivar recommendations.

The current field trials program for cultivar testing could be modified to generate descriptions of environment and cultivar required by crop models. This may mean setting up additional trials initially to establish appropriate parameters and methods of measurement, and an extension of trials to include some exceptional combinations of genotype and environment so that the scope of the model can be established. The ultimate goal is a reduction in the number of field trials required and an increased confidence in new cultivars or crop management schemes. One likely outcome is that a precise specification of data collection and recording methods for field trials is proposed to allow direct comparison between observed and predicted crop performance. The model can give then information on the growth of the whole crop (eg. gross yield) or used to investigate a sub-system within the crop such as development, water requirements or nitrogen balance.

2. THE MODELLING APPROACH

The rise in prominence of *simulation modelling* as a research tool in agriculture can be directly attributed to the advent and widespread availability of computers combined with an increased emphasis on mathematics and statistics in research together with the problems and cost of large scale field experimentation. Within modelling, there has been a shift in emphasis from *analytical* and *statistical* models to *simulation* or *dynamic* models (Jeffers, 1978; Csaki, 1976). Key modelling terms (in italic script) are defined in the glossary.

The first models of aspects of the farm system were economic models (Babb & French, 1963; Hardaker, 1967): models can now be found in the literature describing every aspect of crop production. Each level in the biological hierarchy of organisation is explored by the mathematical modellers, from the sub-cellular level to whole farm systems, but each group of modellers tend to work independently and design highly specific models with limited practical application. Models have been formulated for soil water and nitrogen balances (eg. Nye, 1973; Francis & Pidgeon, 1982, Addiscott & Whitmore, 1987), crop water use (eg. Feddes, Kowalik & Zaradny, 1978; Aslyng & Hansen, 1982), nutrient uptake (eg. Brouwer & de Wit, 1968), photosynthesis (eg. Duncan *et al.*, 1967; Day & Parkinson, 1982), canopy development (Goudriaan, 1988) and respiration (de Wit *et al.*, 1978). Models for whole plant systems draw on this work and provide a framework in which the component submodels can operate together. Probably the most widely used simulation-type model has been the Penman-Monteith equation which describes water use by crops (Monteith, 1965).

2.1. METHODOLOGY OF MODELLING

Simulation models may be *deterministic* (producing a unique solution dependent on proportions) or *stochastic* (many solutions dependent on probabilities) or a combination of the two (Carter *et al.*, 1982; France *et al.*, 1984). The stochastic model uses more computer time, since each simulation has to be repeated possibly thousands of times to echo the full range of natural variation and attach confidence limits to predictions. It can also require extensive data. The advent of parallel computing adds a new dimension to stochastic modelling and to *optimization* procedures. Biologists tend to prefer deterministic models because they are easier to interpret (Chalabi, 1991) but they may be inadequate for detecting changes in a random environment. Within the family of deterministic models, a choice lies between an *empirical* or *mechanistic* approach. The empirical modeller describes a level of biological organisation by experimental results; the mechanistic modeller describes one level by the mechanisms operating in the lower levels of the organisational hierarchy (France *et al.*, 1984). Stapper (1986) distinguishes four type of model based on the techniques used to formulate relationships (*empirical*, *phenomenological*, *correlative*, *mechanistic*). Alternatively, he defines five types based on the criteria of the elements modelled, the source of data and the model complexity (empirical, crop-weather, crop-growth, crop-system, crop-process). A combination of approaches may be used in any one model, which confounds precise model classification.

The mechanistic approach analyses the behaviour of a whole system in terms of individual components and their interactions, built from an understanding of their cause and effect. Many of the processes included are expressed in terms of empirical relationships, based on observation and experiment, with expression of the inherent variation in a set of mathematical equations. Empirical models often give better results, but the regression coefficients used may be crop and location specific. Certain parameters are conditional on the value of others and may have to be estimated, leading to correlation between estimates. However, the basic assumptions underlying relationships can be applied to other situations after careful adjustment of some parameters, or expression of the coefficients as functions of crop and location. Extrapolation of model results to other sites and seasons, for which the environmental data are less well defined or only partially observable, introduces inaccuracy.

Mechanistic models can be used to predict 'mean' crop behaviour or investigate the underlying biological principles, but stochastic models are required to analyse the variability. The random nature of some of the uncontrollable variables (Csaki, 1976) leads some modellers to the conclusion that every model should contain a stochastic element. The values of these variables depends on knowledge of the processes that occur during the growing season and not on a statistical analysis of the system.

The threefold purpose of modelling is summed up by Dent & Blackie (1979) as researcher, research, or application oriented. The modelling literature contains many papers on the development and validation of prototype models of crop systems, in some cases without a clear definition of objectives or justification of the modelling approach. Jeffers (1980) gives a check-list of points to consider in planning any model, and asks the fundamental question, "Are you satisfied that modelling of some part of the system through a formal statement of relationships in physical or mathematical terms will help in the achievement of the objectives of the research ?" A good model should be readily understandable, applicable, and easily adapt to new postulates (Csaki, 1976) and

1. Show a sound appreciation and understanding of the biological problems, though not necessarily including the intricate details
2. Show a realistic mathematical representation of the important phenomena
3. Find a solution, quantitative if possible, of the resulting mathematical problem
4. Give a biological interpretation of the results.

2.2. ADVANTAGES AND DISADVANTAGES OF MODELLING

The modelling approach has both advantages and disadvantages over more traditional analytical methods and makes an important contribution to agronomic research. A model is easier to manipulate than the real world enabling crop management decisions to be evaluated without recourse to field experimentation. The model reduces the complex real world to manageable proportions by the use of a few parameters that can be measured accurately. Potential crop performance can be assessed for any situation, with the results used to identify areas in which crop husbandry might be improved.

A good model should highlight gaps in our present understanding and stimulate new ideas to investigate relationships and formulate and test hypotheses. As the complexity of a model increases during its development it requires greater structure and its sensitivity to any one parameter decreases (Penning de Vries & van Laar, 1982). In principle, models are themselves testable hypotheses (Passioura, 1975), and as such can be treated in the same way as other research hypotheses - they can be examined by experiment that others are able to repeat and verify, and be backed by documentation in a reputable scientific journal. In extreme, models can be used to explore systems that do not exist in nature.

A model summarises research knowledge in an accessible form and can be used to aid decision-making by the agricultural adviser or farm manager (France *et al.*, 1984). It can be used to access and accumulate the results of experimental work and give a method for interpolation, careful extrapolation and prediction of crop results under a range of potential conditions (Stapper, 1986). Once developed, relatively minor modifications may enable a model to be used to study problems beyond the scope of the original design. The modelling approach also encourages communication and co-operation between disciplines (IBSNAT, 1986a; Dent & Anderson, 1971), and forces thorough, objective study.

However, there are several disadvantages to the modelling approach:

There is great difficulty in proving a model 'true'. The lack of suitable data for model development and *validation* is a common problem: realistic interpretation of results relies on the validation with independent data (Ritchie, Otter-Nacke & Godwin, 1984). The initial specification of the model is often influenced by data availability - a model built on data which is only partially observable or available has little chance of practical application. Generally speaking, the simpler the model, the greater its chance of application. Problems may arise if variables such as rainfall are expressed *stochastically*, which in theory have a *continuous distribution*, but become *discrete* due to the sampling and recording methods. Long runs of data, for example weather data recorded over 25 years, exhibit a lack of smoothness due to the sampling, rather than the underlying process. To counteract this, some of the data may have to be mathematically 'smoothed'. One could equally well use a fitted theoretical distribution to describe stochastic elements in the model (Dent & Anderson, 1971). The purely empirical part of any model reduces its application to different climate or soil conditions (Seeman *et al.*, 1979), however, the non-empirical part requires collection of detailed environmental and physiological data.

There is a strong temptation to adjust the model parameters until a 'good fit' is obtained with test data, if necessary by altering some of the relations upon which the model is built (Passioura, 1975). This may not improve the model performance when it is validated using independent data. A model which simply echoes the results of a field experiment has not added to our understanding and the data would be better described by conventional analysis. Model development is very time consuming and expensive and should only be used if the problem cannot be solved by simpler techniques (Wright, 1971). Ralph (1982) described a new irrigation model for soya beans in Australia which recommended an application of 2m litres ha^{-1} water to produce the best long-term profits - a figure which the authorities had been recommending for many years as standard allocation.

Speculative assumptions may be given credence by their use in a respected model. Passioura (1975) predicted a 1 in 3000 chance of producing a correct model based on just five such speculations. There is also the danger of the 'tyranny of the mean' - farmers relying too heavily on models built using average data for decision making, can expect only average performance as a result. There is no such thing as a 'correct' model: the model that has to integrate all the details of plant growth will be as complicated as the plant itself (Brouwer & de Wit, 1968).

2.3. MODEL CONSTRUCTION

Carter *et al.* (1982) give a brief account of model methodology, summarising model construction and testing, by reference to a model to predict outbreaks of wheat grain aphids. The starting point for any model should be a clear statement of the research objectives which should combine the requirements of the end user with the amount and precision of the input data and provide points of reference throughout model testing. The model requires only the level of detail and accuracy necessary for its developer's purpose.

The modeller defines a *system*, with a finite boundary, as a limited part of reality (de Wit & Goudriaan, 1978) containing independent and interdependent elements, or *variables*. A *model* describes this system, not necessarily in mathematical terms. The system boundary establishes the *scope* of the model (Kimmins & Scoullar, 1984). The *resolution* of the model refers to the level of detail it covers, and its *complexity* is a combination of scope and resolution. Complexity is partly governed by the storage capacity and speed of the computer: greater complexity usually requires more input data and computational time without always giving improved performance. Whilst low complexity may be sufficient to predict final grain yield, more complex models are needed to investigate individual plant processes. There is a danger that in trying to encompass all the current understanding of the underlying principles, models become too large and unwieldy to be properly evaluated (Passioura, 1975), whilst over-simplification of complex phenomena may make the model unrealistic (Kimmins & Scoullar, 1984). Excessive detail may hide the significance of results, or properties of the mathematical functions used become confused with the true nature of the system.

Mathematical modelling of the system involves five stages

a. definition of variables
b. choice of continuous or discrete time
c. rules for transformation of the variables through time
d. programming and testing of the model
e. *sensitivity analysis*

The problem is first specified in detail using relational diagrams to identify any obvious linkages between sub-systems and relationships between the main variables. This identifies the type and form of data required. Formulation includes definition of the variables within the system boundary, and the expression of the measured variation in precise mathematical relationships. The evaluation of this 'model blueprint' (Muetzelfeldt *et al.*, 1989) is an on-going process.

The system is described as a set of *state variables* (eg: leaf area index, dry matter, yield), which in the *dynamic*, or *simulation* model, are updated at a certain time interval by *rate variables*. Values of rate variables are dependent upon external *forcing*, *exogenous* or *driving variables* and internal *auxiliary variables* drawn from the current state of the system. The forcing variables represent the only contact from beyond the system boundary. Some are controllable by management (eg: fertiliser application, sowing date), others such as rainfall, solar radiation and temperature are uncontrollable. 'Auxiliary' variables (cf. de Wit & de Vries, 1983) are those calculated from other variables, for example, the average assimilation rate.

The processes of crop growth and development are described by a series of rules, expressed as mathematical equations integrated over time. Most biological systems are non-linear, but simplifying them by linear models reduces the complexity of the sensitivity analysis. In continuous time, rules are expressed as a set of *k* differential equations, giving a rate of change for each of *k* state variables over time.

$$\frac{dX_1}{dt} = f_1(X_1, \ldots X_k)$$

$$\frac{dX_k}{dt} = f_k(X_1, \ldots X_k)$$

Discrete time intervals can be modelled by a set of recurrence equations for each variable:

$$X_{1,t+1} = g_1(X_{1,t}, \ldots X_{k,t})$$

$$X_{k,t+1} = g_k(X_{1,t}, \ldots X_{k,t})$$

where each variable is updated as a function of the variable values at the previous time interval. The value of the state variable at time *t* can be computed. Either:

1. a complete general solution is possible, with the equation written as an explicit function of time if the model is simple enough, or
2. no complete general solution is possible: several possible stable or unstable solutions.

In practice, the classification of processes as continuous or non-continuous depends on the nature of the observations. If the discontinuities are less frequent than the observations, there is no advantage in modelling in discrete time intervals. The choice of time scale for dynamic models is dictated by the complexity required. Time can be measured in real time, or in some developmental time scale. Brouwer and de Wit (1968) use an interval of 0.05 day; Hough (1975) used 10 day mean weather data; Ritchie *et al.*, (1984, 1987) and Jones and Kiniry (1986) used the phyllochron ('the time interval between the appearance of two successive leaves above the ligule of the previous leaf' : Faivre & Masle, 1988), measured in degree days above a certain base temperature, as the time scale for their developmental sub-models. Generally, the more detailed the model, the shorter the time scale, with an interval of one day being the most common in whole crop models. The advantage of using a daily scale is that the model results can be compared more readily with field or laboratory observations.

The model is built using historical data from a wide range of field experiments conducted over different environments and seasons. Data from a single series of experiments could be more accurately described by a statistical or correlative model, but extrapolation of the results would be less reliable. Many years of climatological data are necessary, since the return period for infrequent, or random events like periods of drought, prolonged frost or snow may be several years. For such variables, data on their frequency of occurrence may play an important role. For evaluation of phenological observations, data is required on the duration of developmental phases over a number of sites in one year, in comparison to other years, and on their duration at one site over a number of years, in comparison to other sites. Also of importance are the extreme dates for start and finish of developmental phases over all sites and seasons measured (Seeman *et al.*, 1979). The apparently random nature of some weather parameters, together with the large volume of historical data that may be required, argue the case for using weather generators, based on the probability distributions of the variables taken from historical data (Dent & Blackie, 1979).

2.4. MODEL PROGRAMMING

The choice of programming language lies between general purpose, widely available languages (FORTRAN, BASIC, C++, PASCAL, PL/1, ALGOL, etc.) including functional and logic programming languages (LISP, PROLOG etc.) or the more expensive, special purpose simulation languages (SIMULA, CSMP, GASP etc.). Each has its advantages, but none is ideal. Special purpose simulation languages are quickly compiled and efficient in terms of computer time and memory use, with special data input and output provision. Numerical methods such as integration are particularly well handled. Editing, debugging facilities and graphical output displays are other advantages claimed in the literature, but these are also available for both main-frame and microcomputer implementations of general purpose languages.

Dent & Blackie (1979) distinguish two kinds of special purpose language, the integrating or continuous languages such as CSMP/1130, DYNAMO, SIMULATE and FORDYN and the non-integrating or discrete languages such as GPSS, SIMON, SIMSCRIPT, SIMULA. Many of the Dutch models have been written using CSMP - a language which contains FORTRAN 77 as a subset, but has additional functions for integration, or a related language, DYNAMO (DYNAmic MOdelling Language). ACSL (Advanced Continuous Simulation Language) allows model equations to be entered in any order, before sorting them into the optimum order for evaluation.

The logic programming language, PROLOG, has also been used to systematize modelling knowledge (Muetzelfeldt *et al.*, 1989; Muetzelfeldt, 1991) and interpret the problem description to generate a model program. One of the most useful features is that of back-tracking to enable the user to trace the model's decision path. It also has access to a set of dialogue and graphics routines. C is often the programmer's choice because of the additional data structures offered, but FORTRAN remains the most widely used language by modellers within the United Kingdom because data are more easily transferred between computer systems and programming expertise and guidance are readily available. Double precision numeric data reduces the error where very small or very large numbers are used in calculation. FORTRAN programs can easily be linked to expert system shells (SMALLTALK, CRYSTAL etc.) or to parallel programming applications (OCCAM etc.) which increases their versatility. This can add window, screen and database management support programs which are already well developed for other implementations. However, graphics are easier to program in BASIC, and thus more than one language may be used in a model (eg. PNUTGRO, Boote *et al.*, 1988)

Whichever language is chosen, a model should be written in a 'user-friendly' form with sufficient, simple user guide and documentation for a non-specialist to use (Wilson, 1991). Once the model has been formulated, programmed and tested satisfactorily, the user interface must be carefully planned, as this will play a large part in determining the usability of the model, and the ease with which the model program can be linked to other routines, updated and maintained. The Windows programming environment lends itself particularly well to linking model elements and is rapidly becoming more accessible, offering more sophisticated methods of object embedding.

Key features of good programming include:

- Functional description - to build a conceptual understanding of the model
- Installation and start-up procedures - simple enough to keep the computer 'Luddite' interested
- Example walk-through - particularly for input file structures

- Error trapping - giving helpful error messages on screen, cross-referenced to the User Guide and trapping errors in user input
- Tables of contents, glossaries and indexes - providing task-oriented and command-name listings
- Clear programming style - comment lines within the program code, pre- and post-conditions for each subroutine, data type, unit and status of each variable, meaningful variable names and version number and date of production
- Clear screen appearance - defined areas for input, output and error messages, uniform throughout the program, give a professional look (Ormerod, 1991)
- Simple input file structure
- Graphical support for displaying model results

2.5. MODEL TESTING

Verification and *validation* are seen as synonymous in some of the literature. Verification of the model compares the structure and general behaviour with reality. The model is checked for mathematical and logical correctness against the design objectives to ensure that it behaves as intended. Inaccuracies in the model may provide the basis for cautious 'fine-tuning' of equations or parameters, but this may obscure errors or incompleteness in the implicit assumptions on which the model is based. Alteration of the parameters to improve the model performance can degenerate into an expensive method of curve fitting (Loomis *et al.,* 1987). Errors of programming, data handling or operation should be corrected during the on-going process of model testing and development. Validation is the more rigorous statistical comparison of predicted results from those from independent observation and calculation of confidence limits. Deviation in the simulated results from those obtained by experiment illustrate the inadequacy of the current understanding of the basis physiological processes at work in the system.

A model should be subject to sensitivity analysis throughout its development to study the effect on model output of small changes in the structure and formulation of relationships or parameter values, to gain a full understanding of the processes governing model output. When the user makes a primary change, the model should cope with the various ramifications of that change. A sensitive parameter is one which causes a major change in output. There are naturally sensitive parameters in the real system which should show up in the model. The analysis provides guide-lines for validation and indicates priorities for conventional research.

The main costs of modelling occur primarily during the testing stage. Labour costs will form the largest part depending on the number of specialists required, but model building relies on results from field and controlled environment experiments to measure parameters, so the burden of field trials is initially increased. Indeed, whereas observations are only made at key growth stages in the CVT programme, regular, frequent measurements must be made to gather information on, for example, the effect of environmental factors on the rate of photosynthesis, or development of green leaf area, rate and duration of spikelet development, or grain fill. The more complex the model, the greater the cost of its construction and maintenance.

2.6. CRITERIA FOR JUDGING MODELS

The success of the modelling approach depends on its ability to extrapolate field trial results accurately, including simulating the consequences of G x E interactions, and to form a cheaper, widely available complement to field trials. The model should be able to echo the results of actual field trials in each season as a continual check on its performance, but should also predict results for other cultivars and environments not tested by the particular series of field trials so that it can be used to compare alternative management strategies for crop production. It can be used to explore the response of the system to changes in the level of a single input, or combination of inputs in a sensitivity analysis, or the estimation of inputs for optimal input. Here regression methods are used to estimate a function that relates input to output, and the function can be maximised or minimised to obtain the optimum input levels.

The simplest experiments can be performed on models with few variables to work with. Evaluation of the results of deterministic models is also easier than evaluation of stochastic models, where the effects of experimental changes may be obscured by random elements in the model. A deterministic model can be made to resemble a stochastic one by repeating the experiment several times with different parameter values for the variable in question. ANOVA can be used to analyse the results providing the statistical assumptions of homogeneity, independence and normality are satisfied.

Statistical criteria such as F tests or Runs tests provide objective means of testing the fit of models. A correlation between predicted and observed results of +/- 5% variability can be valid since there is proportionally greater natural variation in such attributes of the crop as yield and ripening date (Seeman *et al.*, 1979). Errors in field trial technique, or differences in definition of terms of measurement may also cause 1% of the results to be outliers (Nelder, 1972). Thus, even if model results swing significantly from observed data it need not necessarily be rejected; it might act as a first approximation until such time as a more reliable model is formulated. Dillon (1971) gives an entertaining warning against placing too much importance on the statistical significance of model results in the context of decision-making, since there are likely to be subjective assumptions in the model which reflect the designer's own strengths of conviction. One of the main problems for the modeller is the unpredictability of weather, despite the fact that it obeys well-defined physical laws.

The remainder of this thesis describes the search for a suitable crop growth model for Scottish barley growth and development, and the collection of data and adaptation of existing models to local conditions. Assessment of the models was by two techniques:

a. simple regression between observed and predicted measurements. An error level due to the formulation of the model of 10% was considered unavoidable due to the uncertainty of some of the underlying relationships in the crop system. This brought the overall model acceptance level down to $r^2 > 84\%$.

b. the proportion of the simulations within 1 standard deviation of the mean of observed measurements.

3. METHODOLOGY OF CURRENT MODELS

Most of the published research on whole-crop models relates to maize, soybeans, rice and wheat rather than barley. However, wheat and barley are both temperate C3 crops from the same plant family and share many common features of growth and development. They are often grown sequentially on the same farmland and require similar husbandry (Russell, 1990; Russell & Wilson, in prep.). Thus work on wheat modelling is of direct relevance to this project. Similarly, aspects of environmental modelling, such as movement and uptake of soil water and nutrients may apply to a wide range of crops. Using a wheat model for barley depends on the two crops having a similar response to factors such as temperature, daylength, water and nutrients, and morphological and phenological differences being embraced by minor modification of parameters rather than alteration of the model structure.

3.1. DIFFERENCES BETWEEN WHEAT AND BARLEY

Winter barley is generally sown earlier than winter wheat to give it a better chance of strong establishment before winter, because it is less hardy than wheat. Similarly, spring barley will be sown later than spring wheat. This has the secondary purpose on the farm of staggering field operations for greater efficiency. The early development of the two crops will thus be under slightly different temperature and daylight regimes.

Barley develops fastest in the early stages (Kirby & Appleyard, 1984) and remains vegetative until 3-6 leaves have emerged on the main shoot (cf 4 - 8 leaves in wheat) and tends to reach double ridge stage sooner (depending on season and cultivar). Stem elongation begins earlier in barley, at the lemma primordium stage (cf floret primordium stage in wheat), however, barley then takes longer to reach Maximum Primordium Number (MPN) than wheat to reach the equivalent stage of Terminal Spikelet (TS). At this stage the barley ear has typically 45 spikelet primordia, initiated more rapidly than those of wheat, but some 15 spikelets subsequently fail to become fertile. The wheat ear at this stage has about 20, larger, spikelets, each with 8 - 10 florets. Later developmental phases are of similar length in the two crops.

Changes in partitioning of assimilate between roots, stem, leaves and grain are associated with progression through the phenological stages. Thus differences in development rate may affect the evaluation of final yield and its components, although the morphological differences are relatively small.

Grain yield is more highly correlated with grain number per ear than with the number of ears per unit area or grain weight, however, higher grain weights in wheat contribute to the higher yields acheived. In barley, the final grain number is determined by anthesis, but in wheat, may be influenced by environmental conditions during the following week. Most spring barley cultivars are closed-flowering types, which makes it more difficult to tell the exact date of anthesis than in open-flowering winter barley or wheat cultivars and thus makes the accuracy of models in predicting this date harder to assess.

Greater variation in final yield and its components is attributable to site and season than genotypic effects within either crop. The use of a wheat model for barley can be further justified by a lack of precision and confidence in the equations used to model the mechanisms of crop growth and development.

3.2. SURVEY OF CURRENT MODELS

Crop models vary in complexity from the Hough's (1975) simple 7 component model using the matrix approach, whereby Principal Components Analysis is used to summarise meteorological effects on barley, to the complex models of Ritchie *et al.* (1984, 1987) and Jones & Kiniry (1986). The UK ARCWHEAT winter wheat model (Porter, 1984; Weir *et al.*, 1984), the Australian wheat model, SIMTAG (Stapper, 1984), the Dutch models (e.g. BACROS, de Wit, *et al.* 1978; ARIDCROP, van Keulen, 1985; WOFOST, van Keulen & Wolf, 1986) and the American CERES wheat model (Ritchie *et al.* 1984) are amongst the better known in the UK (Table 3.1).

"Crop-process" (Stapper, 1986) models describe many aspects of crop growth and development, however, small errors may add up to an unacceptably large deviation of the predicted yield from that observed. They do however, have the advantage of being applicable to a wide range of environments and seasons and thus this type was chosen for further study. Publication of the many simulation models has confirmed that, at least for particular applications, crop-process mechanistic modelling can be an efficient and/or informative practice. This begs the question: 'Is there a suitable existing model for Scottish barley which can distinguish between cultivars and handle G x E interactions as well as the main effects due to site, season and cultivar ?'

Not all wheat or barley models were studied in the same detail, partly because many models are little more than research prototypes, lacking comprehensive documentation.

Of 167 agricultural models registered in the UK (Squire & Hamer, 1990), most were still in the development stage, with approximately half cited as being used for research purposes only. Of 15 models of cereal plant production, only 2 are developed to the level of use for advisory, educational or managerial purposes, and none of these were for barley.

Table 3.1. Survey of general crop, wheat and barley models

CROP	MODEL	REFERENCE
GENERAL	PHOTON	de Wit *et al.*, 1971
	ELCROS	Brouwer & de Wit, 1968
	DAISY	Hansen *et al.*, 1990
	BACROS	de Wit *et al.*, 1978
	***	Baier, 1973
	WOFOST	van Keulen & Wolf, 1986
	DAISY	Hansen *et al.*, 1990
WHEAT	MAQUARRIE	Morgan, 1976
	LA TROBE	Goutzamanis & Connor, 1977
	TAMW	Maas & Arkin, 1980
	ARCWHEAT	Porter 1984; Weir *et al.*,1984
	SIMTAG	Stapper, 1984; Stapper & Harris, 1989
	WERRIBEE	O'Leary *et al.*, 1985
	FUNGIC	England, 1985a, 1985b
	SPRING WHEAT	van Keulen & Seligman, 1987
	CERES WHEAT	Ritchie *et al.*,1984
	EPIC	Cabelguenne *et al.*, 1986
	PACV	Reinink *et al.*, 1986
	NWHEAT	Groot, 1987
	***	Andrew, 1987a, 1987b
BARLEY	***	Hough, 1975
	WATCROS	Aslyng and Hansen, 1982
	CERES BARLEY	Ritchie *et al.*, 1987

The CERES barley model was the first model investigated since a copy was obtained at the start of the project and advice given in its use by two of the authors (Godwin & Otter-Nacke, pers. comm.). It was the only barley model found which distinguished between genotypes and also included a variety of options for nitrogen and water balance calculation. Growth and development aspects of two wheat models were studied for comparison: the ARCWHEAT winter wheat model and the van Keulen and Seligman spring wheat model, despite differences in morphology and development between the two crops. Each model operates on a daily time scale so was compatible with weather data collected at trial sites in Scotland.

In an attempt to standardise the approach of crop system modellers, the IBSNAT projects rigidly define the inputs and outputs from a set of 10 crop models written in FORTRAN, so that sharing of (at least) soil and climate data between modellers of different crop species can be achieved. The models use common program modules for input and output, soil water balance and calculation of nutrient availability, which conform to the data definitions laid down in the IBSNAT recommendations (IBSNAT, 1986b, 1988, 1990). They differ only in details of crop growth and development. This structure has the advantages of supporting separate validation of the subsections, the transfer of data between researchers and the option of adding modules to include pest or weed competition, post-maturity losses etc.

This philosophy is encompassed in the CERES family of models. The soybean (BEANGRO, Hoogenboom *et al.*, 1990), peanut (PNUTGRO, Boote *et al.*, 1988), wheat (Ritchie *et al.*, 1984) and maize (Jones & Kiniry, 1986) models have been tried and tested over a wide range of latitudes and soil types (eg. Hodges *et al.*, 1987; Carberry *et al.*, 1989) and predict crop yield and performance better than most other models of their type. The CERES barley model is based on the CERES wheat model from the US Department of Agriculture, Crop System Evaluation Unit at Temple, Texas. It is heavily based on the FORTRAN code of the wheat model, with small modifications to some parameters. This model has not yet been fully validated or documented although it is being used for research at several centres.

The crop is viewed as a population of individual plants in which the overall yield is the product of the yield of a single plant and the population density. Genetic specific coefficients are used to account for cultivar differences in the rate and timing of development and in sensitivity to cold and photoperiod and thus cater for both spring and winter cultivars. It is a phasic model in that the growth cycle of the crop is divided into developmental phases, with each phase distinguished by its own parameters for growth rate and dry matter partitioning, modified by cultivar, weather and water and nutrient availability. The model can be run under the assumption that water and nitrogen area non-limiting for all plant processes.

ARCWHEAT was the result of a collaborative project involving four (originally) AFRC funded research institutions (PBI, LARS, Letcombe and RES) to model winter wheat growth and canopy development in the UK. The FORTRAN model uses time, temperature and daylength as driving variables and includes soil water and nitrogen movement and effect on plant growth. Other environmental factors are assumed to be optimal and the crop to be healthy. Photosynthesis, respiration and canopy growth are treated in greater detail than the CERES models. Field studies of tillering and shoot growth were used to provide empirical rules for canopy development.

The van Keulen and Seligman (1987) model is a deterministic, modular, crop-process model essentially to model the water use and nitrogen nutrition of a spring wheat crop. Crop development was of particular interest in that different methods were used to predict intermediate stages of phenological development.

ARCWHEAT and the van Keulen and Seligman models were not tested in their entirety because they used a number of parameters related specifically to wheat which could not be assumed to apply to barley winter and spring cultivars. They were studied to look for alternate methods for modelling those aspects of crop production, and phenological development in particular, which had given cause for concern in the CERES barley model. Equations were extracted from the models out of context, and programmed for the data sets of the barley database (Chapters 5 and 6).

3.3. ELEMENTS OF MECHANISTIC MODELS

The seven chief elements of a deterministic, mechanistic, process-oriented model are:
1. input routines for soil, weather and crop data
2. simulation of soil water availability
3. simulation of soil nitrogen availability
4. simulation of phenological development
5. simulation of root, leaf, stem and grain growth
6. calculation of components of yield
7. output routines in which the results are displayed, saved to file and printed

3.3.1. MODEL INPUTS

Model inputs fall into three categories:
a. Measured, known variables - latitude, altitude, sowing date, fertilisation, irrigation
b. Measured, unpredictable variables - rainfall, solar radiation, temperature
c. Unmeasured, predictable variables - soil moisture and nutrient availability, crop residues

Models which estimate the majority of parameters they require will be the most widely and easily applicable. The use of interactive data entry routines which enable parameter values to be altered during the run of the program, or successive runs to be made with different values have an added advantage for model testing. Expert system technology may provide methods to drive the model and interpret the results. Menu driven interfaces with comprehensive error checking are the most reliable for single model runs but are inefficient for multiple runs to systematically vary certain input values. In this case, files, spreadsheets or database systems provide quicker access to the model. Spreadsheet-based interfaces using the features of the software for easy input file creation and output file viewing may increase the feasibility of use of PC-based models on-farm by crop production managers in testing management strategies, but spreadsheet macro programming has some limitations compared to compiled programming languages, notably in speed of execution.

The Decision Support System for Agrotechnology Transfer (DSSAT) from IBSNAT provides users with access to data on crops, soils and weather, CERES crop models and expert knowledge (IBSNAT, 1986b, 1988). Collaborators developed the concept of a Minimum Data Set to compare crop productivity between different locations, and programs in the DSSAT can convert this data from a database system to the input formats specified by the models. This approach was found particularly useful when the required input file structures were complicated and was adopted for this project.

3.3.2. SIMULATION OF SOIL WATER AVAILABILITY.

Many models of soil water availability are based on the work of Penman (1948) in which the potential evapotranspiration rate (E_t) is related to the evaporation rate from a free water surface (E_o) by the equation:

$$E_t = f.E_o$$

The crop factor (f) is related to the crop development stage, height and genotype, whereas E_o is dependent on the temperature, humidity and solar radiation. Actual transpiration rate (E_a) is related to potential transpiration by a factor which indicates the level of stress. The Penman-Monteith equation (Monteith & Unsworth, 1990) that calculates E_a directly, requires additional data on wind speed and vapour pressure.

de Wit & van Keulen (1972) model transport of heat, water, solutes and gases in soils. Their work on water movement illustrates the general principle used in many models of dividing the soil into homogeneous compartments or layers. A widely-used basic model for incrementing soil water (θ) in the rooting zone over time (t) is

$$\theta_{t+1} = \theta_t + P + C - E_a - D - R$$

P	precipitation + irrigation (surface layer only) or infiltration from layer above
C	capillary rise from layer below
D	drainage to layer below
R	runoff (surface layer only)

Water reaching the surface as precipitation or irrigation is assumed to successively wet each soil layer to field capacity with excess draining to the layer below (the cascade approach). All irrigation water infiltrates into the surface layer. The duration and intensity of rainfall events are not considered.

The CERES models divide the soil into up to 10 layers. Movement of soil water into any one layer is restricted by the saturated upper limit (estimated as field capacity) of the layer. Movement out of the layer by drainage, or evaporation from plant or soil is restricted by the drained upper limit, and the lower limit of available plant water (estimated as wilting point) for that layer. These values depend on soil type and are read into the model as inputs. Water supply to the roots is related to the soil water potential and the rooting depth and density, it is 'available' to the roots between -5 kPa (approximate field capacity) and -1.5MPa (approximate permanent wilting point). Three soil water deficit factors are calculated from the ratio between soil plant extractable water content and root water uptake required to satisfy the potential transpiration demand. These take values from 0 to 1 (0 - severe limitation, 1 - no water deficit) and are used to modify potential crop growth. Provided transpiration is less than water uptake, water availability does not limit dry matter production or partitioning. If transpiration accounts for more than two-thirds of water uptake, then leaf area expansion and tillering are affected.

The van Keulen and Seligman spring wheat model uses plant nitrogen status to influence water uptake such that water use efficiency (dry matter produced per unit of water uptake) increases with nitrogen availability. This is achieved by a decrease in stomatal resistance as leaf nitrogen level increases. The ratio between actual and potential transpiration (van Keulen, 1975) is used to modify assimilation rate as in other models. However, the effect of prolonged stress is included as a cumulative relative transpiration deficit which may affect crop growth. Rooting density is not considered a limiting factor to water uptake.

3.3.3. SIMULATION OF SOIL NITROGEN AVAILABILITY

Soil nitrate and ammonium levels are in a state of flux throughout the growing season, as the continuous processes of nitrification, denitrification, mineralisation and volatilization are highly dependent on the weather conditions, notably temperature and rainfall. Nitrogen levels influence crop yields greatly, and the effect of nitrogen level on crop production is an important research area (eg Jenkinson & Smith, 1988). The main assumption in modelling is that deficiency in major nutrients, including nitrogen, alters the partitioning of assimilate to increase the root fraction, and reduces the photosynthetic area and growth rate of the crop (Andrew, 1987b).

The general structure of Beek and Frissel's (1973) simulation model of nitrogen availability is representative of many others, and utilises the compartment principle outlined above for soil water modelling. All nitrate in any one soil layer is in solution uniformly throughout that layer. Nitrate and ammonium are considered separately, since nitrate is intensively leached from the soil complex in the soil water, whereas ammonium is assumed to be adsorbed completely. In this simple model, ammonium is nitrified directly to nitrate; intermediate stages, or absorption of ammonium by nitrifying bacteria are not included. Fresh organic material is divided into six fractions (humus, proteins, sugars, cellulose, lignin and biomass): decomposition of each fraction is treated separately. Nitrogen fixation from atmospheric nitrogen and denitrification are not considered. The rates of the various processes are dependent on soil water content, temperature, and relative concentration of ammonium and nitrate in the soil. The model can be summarised as follows:

$$A_{t+1} = A_t + M - N_f - C$$

A_t	amount of ammonium in soil layer at time t
M	mineralisation of organic nitrogen into ammonium
Nf	nitrification of ammonium to nitrate
C	consumption of ammonia by the biomass

$$N_{t+1} = N_t + N_f + M + L_a - L_b - I - U$$

N_t	amount of available nitrate in the soil layer at time t
L_a	leached into layer from above
L_b	leached into layer below
U	uptake by plants
I	incorporation of inorganic nitrogen into biomass

van Keulen and Seligman (1987) have developed this model for a dryland application, and divide soil nitrogen into four components:

a. mineral nitrogen, including nitrate, nitrite and ammonium
b. nitrogen in fresh organic material
c. nitrogen in stable organic material
d. nitrogen in the microbial biomass.

Transformation of organic nitrogen to nitrate can then be treated as a single process. The fresh organic material is divided into three fractions according to the ease with which it is decomposed - easily decomposable, moderately decomposable and resistant to decomposition. The uptake of nitrate by the plant is controlled by root distribution through the soil layers, soil nitrate concentration, and plant nitrate demand. Uptake ensues from the transpiration flux and from diffusion in the root zone. Total uptake is limited by the capacity of the plant transport system, and available nitrate in soil layers above plant wilting point.

The CERES models include the process of denitrification:

$$N_{t+1} = N_t + F + M + N - D - L$$

F	input from fertiliser (includes hydrolysis of urea fertilisers if appropriate)
M	mineralised from organic matter
N	nitrification from ammonia
D	denitrification
L	leaching loss

Nitrogen availability is compared with potential demand to calculate two soil nitrogen deficit indexes. These take values from 0 - 1 (0 - no available nitrogen, 1 - no deficit), and are used in conjunction with the water deficits to modify potential growth rates.

3.3.4. SIMULATION OF PHENOLOGICAL DEVELOPMENT

Models commonly simulate phenology by assuming that key stages in crop development are reached after the passage of a certain thermal time interval, measured in degree-days above a specified base temperature (T_b) below which development ceases. Models differ in the values for T_b and thermal time intervals used, depending both on the maturity of the crop and the model origin. All models commonly predict emergence and anthesis, but the number of intermediate stages recognized varies between models. Intervals for wheat models for the period germination to emergence range from 70°Cdays, T_b 2°C (CERES) to 150°Cdays, T_b 1°C (ARCWHEAT). Values for the period from emergence to anthesis range from 490°Cdays, T_b 3°C (SIMTAG) to 1141°Cdays, T_b 2°C (WERRIBEE). The value may be modified by stress or vary with the genotype (CERES).

The period from anthesis to maturity is one of the most difficult to quantify since the final stage is one of physical drying and is highly dependent on the weather. Some models predict only to achievement of maximum dry weight (CERES, SIMTAG), which may be two to four weeks before harvest, and others predict to maturity, defined as 15% grain moisture content (ARCWHEAT, LA TROBE, CABO).

The CERES barley model divides crop development into nine distinct phases and tie apical development to leaf number by measuring duration of development phases in phyllochrons. A vernalisation factor, accumulated daily whilst the minimum temperature is above 0°C and the maximum temperature below 15°C, is used to determine the period from emergence to MPN. Transition is as follows:

8 **Germination** occurs if there is sufficient soil water at the sowing depth within 90 days of sowing

9 **Emergence** occurs after a certain thermal time interval, dependent on sowing depth ($T_b = 2°C$)
Thermal time to emergence = 50 + (10.4 * Sowing Depth) °Cdays

1 Maximum Primordium Number (MPN) - occurs when 300 Thermal Development Units (TDU) have accumulated, modified by sowing date. Each TDU is a function of accumulated temperature from emergence (T_b = 0°C), reduced by incomplete vernalisation and genotype daylength sensitivity.

2 Beginning of ear growth after 225 °Cdays

3 End of pre-anthesis ear growth after 150 °Cdays

4 Start of grain fill occurs after 200 °Cdays have passed since the end of pre-anthesis ear growth. Ear Emergence occurs 60 °Cdays into this phase.

5 End of grain fill equivalent in the model to the date of physiological maturity - determined by a genetic coefficient ranging from 300 °Cdays to 540 °Cdays (T_b = 1°C).

6 Harvest date not predicted by the model.

ARCWHEAT measures pre-emergence and post-anthesis phases in thermal time, but photoperiod and vernalisation effects are incorporated between emergence and anthesis. Van Keulen and Seligman (1987) base their model of phenological development on controlled environment measurement of temperatures required to reach each stage of development. Development is divided into pre-anthesis and post-anthesis phases, with intermediate stages of development expressed as a proportion of the duration of the total length of the phase (Table 3.2). Thus the rate of development during each phase can be integrated to give development stage directly. Duration of each phase is linearly related to mean temperature during the phase. The sowing to emergence phase is treated separately.

Table 3.2. The van Keulen and Seligman development model

Phase	**Proportion of thermal time**	
	pre-anthesis	**post-anthesis**
Floral Initiation	0.22	
Spikelet Differentiation	0.24	
Stem Extension	0.35	
End of tillering	0.5	
Terminal Spikelet	0.52	
Anthesis	**1.0**	
Start of grain fill		0.11
End of grain fill		0.7
Maturity		**1.0**

Expression of genotype

Differences between cultivars are primarily modelled by their effect on development. Differences in photoperiod sensitivy and vernalisation requirement will result in different rates and durations of the vegetative phase. Differences in grain growth rates and kernel size will affect the rate and duration of grain fill. Earliness of maturity will affect the date of physiological maturity and harvest.

The CERES barley model uses six genetic specific coefficients to describe cultivars, scaled to unitless values between 0 and 10.

P1D sensitivity to photoperiod - estimated from the date of ear emergence, since more sensitive cultivars take longer to reach ear emergence. The time from MPN to ear emergence is constant in the model so differences in the date of ear emergence are due to variation in the date of floral initiation and MPN. Low values indicate early ear emergence, high values, late ear emergence.

P1V vernalisation requirement - a straightforward switch between those with no vernalisation requirement (spring cvs) and high requirement (winter cvs).

P5 duration of grain fill phase, thermal time from the start of grain fill to maturity.

G1 potential maximum grain size, based on the average number of grains per ear (range 15-30). Low values indicate cultivars with few grains per ear. Grain number is proportional to the weight of stems+ears at the end of stage 4 (G3).

G2 potential grain fill rate. Range 0.08 - 2.0 mg grain^{-1} day^{-1}. Related to the mean grain weight and mean temperature during the phase (Tn) by the equation:

Grain weight = G2 x P5/Tn

G3 potential weight of a single stem (excluding leaves) and ear at the end of stage 4 when the stem and ear stop elongating. It is used to determine ear number. Values indicate tillering capacity with low values resulting in more tillers.

When the model is run, P1V is set first using intermediate values of the other coefficients which do not affect pre-anthesis developemnt, and then P1D is adjusted to align the predicted development with the observed date of ear emergence.

The ARCWHEAT winter wheat model incorporates genotypic differences by defining phase durations in thermal time as model inputs. Since it explicitly refers to winter wheat, the vernalisation process is common to all cultivars. Conversely, the van Keulen model refers to spring wheat and does not consider differences in vernalisation requirement between cultivars or include photoperiod effects.

3.3.5. GROWTH AND PRODUCTION OF DRY MATTER

Assimilate production is a function of intercepted solar radiation and the efficiency with which it is utilised. At the canopy level, dry matter production can be related to the photosynthetic efficiency of the crop as a whole (CERES): at a lower level of organisation, the processes governing photosynthesis, stomatal behaviour, photorespiration and dark respiration are modelled separately (ARCWHEAT).

50% of incoming solar radiation (Szeicz, 1974) is assumed to lie within the photosynthetically active (PAR) waveband (400-700nm). Calculation of intercepted PAR (Io) from measured incident solar radiation requires information on canopy reflectance (Duncan *et al.*, 1967) and leaf area. Radiation absorbtion (I) is related to Leaf Area Index (l) by a form of the Monsi and Saeki (1953) equation:

$$\mathtt{I} = \mathtt{I}_{\mathtt{o}}\mathtt{e}^{-k\mathtt{l}}$$

k, the light extinction coefficient, is related to the distribution of leaves within the canopy (Goudriaan, 1988) and geometry of the crop and the definition of LAI. It may range from 0.3 for erect leaves to 0.7 for horizontal leaves. Low values of LAI according to the CERES definition (leaf blade area only) are offset by using a higher *k*.

The potential dry matter accumulation rate is the product of Io and the photosynthetic efficiency, measured as the Dry Matter Radiation Quotient (Russell *et al.*, 1989) (ARCWHEAT: DMRQ=2.3 g MJ^{-1} $\mathtt{I}_{\mathtt{o}}$). ARCWHEAT uses additional input parameters for mesophyll conductance, growth respiration, ambient CO_2 concentration, leaf boundary layer resistance, Blackmann photosynthesis parameter and McCree maintenance respiration parameter. The CERES model summarises potential dry matter production in one equation:

$$\mathtt{dry\ matter\ production} = 7.5 * \mathtt{I}^{0.6}.$$

The actual assimilation rate depends on stresses acting on the plant. For example, van Keulen and Seligman (1987) use a linear relation with leaf nitrogen concentration to modify the value of the light-saturated CO_2 assimilation rate. Atmospheric CO_2 concentration affects photosynthetic performance, so models which include this as an input (ARCWHEAT, BACROS) can be used to look at the long term effects of climatic change on crop growth.

Canopy development.

de Wit *et al.* (1978) uses LAI as a model input: ARCWHEAT gives the option of reading Green Area Index (GAI) from input or modelling it from the number and size of leaves: van Keulen (1975) and CERES calculate LAI as a function of dry matter. Leaves are produced on the main stem in proportion to the accumulated temperature from emergence (Kirby and Appleyard, 1984). ARCWHEAT, CERES and Delecolle *et al.* (1985) then vary the phyllochron according to the rate of change of daylength at plant emergence. Many leaf development models maintain a constant number of actively-photosynthesising green leaves on the main stem: four are allowed in the CERES models, three in the ARCWHEAT model. After flag leaf appearance, leaf area declines steadily at a rate dependent on temperature and water stress.

For crop-growth models it is sufficient to model canopy LAI and main stem leaf number: crop-process models simulate total leaf area by addition of individual leaf areas. Leaf size depends on the position on the stem, and the stresses acting on the plant. In the ARCWHEAT model, the first six or seven leaves produced up to double ridge stage are of a similar size and relatively small: subsequent leaves up to the twelfth leaf are progressively larger. The maximum number of leaves produced is in part genetically determined, but is also highly dependent on environmental conditions, particularly on temperature. The end of leaf appearance is timed so that the flag leaf will reach full size by anthesis. Each leaf is totally senesced by the time the third leaf above it reaches maximum expansion. Leaves grow on tillers in the same way.

CERES first calculates a potential plant leaf area growth rate as a function of accumulated temperature and tiller number, and the weight of leaf tissue required to support this rate is determined from an Area to Weight Ratio (AWR). If the assimilate supply is insufficient to maintain this potential rate, then the new leaf area is determined from the weight of available assimilate. The AWR gradually falls from 150 cm^2g^{-1} to 127.5 cm^2g^{-1} at MPN as the first leaves produced are thinnest, and is thereafter maintained at 127 cm^2g^{-1}.

Tiller development

Tillers are produced at regular, temperature dependent intervals after the appearance of three (ARCWHEAT) or four (CERES) leaves on the main stem. Tillering continues until double ridge stage (ARCWHEAT) or the beginning of ear growth (CERES). Tiller death is related to population density: tillers are less likely to survive in denser crops. It is also related to the age of the tiller at MPN: early formed, larger tillers having the highest chance of survival. Those surviving at anthesis are assumed to bear ears, but the proportion which survive is influenced by user inputs (ARCWHEAT). High temperatures, water and nutrient stress increase tiller death.

Root growth and development

Root system growth and morphology are seldom treated in great detail in 'whole crop' models. There are models for water and solute uptake on the scale of individual roots (ie. Caldwell, 1976, Nye and Tinker, 1977) but the competition between overlapping root systems in a whole crop has received less detailed attention. In radial and cylindrical flow models, absorption of nutrients by a single root is related to its radius, the concentration of solute, and its absorbing power (Nye, 1973). On a larger scale, absorption is also related to age and morphology of the root system (Hackett, 1968; Baldwin, Nye and Tinker, 1973; Robinson and Rorison, 1983; Fitter *et al.*, 1991).

Partitioning of assimilate

Under optimum conditions of water and nutrient availability, a maximum proportion of assimilate is utilised in leaf and tiller production before anthesis, modified according to stresses acting on the plant. Drought, nitrogen shortage, or extreme temperature may direct a greater proportion of the dry matter into further root development. The proportion partitioned to the leaf, stem, root and grain depends on development stage. The ARCWHEAT model introduces an additional storage pool in the stem, which can be diverted to any of the other pools according to stresses acting on the crop (Table 3.3). Each pool must receive at least the minimum amount of assimilate for maintenance respiration. After anthesis, all new dry matter produced is available for grain growth. In addition, the ARCWHEAT model mobilises up to 30% of the reserve pool for grain growth if the assimilate supply is insufficient to maintain the temperature dependent rate of grain fill. A balance is struck between the two prevailing theories that availability of assimilate limits the eventual grain size ('source'), and potential grain size limits the rate of assimilation ('sink').

Table 3.3. Table to show the partitioning of dry matter in the CERES model

	Maximum % dry matter allocated to			
Development stage	Roots	Stem	Leaves	Grain
Emergence to MPN	35	0	65	0
MPN	30	10.5	59.5	0
MPN to start ear growth	30	28.7	41.3	0
Ear growth	25	75	0	0
End ear growth to start grain fill	20	80	0	0
Grain fill to maturity	<35	65	0	genetically determined

b) ARCWHEAT model

Development stage	**Maximum % dry matter allocated to**				
	Roots	Shoots	Store	Leaves	Ear
Floral Initiation	5.8	10	0	54.2	0
Double Ridge	35.8	10	0	54.2	0
Terminal Spikelet	20.5	40	0	39.5	0
Beginning ear growth	20.5	40	0	39.5	0
Anthesis	10	10	0	30	50
Start grain fill	5	0	95	0	0

3.3.6. COMPONENTS OF YIELD

Total grain number is calculated as the product of ears per unit area and grains per ear. Masle (1985) describes a model which calculates ear number according to the number of tillers with three leaves at the time when nitrogen becomes a limiting factor for plant growth and production of new tillers ceases. The total grain number and number of grains per ear is calculated in several models from the weight of the ear at anthesis and the number of fertile tillers. In the ARCWHEAT model, 10mg of ear weight at anthesis is equivalent to one grain set (Wood & Thorne, 1986).

Stem number is modelled on a daily basis in both the CERES and ARCWHEAT models, and is fixed by ear emergence. Grain number is predicted from the crop dry weight, assuming 10 to 30 grains set per 1g stem dry matter at ear emergence, depending on genotype (CERES), or 100 grains per 1g ear dry matter at anthesis (ARCWHEAT). Grain number per ear is a calculated value at maturity. Kernel weight in the CERES model is calculated from total grain yield and grain number.

3.3.7. OUTPUT ROUTINES

Elaborate output routines are costly in terms of computer time and memory required, although graphical display simplifies interpretation of results. Statistical analyses for comparing model performance with field measured data are perhaps more useful. Results from most models are flexible enough to extract additional data about aspects of the crop and its environment at intermediate points in the season.

4. EVALUATION OF THE CERES BARLEY MODEL

The CERES barley model was tested after correcting errors in the program code. Unfortunately, data were not available for mid-season soil water or nitrogen values, so the internal accuracy of the soil water and nitrogen modules could not be assessed. This concentrated the effort on the crop growth and development modules. The model was run according to the authors' directions (Otter-Nacke, pers. comm.). The internal consistency of the model was checked using the five data sets provided with the model. These were data from four research stations in the Aleppo area of Northern Syria and one set from Rothamsted, 1976. These were interesting in that the descriptions of the soils were taken from the DSSAT database and provided an example of the detail and format of soil input data required. The data from Rothamsted were for a range of sowing dates at fortnightly intervals between March and May 1976 but the observed final yield data was not available which limited their usefulness. 1976 was a dry year and even the high available water content of the Rothamsted silty clay loam was insufficient to prevent water stress. These data sets were later discarded because the droughty locations could not be compared with the climate of the barley areas of Scotland and independence could not be assumed.

4.1. DATA FOR MODEL TESTING

Data for model testing had to satisfy several criteria:

- Independence from the data used to build the model - this was immediately satisfied by using data from barley trials rather than wheat since the original model had been developed using wheat trial data.
- Span a broad range of sowing dates - for the double purpose of testing with autumn and spring sowings and reducing the number of years needed for a representative range of weather problems.
- Include several contrasting cultivars in each trial - notably those with different vernalisation requirement and photoperiod sensitivity.
- Include mid-season measurements of crop biomass, canopy characteristics and phenology - correctness of method being as important as a correct end result. Data from CVT experiments were not included for this reason.
- Weather data collected on or close to trial site, ideally including solar radiation.
- Data from field sites in Scotland - to comply with the original purpose of the project. Data from controlled environment experiments were not used.

- Access to the 'raw' data - to check definitions of measurement and calculated values.
- Trials not subject to undue stress due to water or nutrient shortage, weed or disease.
- Measurements from row plots rather than spaced plant trials.

Table 4.1. Data for model testing

Reference	**1**	**2**	**3**	**4**
Range of sowing dates	25.3.76 4.4.77	19.11.79, 8.4.80 10.10.80, 13.11.80 19.3.81, 23.4.81	17.9.80, 17.3.81 17.9.81, 27.3.82	March & April 1970 - 1975
Cultivars used S = spring W = winter	Golden Promise (S) Maris Mink (S)	Golden Promise (S) Maris Otter (W) Video (W) Igri, Crosier (W)	Athene (W) Golden Promise (S) Igri (W)	Zephyr (S) (1970) Golden Promise (S)
Mid-season measurements	leaf number spikelet number apical development tiller production	leaf number spikelet number apical development tiller production	leaf number development stage biomass nitrogen content	leaf number development stage tiller production growth rate
Final measurements at harvest	components of yield distribution of weight per grain	components of yield absorbed PAR	components of yield nitrogen content	components of yield nitrogen content
Site	PBI, Edinburgh PBI, Cambridge	Pentlandfield, (Edinburgh)	Aberlady (East Lothian) Balerno (Midlothian)	Drumforber, Wartle (Laurencekirk) Shaggart, Logie Newton (Aberdeenshire)
Soil	sandy loam brown clay loam	sandy loam	calc brown sand imperfectly drained clay loam	sandy loam
Seed rate	258 seeds m^{-2} hand sown in rows	258 seeds m^{-2} hand sown in rows	400 seed m^{-2} spaced rows	4 seed rates 10, 20, 30, 40 gm^{-2}
Solar radiation recorded on site	no	no	no	no

Published data sets used were those of :-

1. Russell & Ellis (1988) and Ellis & Russell (1984)
2. Kirby & Ellis (1980) and Ellis & Kirby (1980)
3. Dyson (1977)
4. Elmes (1985)

In addition, a field experiment was conducted in Edinburgh in 1988 (Appendix D) to test the hypothesis that spring cultivars do not differ significantly in their development rates, when grown under similar conditions. A second objective of this study was to derive values for the genetic specific coefficients for the CERES barley model. Appropriate parameter vales were calculated for ten spring barley cultivars, including cv. 'Golden Promise', which featured in each of the data sets used.

A list of suitable values for the genetic specific coefficients for some barley cultivars was provided with the model. First estimates for the coefficients for the cultivars in Table 4.1 were based on those for similar or related ones. Actual values should be derived from field and controlled environment experiments (Hunt, 1988a, 1988b), or found by running the model iteratively (Ritchie *et al.,* 1984) for each new cultivar over a range of sensible values, selecting those values which give the best predictions. This process is lengthy and can entail many iterations. The coefficients obtained from one site in one year should then be appropriate for any site in any season according to the model authors. However, when any of the genetic parameters are fit from experimental data, the model accuracy cannot be validated with the same data set.

Initially, the model was found to be very sensitive to the genetic specific coefficient input values. An optimisation procedure was carried out for some cultivars in the data set by running the model with additional data (Russell *et al.*, 1982) to ascertain the best values to use as inputs for cvs 'Golden Promise', 'Maris Otter' and 'Igri' to minimise the deviation in two factors: firstly the date of ear emergence and secondly the grain number. These optimum values were then used with the test data set.

Meteorological data for each site were taken from the nearest Agrometeorological station via the METDATA database (Crouch, 1985, with permission from AFRC and the Meteorological Office).

Soil data were prepared using the SOILDATA program (Bradshaw, pers. comm.) which generates estimates of soil water holding capacity and soil chemical composition from the physical description of the soil profile (Ragg & Claydon, 1973).

A suite of programs were prepared to simplify use of the CERES barley model. Input files were prepared in the correct fixed file format using a FORTRAN file generation program DATALOAD (Appendix B). This calculated site latitude from the grid reference, selected the nearest agrometeorological station on the Metdata database and used the figures for sunshine hours for that station to calculate daily solar radiation (McGechan, 1985). The program also provided interactive data entry screens for the entry of field trial management information and observed crop yield measurements. A second program, READOUT, extracted the summary yield information from model output files (eg. Figure 4.1.) and diverted the output to the MINITAB statistical analysis package (Ryan, Joiner & Ryan, 1985) for analysis.

4.2. RESULTS

Field measured genetic coefficients were not significantly different for the ten spring cultivars under consideration. However, these measured values were dissimilar from the coefficients obtained from model calibration. Predictions of all aspects of growth and development could be brought within +/- 5% of observed values by the calibration process for an individual cultivar/year/location combination, but the model gave poor results when the same values for the coefficients were used for a different year/location (Table 4.2). The difference in results between Scotland and Cambridge points to the poor stability of the genetic specific coefficients, with the prediction of grain yield being particularly poor.

Table 4.2. Percentage error for selected attributes of predicted development and yield of cv 'Golden Promise' from the CERES barley model.

	SCOTLAND		CAMBRIDGE	
	1976	**1977**	**1976**	**1977**
Ear Emergence	0	+1	-3	+4
Maturity	-2	+8	+9	+21
Grain yield	+2	-22	+39	+68
Grains/ear	+3	+7	0	+20
Tiller number	-5	-2	+48	+58
Kernel weight	+3	-24	+1	-12

Data: Ellis & Kirby 1980. Model calibrated using data from Scotland, 1976

Since fixing the date of ear emergence was central to the calibration process, the best fit between predicted and observed values (Table 4.3) for this character was not unexpected. Final yields of grain, straw and biomass were less well predicted, particularly from trials with unusually high or low values for any character (Figure 4.2a). There was little difference in accuracy between spring and winter cultivars.

Figure 4.1. Sample output from the CERES barley model

```
 RUN   1 OUTPUT SUMMARY
 INST_ID :ES  SITE_ID: AB  EXPT_NO: 02  YEAR : 1982  TRT_NO:  6
 EXP.    :Aberlady (Ann Elmes) Winter 81/82
 TRT.    :150 kg N / ha
 WEATHER :Edinburgh Bush_House, 1980 - 1982
 SOIL    :Typic Udipsamment. Calcareous Brown Sand
 VARIETY :Igri (2)
 IRRIG.  :NEVER IRRIGATED, RAINFED.
 LATITUDE=56.0  SOWING DEPTH=5.CM PLANT POPULATION=400 PLANTSm¯²
 GENETIC SPECIFIC CONSTANTS   P1V = 6.0  P1D = 3.0  P5 = 4.0
                              G1 = 2.5   G2 = 4.0  G3 = 2.5
 SOIL PROFILE DATA [ PEDON: Fraserburgh  ]
 SOIL ALBEDO= .13  U= 6.0  SWCON=.64   RUNOFF CURVE NO.=  67.0
 FERTILIZER INPUTS
 DAY OF YEAR    KG/HA     DEPTH   SOURCE
      77     150.00       .00   CALCIUM NITRATE
           THE PROGRAM STARTED ON DAY  261
DATE  CDTT PHENOLOG STAGE    BIOM   LAI NUPTK   N% CET RAIN PESW
18 Sep   0 SOWING           g/m^2       kg/ha       ----mm----cm
19 Sep   11 GERMINATION                              4.   0.  13
 1 Oct  105 EMERGENCE PHINT=95.8 CHGDL= -.079       15.  86.  15
24 Apr 1044 MPN  VE DAYS=50.  105. 1.28  30.5  2.90 152. 696.  7
22 May 1280 END VEG. BEG EAR  390. 3.56 105.0  2.69 217. 745.  6
 2 Jun 1419 END    EARS= 639  524. 3.47 116.4  2.22 245. 760.  5
Ear Emergence occured on  5 Jun Day of Year = 156
18 Jun 1625 BEG GR FILL       688. 3.21 115.1  1.67 274. 838.  9
26 Jul 2084 MATURITY         1001.  .01  49.8   .91 366. 940.  8

YIELD (KG/HA)=4537 (BU/ACRE)=67.7
FINAL GPSM=7157 KERNEL WT=63.4mg
 ISTAGE     CSD1     CSD2   CNSD1    CNSD2   STAGE OF GROWTH
      1      .00      .00     .12      .21  EMERG -  MPN
      2      .07      .17     .15      .33  MPN - BEGIN EAR GROW
      3      .25      .32     .00      .04  BEGIN EAR - END EAR
      4      .22      .28     .00      .00  END EAR - BEGIN GRFIL
      5      .00      .00     .00      .00  LINEAR GRN FILL PHASE
 * NOTE: In the above table, 0.0 represents minimum
    stress and 1.0 represents maximum stress for water (CSD)
    and nitrogen (CNSD) respectively,
                             PREDICTED      OBSERVED
 EAR EMERG DATE                 156
 MATURITY DATE                  207           204
 GRAIN YIELD (KG/HA)          4537.         5099.
 KERNEL WEIGHT (MG)             63.4
 GRAINS PER SQ METRE          7157.
 GRAINS PER EAR               11.21
 MAX. LAI                      3.56
 BIOMASS (KG/HA)             10011.        10916.
 STRAW  (KG/HA)               5474.         5817.
 GRAIN N%                      1.37          1.53
 TOT N UPTAKE (KG N/HA)       111.9         159.5
 STRAW N UPTAKE                49.8          71.4
 GRAIN N UPTAKE                62.1          78.1
```

Table 4.3. Correlation of predicted and observed data.

	CORRELATION COEFFICIENT
DEVELOPMENT	
Phyllochron	0.672
Date of MPN	0.507
Date of ear emergence	0.874 ***
Date of maturity	0.635 ***
COMPONENTS OF YIELD	
Biomass (kg ha^{-1})	0.471 ***
Grain yield (kg ha^{-1})	0.514 ***
Straw yield (kg ha^{-1})	0.421 **
Harvest Index (%)	0.504 ***
Kernel weight (mg)	0.325
Grains per m^2	-0.028
Grains per ear	0.453
CROP NITROGEN BALANCE	
Grain N%	0.813 ***
Total N uptake (kg N ha^{-1})	0.848 ***
Straw N uptake (kg N ha^{-1})	0.831 ***
Grain N uptake (kg ha^{-1})	0.765 ***

Results of regression of predicted characteristic against observed. Number of data points vary.

*** Significant at $p>0.01$

** Significant at $p>0.05$

Grain number was calculated in the model from the number of ears per plant and final grain yield. The number of ears per plant was underestimated in all cases for spring cultivars, and in most cases for winter cultivars. Since the predicted total grain yield figure was only reliable for trials with yields between 3.5 and 6 t ha^{-1}, the components of yield showed a poor correlation with oberved values (Figure 4.2b). In particular, kernel weight was overestimated. This may have been partly due to the model origins as a wheat model, with higher number of grains per ear in winter wheat than two-row winter barley (Bragg *et al.,* 1984) and lower tiller numbers in wheat as compared to spring or winter barley (Kolbe, 1984). Observed differences in grain number per unit area were not reflected by the model. The results for development stage are plotted (Figure 4.2c) against sowing date, expressed as the number of days the predicted values deviated from observed. Points above the central line are overestimates, those under the line are underestimates of the dates of the different phases. The test data had a range of genotype x sowing date combinations, including spring cultivars sown in the autumn and winter cultivars sown in the spring. The model failed to predict these differences for autumn sowings especially, highlighted by one case where autumn-sown 'Golden Promise' was predicted to reach MPN 72 days early and anthesis 30 days early. Development stage was closely linked to leaf appearance in the model, so the predicted phyllochron, measured in thermal time, is also shown.

Both grain and straw nitrogen uptake were underestimated (Figure 4.2d) over the range of nitrogen treatments studied (0 to 150 kgN ha^{-1}). The error was compounded in the calculation of total nitrogen uptake, although uptake rightly increased at higher nitrogen levels. Total nitrogen accumulation in both the whole plant and the grains was more closely related to biomass production than to tissue nitrogen concentration. At low nitrogen levels, grain yield was proportional to total uptake: with increasing nitrogen uptake, grain yield per unit nitrogen taken up decreased but the protein content of the grain increased. Observed grain nitrogen percentage varied between narrow limits (1 to 2%) although was only effectively simulated for mid-range values.

4.3. DISCUSSION

Six areas gave particular cause for concern with the model:

a. Phasic development
b. Leaf canopy development
c. Tillering
d. Specification of genotype
e. Components of yield
f. Interaction between soil water and soil nitrogen deficits

4.3.1. PHASIC DEVELOPMENT

The developmental submodel is temperature dependent, modified by genotype, water and nitrogen availability. Additional parameters affect the rate of development:

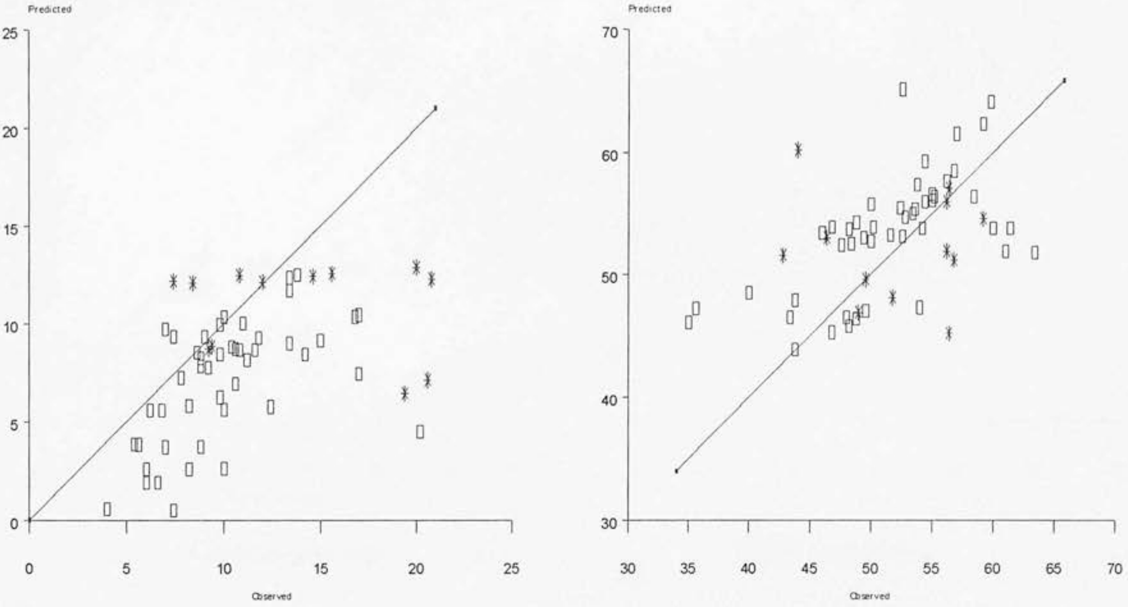
P9	thermal time from germination to seedling emergence
P2	thermal time between MPN and end of vegetative growth
P3	thermal time from end of vegetative growth to end of pre-anthesis ear elongation
P4	thermal time between end of pre-anthesis ear growth and beginning of grain fill

Values varied according to date of emergence, sowing depth and latitude, but overestimated each phase after emergence when compared against field measured values (Table 4.4) for the mean of 10 spring cultivars (Appendix D).

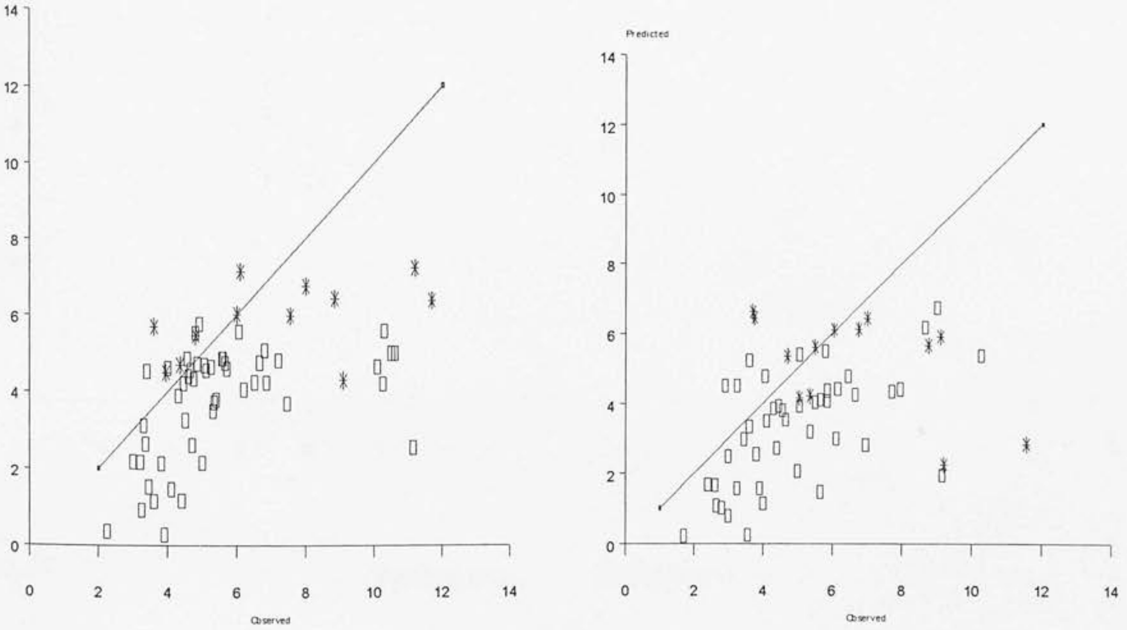
Figure 4.2. Comparison of model predictions with observations for the test data

A. Yield

Biomass (t ha^{-1}) **Harvest Index (%)**

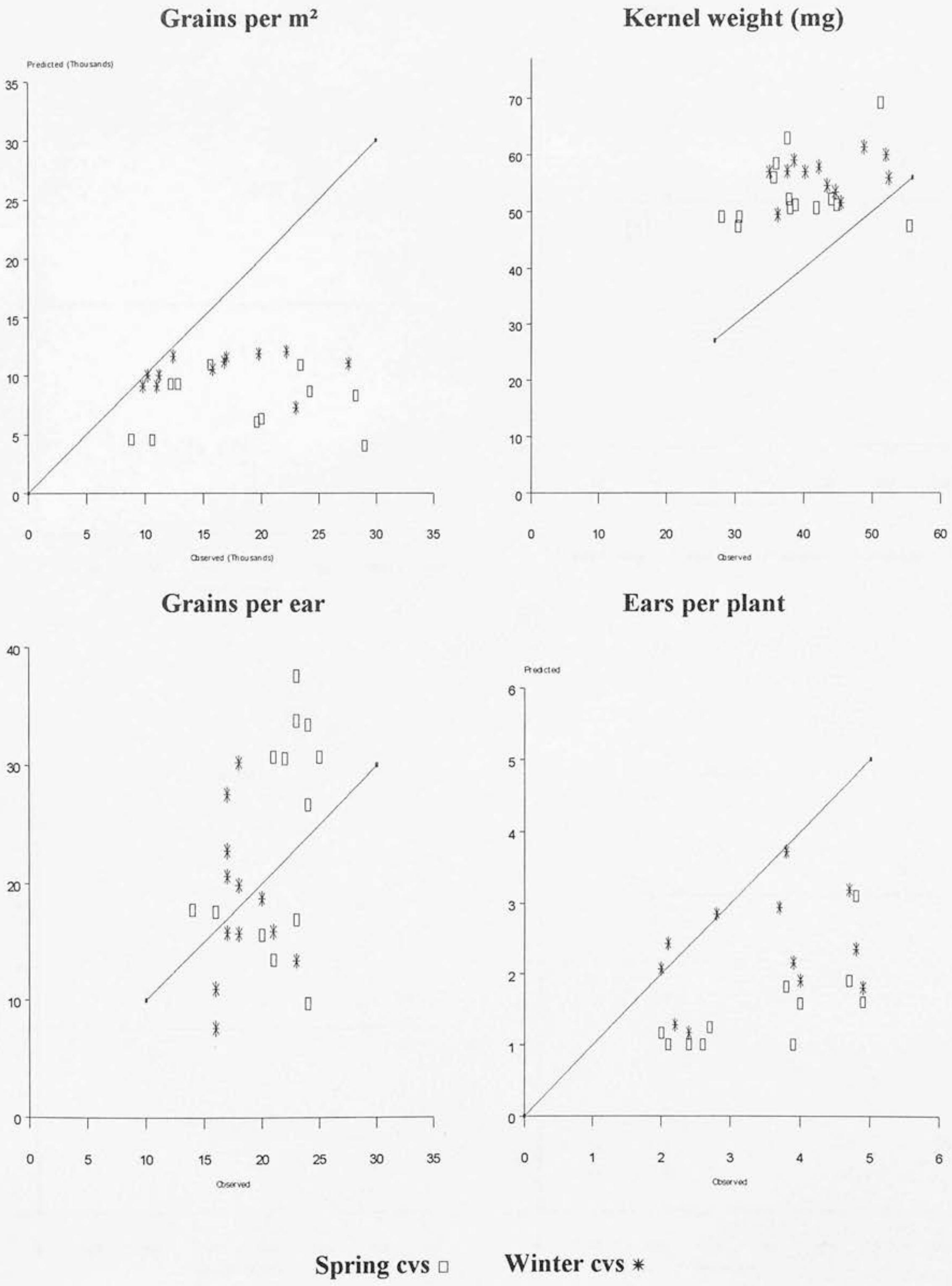


Grain Yield kg ha^{-1} **Straw Yield kg ha^{-1}**



Spring cvs □ Winter cvs ∗

B. Grain number


Grains per m²

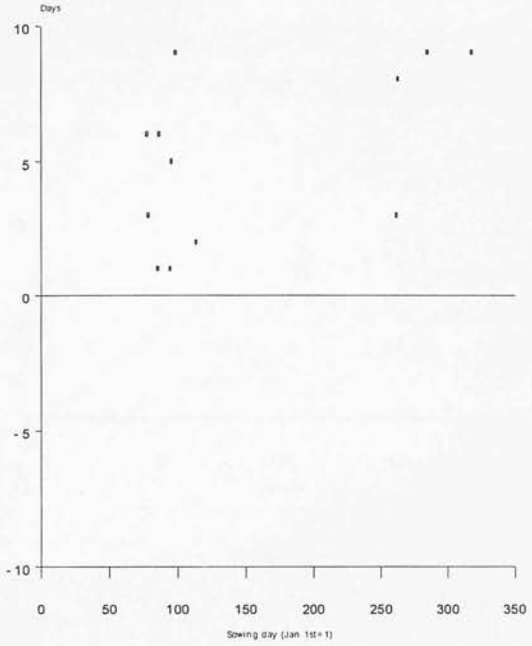
Kernel weight (mg)

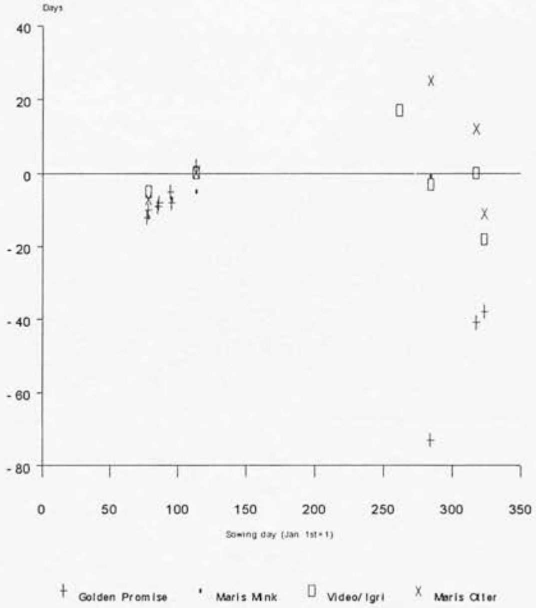
Grains per ear

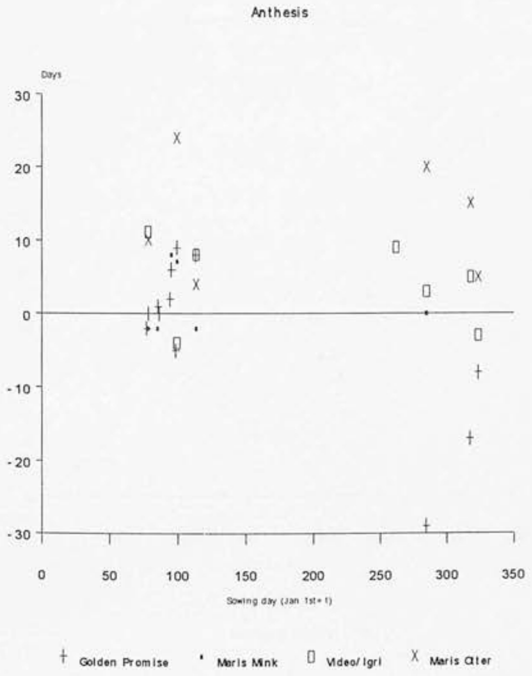
Ears per plant

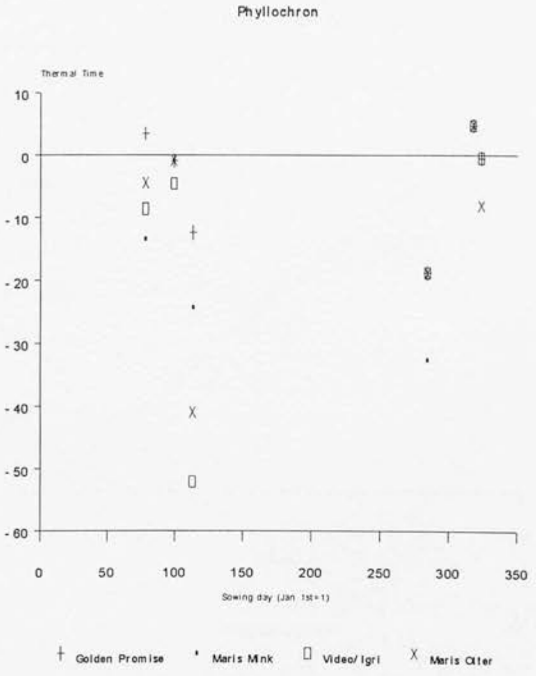
Spring cvs □ Winter cvs ∗

C. Development


Emergence

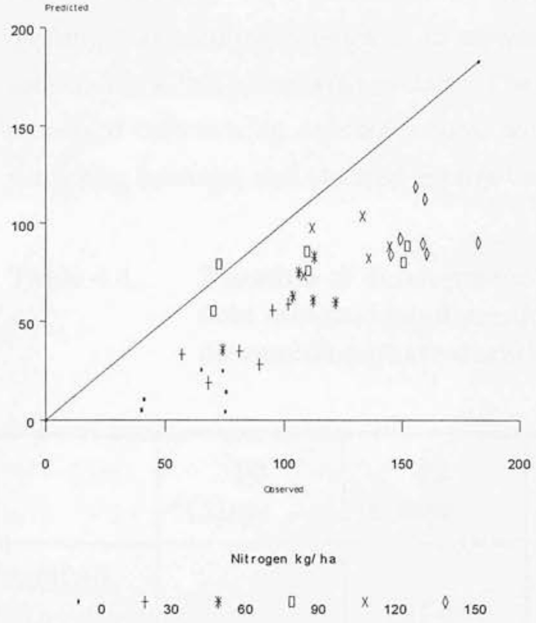

MPN



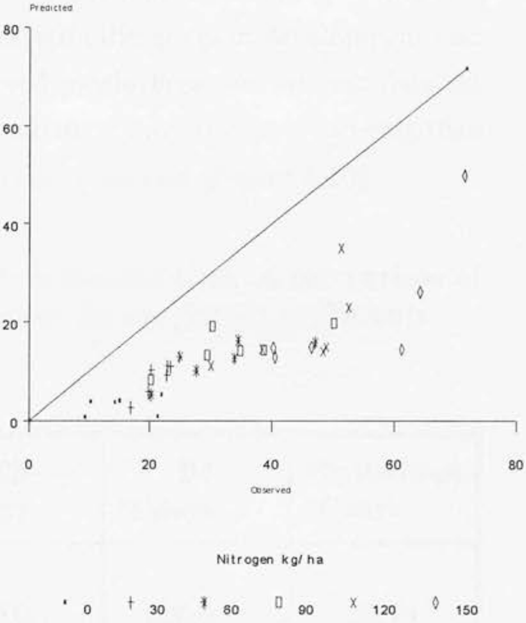


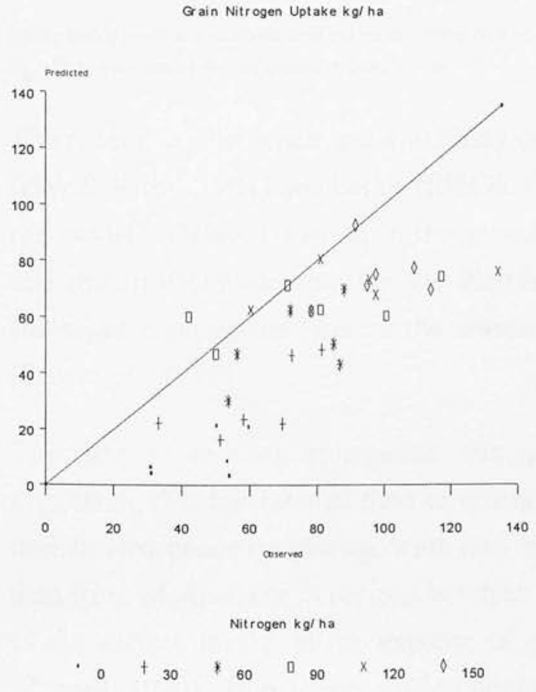
D. Nitrogen uptake

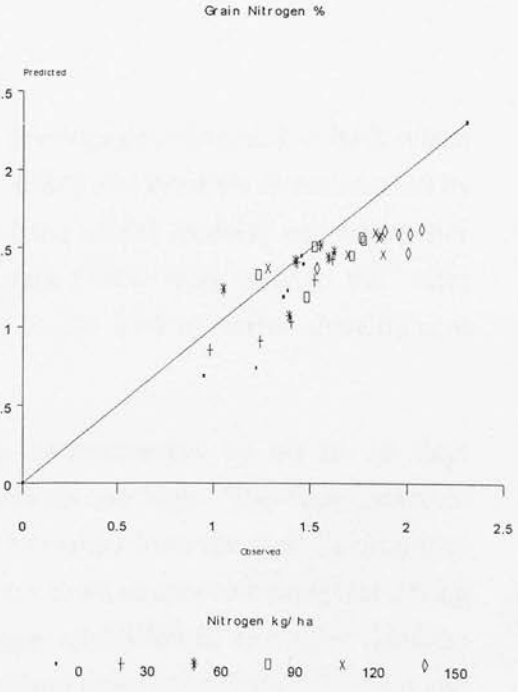
Total Nitrogen uptake (kgha^{-1})



Straw Nitrogen uptake (kgha^{-1})







Default input values for the phyllochron of 95°Cdays (winter cvs) and 75°Cdays (spring cvs) were suggested for the original version of the model. Version 2.00 amended this to 77.5°Cdays for all cultivars, modified by the rate of change of daylength at seedling emergence to simulate observed differences in development rate caused by altering the sowing date The observed phyllochron for the test data set increased with sowing date for autumn sowings and decreased again with sowing date for spring sowings, and showed greater variation than predicted (Figure 6.10).

Table 4.4. Duration of development phases in thermal time. A comparison of field measured and predicted values for the genetic coefficients determining phase duration.

	P9 °Cdays	**P2 °Cdays**	**P3 °Cdays**	**P4 °Cdays**	**Phyllochron °Cdays**
MODEL					
Tb = 0		225.0	150.0	200.0	57.73
Tb = 2	81.2				
FIELD					
Tb = 0	98.6	215.0	142.0	131.0	74.3
Tb = 2	72.6	179.0	122.0	113.0	59.8

Spring barley sown at 3cm depth, emerged on day 108 at latitude 55.85°N

T_b = Base temperature for calculation of thermal time

The natural convergence and synchrony of crop development observed in both wheat (Hay & Kirby, 1991) and barley (Ellis & Russell, 1984) was not fully demonstrated by the model. Delayed sowing in the spring caused the model to delay ear emergence and maturity considerably for the Rothamsted data (Table 4.5), despite the water shortages experienced later in the season which would tend to hasten development (Day *et al.*, 1978).

The date of seedling emergence was generally overestimated by up to 10 days suggesting that the thermal time to emergence was set too high. The dependence of time to emergence on sowing depth may well have resulted from the model's origins in data from Mediterranean regions in which crops are sown deeper to counteract drying of the surface layers, at the expense of percentage establishment and tiller numbers (Russell, 1990). In practice, sowing depth in Scotland only varies from 2.5 - 5cm and a fixed thermal time to emergence of 100 °Cdays (see Appendix D) could be used.

Table 4.5. The effect of delayed sowing date on model predictions

SOWING DATE	**24.3.76**	**7.4.76**	**21.4.76**	**4.5.76**	**19.5.76**
Day number	**84**	**98**	**112**	**125**	**140**
PREDICTED DATE OF					
Ear Emergence	159	163	169	176	184
Physiological Maturity	184	187	192	198	207

Data: Rothamsted, 1976. Day numbers given where January 1 = 1

MPN was correctly predicted from spring sowings but not from autumn sowings. Ear emergence was predicted to within 10 days in most cases, but winter cultivars reached ear emergence earlier than predicted and autumn-sown spring cultivars reached ear emergence later than predicted. The duration of grain fill was well predicted, but the start of the phase was dependent on the predictions for earlier phases.

4.3.2. LEAF CANOPY DEVELOPMENT

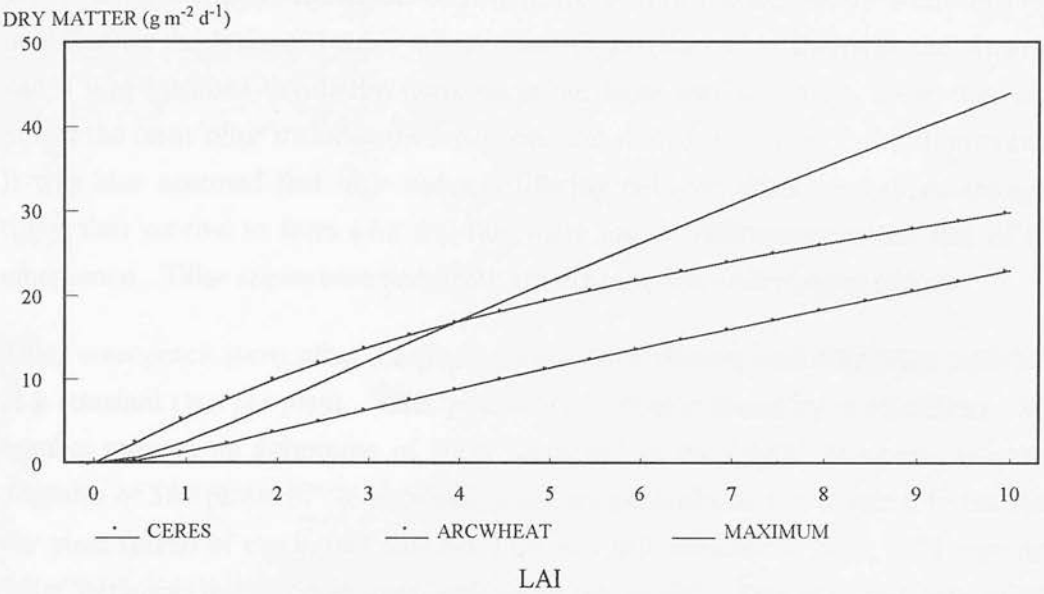
Leaf Area Index (LAI) is ambiguously defined in the model as the upper leaf blade area only. The Green Area Index (GAI) including the sheath and stem area as well is an ambiguous term since the senescing parts of leaves and stems may or may not be included in the definition. The precise relationship between LAI and GAI for the period up to about a week before anthesis for the data presented in Biscoe et al (1975) is given by Russell (1990) as:

$$\mathrm{GAI} = 1.02 \times \mathrm{LAI} + 0.0672 \times \mathrm{LAI}^2$$

However, the model predicted LAIs of less than half the observed values of GAI. The maximum LAI predicted for any test data was 4.31, which would give a maximum GAI of 5.64. Leaf area is often unrecorded in trials, but values of GAI of 10 $m^2\ m^{-2}$ are not unusual in Scotland. Low values of LAI were offset by using a higher light extinction coefficient (k = 0.85) than others have used (For example: k = 0.44, Gallagher *et al.*, 1976a) to calculate I_O, so that the exponent in the Monsi & Saeki (1953) equation ($I = I_O e^{-kl}$) stays more or less the same (ref. page 39).

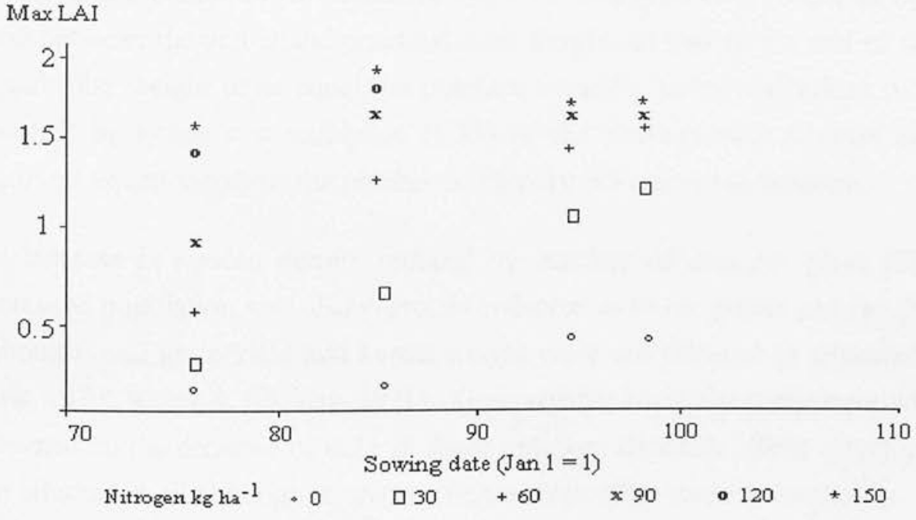
Given an incoming solar radiation of 22 $MJm^{-2}d^{-1}$ on a clear, sunny day (Milthorpe & Moorby, 1974), with 50% in the photosynthetic waveband, the maximum photochemical efficiency is around 4.4 gMJ^{-1}. The model overestimates conversion for low values for IPAR (Figure 4.3)

Figure 4.3. The production of dry matter. The CERES model overestimates dry matter production at low levels of intercepted radiation and LAI.



Low nitrogen levels excessively depressed predicted maximum LAI resulting in low biomass accumulation (Figure 4.4). This in turn affected all the components of yield except kernel weight. Cold winter temperatures similarly affected LAI, particularly for autumn-sown spring cultivars. Leaf area development was also slower for spring cultivars than winter cultivars from similar sowing dates, and in some cases LAI failed to reach 1.0. This also depressed nitrogen uptake figures. The model canopy had all the appearance of being severely affected by drought, but running the model for non-limiting water did not noticeably increase the canopy size or duration.

Figure 4.4. The effect of nitrogen nutrition on leaf area development



4.3.3. TILLERING

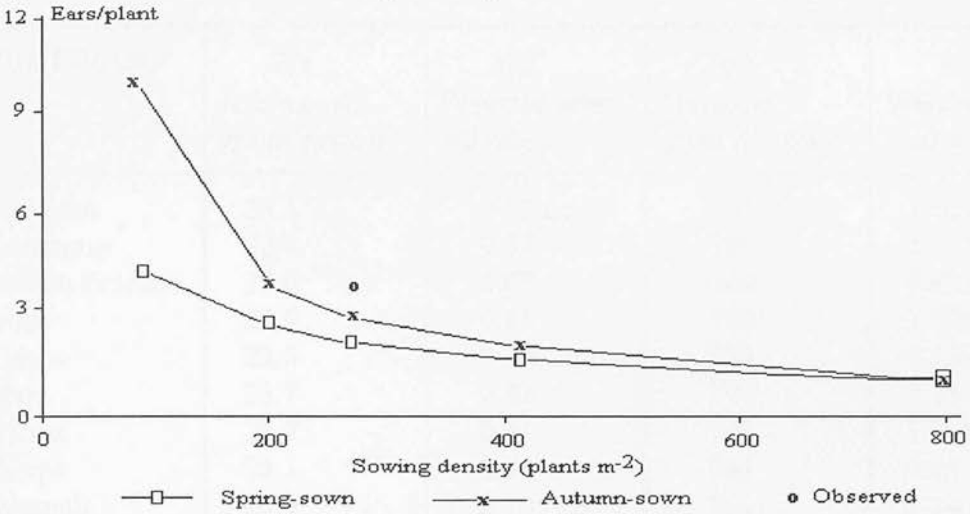
The tillering section of the model originated from work carried out on wheat in Texas, modified on the basis of further wheat research carried out in England and Australia, and it was assumed that barley behaved in the same way as wheat. Note that in the model the term 'tiller' includes the mainstem, and should be equated with stem number. It was also assumed that high and low tillering cultivars differ in the percentage of tillers that survive to form ears and that there are no differences in the rate of tiller emergence. Tiller appearance and death are distinct, non-overlapping phases.

Tiller emergence starts after 2.5 phyllochrons have elapsed and continues until MPN at a constant rate per plant. Tiller production is then reduced by competition. Stem number reaches an asymptote of 3000 stems m^{-2} in the model, however, at sowing densities of 300 plants m^{-2} in Scotland, there are generally no more than 6 fertile stems per plant (mean of cvs in test data set 3.24 ears m^{-2}, maximum value, 4.92 ears m^{-2}). Tiller initiation is not considered limiting in the model. The potential rate of tiller formation depends on the actual length of the phase in thermal time, and the genetic coefficient G3 which gives the average weight of a single stem and ear at anthesis. Cultivars with lower values of G3 produce more tillers although there is a strong GxE interaction. Autumn-sown crops, or cultivars with a high vernalisation requirement will spend longer in phase 1 and produce more tillers. However, the final number of fertile ears for spring-sown spring cultivars was often no more than one per plant, even under low planting densities. Examination of intermediate growth stages showed that some tillering occurs during phase 1 but all tillers produced then die during stage 2.

Tiller death is controlled by a source-sink relationship. It starts at the end of spikelet initiation and continues to the end of stage 3. The process is modelled by using the ratio between the actual and potential stem weight, so that at the end of stage 3, the actual tiller weight must equal the potential weight. Either the values of G3 or the constant by which it is multiplied (1.33) or the biomass must contain an error, or incorrect equations allow the number of tillers to fall below the potential.

An increase in sowing density reduced the number of ears per plant (Figure 4.5). Increased population was also correctly reflected in fewer grains per ear (Table 4.6), although total grain yield and kernel weight were not affected as expected (Kirby & Faris, 1970; Willey & Holliday, 1971). Grain number being the component with greatest influence on the decrease of yield at above optimum densities. Plant development was not affected at all although in practice dense crops often ripen more rapidly.

Figure 4.5. The effect of sowing density on fertile ear number.



Data: T811, T813 Series (Russell & Ellis, 1984) Cv. Video

Autumn sowing: 10th October 1980 Spring sowing: 17th March 1981

Table 4.6. The effect of sowing density on CERES model predictions

SOWING DENSITY	100	400	800	1200
Date of Ear Emergence	162	162	162	162
Date of Maturity	187	187	187	187
Biomass (kg ha^{-1})	3814	4128	4417	4614
Grain yield (kg ha^{-1})	1211	1266	1307	1331
Kernel weight (mg)	31.4	31.4	31.4	31.4
Grains m^{-2}	3853	4028	4159	4234
Grains per ear	38.53	23.02	15.12	11.29
Maximum LAI	1.67	1.90	2.11	2.25

Data set: Rothamsted, 1976

4.3.4. GENETIC SPECIFIC CONSTANTS

Model performance was very sensitive to the input values of the genetic coefficients. Cultivar distinction was not successful for those under test, and failed to predict the effects of inadequate vernalisation on development. Differences between coefficients measured in the field were not significant (Table 4.7; Appendix D) so the unique characterisation of a cultivar was not possible. The assumption that the genetic specific coefficients remain constant over diverse environments from one season to the next was not proved since the interaction effects were confused by larger errors in the modelling of canopy development and biomass accumulation.

Table 4.7. Field Measured Genetic Specific Coefficients

CULTIVAR	G1 Average no. grains per ear	G2 Potential grain fill rate	P5 Duration of grain fill phase	G3 Weight stem +ear at anthesis
Blenheim	23.3	0.82 mg d^{-1}	761 °Cday	1.020 g
Camargue	22.8	0.77	788	1.145
Golden Promise	25.0	0.67	748	0.815
Lotus	22.9	0.83	788	1.025
Klaxon	23.5	0.76	774	1.135
Oboe	25.7	0.83	774	1.385
Prisma	23.7	0.91	748	1.435
Sherpa	26.1	0.84	761	0.91
Triumph	24.9	0.79	761	1.14
Tyne	24.4	0.71	761	1.045
MEAN (SE)	24.3 (0.99)	0.79 (0.07)	767 (13)	1.105 (0.111)

Data: Bush House, Edinburgh, 1988 (Appendix D)
Large values of G3 indicate larger stems

4.3.5. COMPONENTS OF YIELD

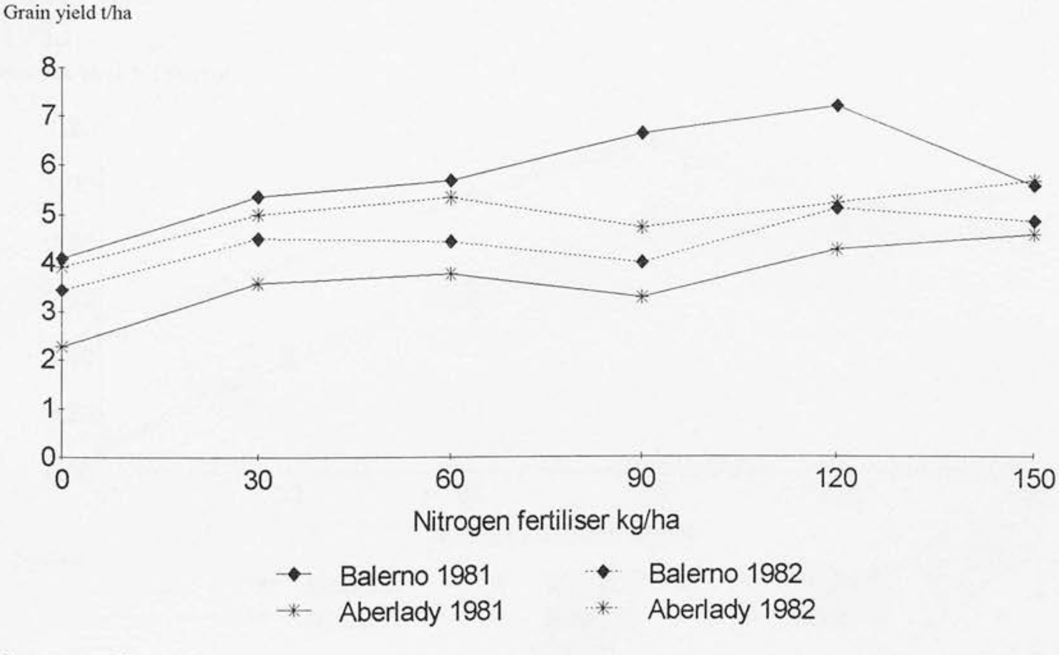
Ear number is derived from a relationship between tiller numbers and biomass at anthesis. All surviving tillers at anthesis are assumed to be fertile. Grain number per unit area is related to the weight of the mean stem plus ear at the end of ear growth using the genetic constant G1. The minimum grain weight is set at 20 mg and the maximum depends on G2 and P5. It follows that if tillering and the genetic constants are sources of error in the model, then the components of yield will be affected. Predictions of grain number, ear number, and total biomass yield underestimated measured yield in all cases, whilst grain weight and the proportion of biomass as grain were overestimated. The model predicted 5000 to 12000 grains m^{-2} whereas the measured values ranged up to 28000 grains m^{-2}.

4.3.6. SOIL WATER AND NITROGEN STRESS: MODELLING THE INTERACTION

The water balance equations are all empirically derived and as general as possible to avoid regionally-fitted parameters. The performance of these sub-models could not be studied separately due to the lack of data sets for which soil water had been measured throughout the season. However, much of the original work on which this section was built applied to dryland situations in sharp contrast to Scottish conditions.

Nitrogen uptake and grain nitrogen percentage were consistently underestimated from a range of levels of fertiliser input. The test data were taken from an experiment to investigate the relative contribution of soil and fertiliser nitrogen to plant nitrogen levels at six fertiliser application rates (Elmes, 1985). Spring barley (cv. 'Golden Promise') was grown at two contrasting sites in 1981 and 1982. Balerno, (altitude: 183m), has a heavy clay loam soil and high annual rainfall (905mm), and soil water levels seldom fall to limiting levels for barley growth. Aberlady (altitude: 12m), is a coastal site with a deep sandy soil and relatively low rainfall (589mm) and barley can show symptoms of soil water stress during prolonged dry periods. The 1981 season was drier than average, although sunshine and temperatures were similar to 1982. Measurements showed that the effects of moisture stress at Aberlady were most pronounced at high nitrogen levels and were experienced early in the season, whilst the crop at Balerno did not show symptoms of moisture stress. Increased nitrogen resulted in increased yield and increased water use over all treatments at Aberlady, with the higher yields in the wetter year, 1982. However, increased nitrogen fertilisation resulted in a greater yield response in the drier year on the heavy soils of Balerno (Figure 4.6). Little difference was observed between the water use at low and medium nitrogen treatments at Balerno, but there was a big response to the high nitrogen treatment.

Figure 4.6. **Modelling the effect of nitrogen and water stress on grain yield. Observed results**



Data source: Elmes 1985

Aberlady - light, sandy, well drained soil: Balerno - heavy soil

1981 - drier than average: 1982 - average rainfall

Figure 4.7a. The effectiveness of the additive (A), multiplicative (B) and geometric mean (C) models on predicted yields at two contrasting sites in two contrasting years.

◆ Balerno   * Aberlady

1981

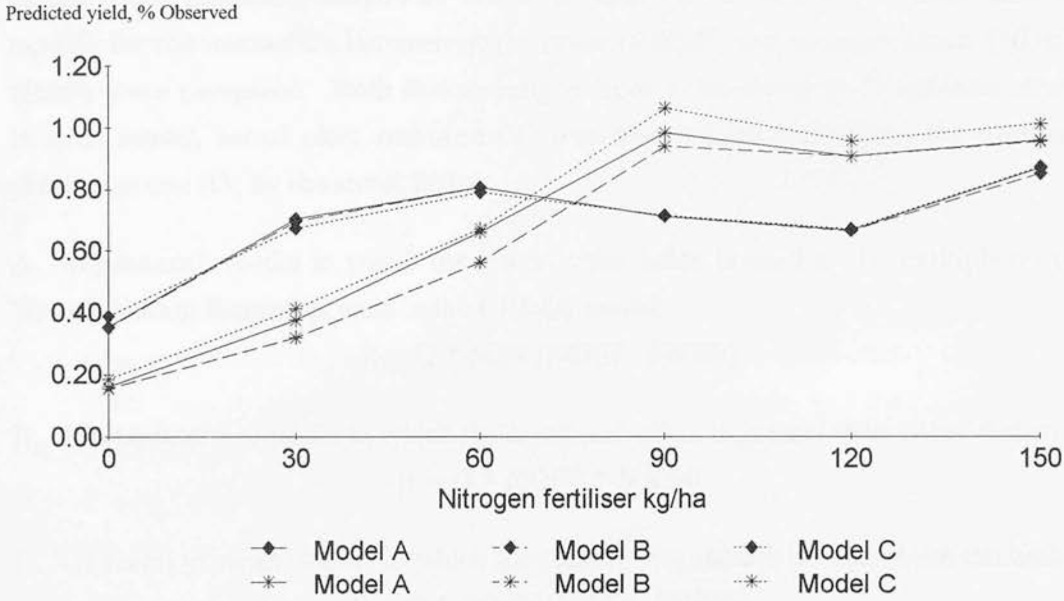
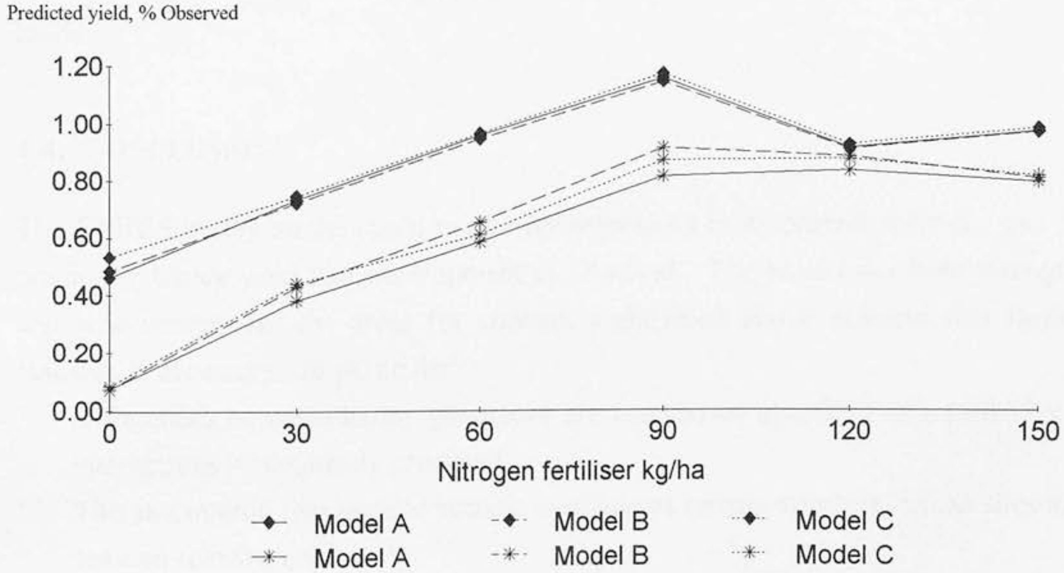


Figure 4.7b
1982



The model correctly predicted an increase in yield with increasing nitrogen application and a corresponding increase in soil water and nitrogen uptake. However, model performance, measured by predicted yield as a percentage of observed yield (Figure 4.7a,b), deteriorated when both water and nitrogen stress were present. The model narrowed the observed contrast between the seasons. It was thought that this might be due to the modelling method by which the stresses were applied, so three different models for the interaction between water stress (SWDF) and nitrogen stress (NDEF) factors were compared. Both factors ranged from 1- no stress to 0- extreme stress. In each model, actual plant response (R) was obtained by multiplying the optimum plant response (O) by the stress factor:

A. 'Minimum' model in which the lower stress index is used as the multiplier - the 'law of limiting factors' as used in the CERES model.

$$R = O * \mathrm{MIN}\ (\mathrm{NDEF}, \mathrm{SWDF})$$

B. 'Multiplicative' model in which the combined effect is greater than either factor.

$$R = O * \mathrm{NDEF} * \mathrm{SWDF}$$

C. 'Geometric mean' model in which the mean of the factors is used as the multiplier.

$$R = O * \mathrm{SQRT}\ (\mathrm{NDEF}, \mathrm{SWDF})$$

The method applied actually had little effect on the overall model accuracy. The largest effect was seen with the Aberlady 1981 data when the most pronounced stresses were present. However, the stresses encountered never reached extreme levels.

4.4. CONCLUSIONS

The CERES barley model could not be recommended in its present form for use for predicting barley yield and development in Scotland. The model has both strengths and weaknesses, but the areas for concern highlighted above indicate that further research is necessary. In particular:

- Differences between barley genotypes are not shown up effectively with G x E interactions inadequately predicted.
- The assumption that genetic specific coefficients remain constant across sites and seasons remains unproved.
- Model performance depends heavily on input parameters which are at best only estimates of the true values

* Weak predictions of tiller number, leaf area index and thus canopy development have major 'knock-on effects' on predictions of components of yield.

* Nitrogen usage and grain nitrogen percentage predictions are inaccurate.

* The model is not truly mechanistic since a combination of methods are used to derive the model equations. Additional statistical modelling may be required to establish suitable ranges for model parameters which can then be built into mechanistic methods.

* The model was developed for wheat. Part of the difficulty may be due to inherent differences between wheat and barley in terms of morphology and phasic development, determination of the components of yield and response of the crop to environmental factors.

Much of the variation in predicted phenology produced by different models can be explained by the built-in vernalisation responses, however, the modular structure of the CERES barley model provided the basis for constructing a model for barley in Scotland. Further data were required to re-construct the growth and development modules, and other methods for quantifying the variation in development rate between cultivars were also required.

5. COLLECTION AND ANALYSIS OF BARLEY DATA

5.1. THE BARLEY DATABASE

Plant growth and development data from 31 references (starred in the bibliography) including the test data set described earlier, were compiled into a database organised in seven linked files for statistical analysis and model testing (Appendix C, Table 5.1). The data described 354 field trials in the United Kingdom, Germany and Denmark, spanning latitudes 51 to 57N and the harvest years 1964-1989 (Table 5.2). 40 cultivars were included, 14 winter and 26 spring types (Table 5.3). The criteria for choosing the test data set (page 43) were relaxed slightly so that other experiments in which stage of development had been recorded could be included. The data set was unbalanced by the plentiful data available for a few cultivars (cv. 'Golden Promise', an early, semi-dwarf, erectoid type, and cv 'Proctor' - a late, tall cultivar).

Table 5.1. The reference data set.

File 1	**Experiment and Treatment description** Cultivar index number, Site/Reference identifier, Sowing density and depth, Dates of sowing, seedling emergence, collar initiation, double ridge, maximum primordium number, ear emergence, anthesis, maturity and harvest, expressed as calendar date, day number (Jan 1st=1) and days after sowing
File 2	**Yield data** Grain, straw and biomass yield, Harvest Index, Components of yield, Maximum stem number, Weight at anthesis, absorbed PAR emergence to anthesis, DMRQ
File 3	**Accumulated temperature, and Photoperiod** Thermal and Photo-Thermal times from sowing to each development stage
File 4	**Canopy structure** Leaf numbers at each development stage, Rates of leaf and spikelet primordium initiation, Rate of leaf appearance, Phyllochron, Maximum and fertile spikelet numbers
File 5	**Reference and Site data** Site/Reference identifier, Author, Journal, Reference description, Latitude, Grid-reference, Altitude, Soil index number, type and series, Plot size and type, Nearest weather station
File 6	**Cultivar data** Name, index number, row number, winter/spring habit, height, leaf type, thousand grain weight, earliness of maturity. Indices of vernalisation requirement, frost tolerance, disease resistance
File 7	**Soil data** Index number, Description, Albedo, and for each soil layer: depth, pH, Organic Matter content, NO_4, NH_3 content, water holding capacity

Table 5.2. Sites and seasons in the database

SITE	LATITUDE	RECORDS	YEARS
Aberdeen	56.85	4	1970 - 1973
Ayr	55.5	5	1986
Cambridge	52.18	107	1964 - 1985
Oxford	52.00	1	1983
Nottingham	52.87	14	1983 - 1985
LARS, Bristol	51.43	4	1985
Leeds	54.00	6	1978
Midlothian	55.67	14	1979 - 1983
Edinburgh	55.85	50	1979 - 1982, 1985, 1988
Tenby	51.67	105	1976 - 1979
Bangor	53.25	14	1982 - 1984
Denmark	55.68	11	1985
Germany	51.67	8	1968 - 1979
TOTAL NUMBER OF RECORDS		354	

Table 5.3. Spring cultivars

NAME	TYPE	EAR	REFS
Proctor	N	2-row	27
Triumph	SD-P	2-row	25
Golden Promise	SD-E	2-row	22
Jupiter	N	2-row	20
Maris Mink	SD-P	2-row	17
Armelle		2-row	13
Ark Royal	N	2-row	8
Hassan		2-row	7
Carlsberg (Danish)	N	2-row	4
Dram		2-row	4
Hood		2-row	1
Kite		2-row	1
Blenheim	SD-P	2-row	1
Prisma	SD-P	2-row	1
Klaxon	N	2-row	1
Sherpa	N	2-row	1
Tyne	SD-E	2-row	1
Lotus	N	2-row	1
Oboe	N	2-row	1
Camargue	SD-P	2-row	1
Zephyr		2-row	1
Mazurka		2-row	1
Lami	SD-P	2-row	1
Georgie		2-row	1
Kym		2-row	1
Clermont	N	6-row	13

Winter cultivars

NAME	TYPE	EAR	REFS
Sonja	N	2-row	36
Igri	N	2-row	29
Maris Otter	N	2-row	15
Halcyon	N	2-row	13
Crosier	N	2-row	9
Video	N	2-row	8
Kiruna	N	2-row	4
Malta	N	2-row	1
Athene	N	6-row	16
Hoppel	N	6-row	12
Esther	N	6-row	5
Vogelsanger Gold	N	6-row	5
Probstdorfer Remy	N	6-row	3
Gerbel	N	6-row	2

N = nutans (tall)

SD = Semi-Dwarf

P = Semi-Prostrate

E = Erectoid

Kiniry *et al.* (1989), working on a similar database of wheat yield data from a number of experiments world-wide, included only those data sets with no apparent water, nutrient, or temperature stress. However, differences in cultivar response to stress could explain some of the yield variation. To overcome this problem, cultivars in the barley database were ascribed indices according to their vernalisation requirement, disease resistance, cold and drought tolerance based on values in the UK Recommended Lists on a scale from 0-9. Data for crop nutrition and soil water status were not always available, so the data sets were restricted to those with no apparent nutrient or water stress or significant yield reduction due to weeds, pests or diseases. In some trial series, this meant only using control data from an experiment to study any of these factors. Changes in potential due to any increase in the ambient CO_2 concentration (320 - 350 ppm between 1964 and 1989) were ignored.

5.2. DEFINITION OF DATA FIELDS

5.2.1. CROP DATA

Sowing date, cultivar and density were recorded for every trial. Fertilisation was recorded as the total amount of nitrogen applied, and date, type and amount of individual applications. Data on crop chemical application were generally given in the references but were not included in the database since the models available did not take account of the effects of pests and diseases. Summary yield data were given in most data sets, however some error was inescapable due to the lack of a standard trial recording method and different definitions of terms used by different researchers. For example, thousand grain weight may have been calculated using all grains or only those over 2 mg. Grain, straw and biomass yields were taken as dry weights; harvest index as the ratio of grain dry weight to total above-ground dry weight (recalculated for all data in case some authors had included root weights).

Leaf Area Index was an ambiguous measure since it may include leaf sheath area, ear and awn area as well as leaf blade area. Borojevic and Williams (1982) define LAI in m^2 m^{-2} as all green parts of leaves and stems but not spikes; Wareing & Cooper (1971) use the area of exposed leaf sheath and laminae only; Legg *et al.* (1979) use a Green foliage Area Index (GAI) and include one side of leaves, stems, ears and awns. Data were standardised using the relationship between LAI and GAI given earlier (page 55); those that could not be standardised were omitted from the database.

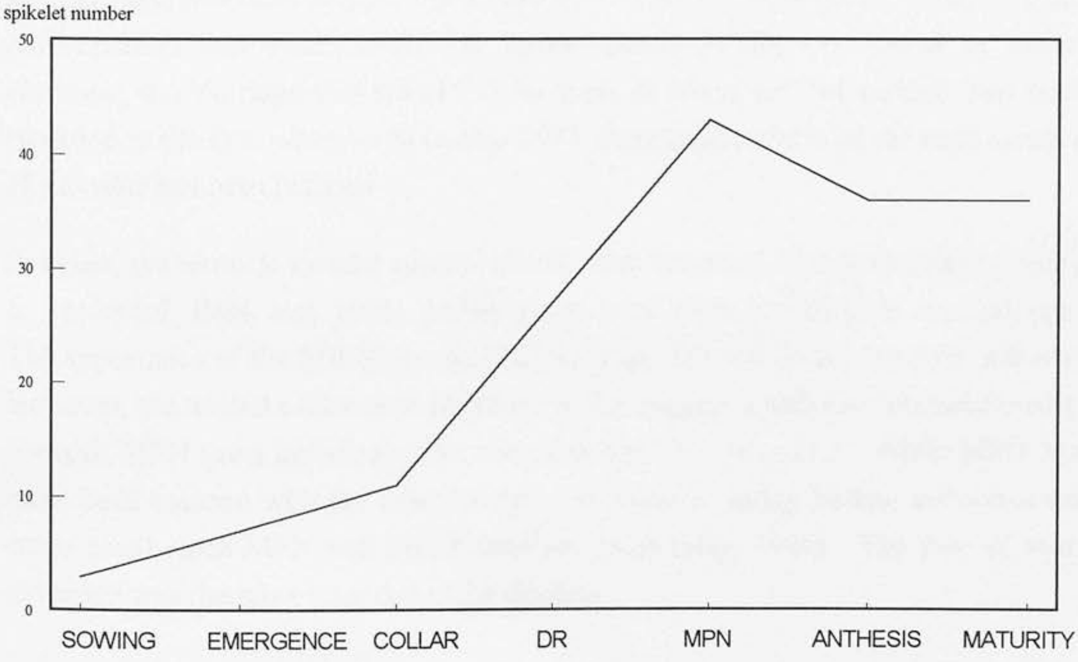
Phasic development was charted by several reference points for the development of the growing apex. The course of barley development has been well detailed elsewhere (Kirby & Appleyard, 1984), and several scales of measurement proposed (see Landes & Porter, 1989 for a comparison between scales), but the points used in this study require careful definition and were related to the external morphology of the crop and the decimal Zadoks scale (Tottman & Makepeace, 1979) used by several authors. Additional points were defined on the ontogenetic time scale equidistant in accumulated temperature between emergence and anthesis, to compare with the time scale used by van Keulen & Seligman (1987) (cf. Groot *et al.*, 1986 for maize). Recording apical development by dissection is very time-consuming, and the accuracy of the data depends on the experience of the recorder and the sampling frequency.

Two parallel approaches for modelling development were considered for the database:

Sowing - emergence - onset of stem elongation - ear emergence - maturity
Sowing - collar initiation - (double ridge) - MPN - anthesis - maturity

The chief developmental difference between autumn- and spring-sown barley lies in the duration of the vegetative period. Thereafter, cultivar and sowing date differences are reduced. Controversy surrounds the definition of the switch from vegetative to reproductive growth and it has been variously equated with the initiation of the collar primordium, double ridge stage, or the moment of acceleration of the rate of primordium initiation. These points were all recorded in the database.

Figure 5.1. The time course of primordium initiation - the general pattern



Collar initiation was taken as the date when the number of structures initiated at the stem apex was one greater than the final number of main stem leaves. This was not found by examination but identified with hindsight once the maximum leaf number was known. This is in contrast to a number of researchers who have equated the initiation of flowering with the appearance of double ridges at the stem apex. The rate of primordium initiation also changes at about this time from a slow phase of leaf initiation to a faster phase of spikelet initiation (Stern & Kirby, 1979; Baker & Gallagher, 1983; Kirby *et al.*, 1987) although the two points do not necessarily coincide (Figure 5.1). In some studies, the initiation of spikelets began at the slower rate (Halse & Weir, 1970; Kirby, 1977). These rates were constant in thermal time within each phase (Gallagher, 1979; Stern & Kirby, 1979, Molina Cano, 1990). Elongation of the apical dome also occurs at about the time of the onset of reproductive growth however the collar has usually been initiated before this can be detected.

The date of collar initiation recorded in the database was calculated by extrapolation for data where several counts of spikelet primordia had been recorded to fix the rate of spikelet primordium initiation in thermal time and the final leaf number was known. However, early counts of leaf primordium number in the raw data for some data sets were inevitably higher than the final leaf number. By implication, the collar is often mistakenly counted as a leaf primordium in which case the total primordium number equals the sum of the numbers of leaf + spikelet primordia, rather than leaf + spikelet + collar.

Double ridge had been recorded in a number of trials as the point by 'when spikelet differentiation was determined'. No further check on this date could be made. However, double ridge was calculated for trials in which spikelet number had been recorded as the date when 50 % (Kirby, 1977; Rasmussen, 1985) of the total number of spikelets had been initiated.

In wheat, the terminal spikelet appears shortly after the onset of stem extension (Kirby & Appleyard, 1984, Hay 1986), so the 'ear at 1 cm' stage is a suitable external sign. The appearance of the first internode (Zadoks stage 31) will follow terminal spikelet. However, the limited evidence available for barley suggest a different interrelationship between MPN (awn initiation) stem extension and tiller mortality. While MPN has often been equated with the onset of stem extension in spring barley, autumn-sown crops could reach MPN well before stem extension (Hay, 1986). The date of stem extension was therefore recorded in the database.

Ear emergence was recorded as the date of emergence of 50% of ears. The date of anthesis ("when anthers dehisce in the central florets in the spike" - Rasmussen *et al.*, 1979), which occurs within the closed floret in many barley cultivars, may be subject to additional error since it may have been recorded in the trial when the anthers were actually visible outside the floret two or three days after anthesis. Anthesis may occur in the field over an 8 to 12 day period for all stems in a plot, with greater differences between the main stems and higher orders of tillers, than between the main stem population. For these reasons the date of ear emergence may be more reliable than that of anthesis. Lack of rigour in experimental description confounds comparison between work by different authors when the terms awn emergence, ear emergence, anthesis, heading or flowering are used synonymously. Physiological maturity, also ambiguous, was recorded as the date of maximum dry weight. The date of harvest was recorded.

Rates of leaf primordia initiation and spikelet primordium initiation in thermal time were recorded (Chapter 6 for full discussion). Maximum spikelet number and the number of grains per ear were used to calculate a percentage spikelet survival rate from MPN to anthesis. It was assumed that the final leaf, the flag leaf, was initiated at or around ear emergence. The rate of leaf initiation in thermal time, and its inverse the phyllochron, were calculated from the final number of leaves and the thermal time from emergence to ear emergence.

5.2.2. WEATHER DATA

Meteorological data for each UK site were taken from the nearest agrometeorological station via the METDATA database. Data included maximum and minimum daily air temperature, rainfall, sunshine hours, and where possible, solar radiation. The chosen station was coastal or inland to correspond with the site. This was considered more important than the distance of the station since proximity to the coast can exert a large influence in local cloud cover conditions. Where a trial site was some distance from the nearest agrometeorological recording station, the data were adjusted by the following correction factors for increased altitude(Barry and Chorley, 1967):

Radiation: 5 - 15% (mean 10%) increase per 1000 m

Temperature: 5 - 7 °C (mean 6°C) decrease per 1000 m

Rainfall: East slopes 253 mm per 100 m, West slopes 83 mm per 100 m
or 10% increase per 100m

Weather data for trials outwith the UK were not included in detail, although figures for accumulated thermal times were taken directly from references where given.

Temperature

Angus *et al.* (1980) compared development rates for a wide range of crop species and showed that duration of phenological phase had a strong linear relation with mean temperature during the phase such that development proceeded faster as temperature increases but that duration of each stage was reduced. Both mean temperature during each stage and accumulated temperatures were stored. Thermal time (H) is the integral of temperature with respect to time above a given base temperature (T_b). It was approximated by calculating accumulated temperature from daily maximum and minimum temperatures (T_b = 0°C) using the standard Agromet method (Meteorological Office, 1969) as follows:

Minimum daily temperature (T_{min}) > T_b	$H = T_{mean} - T_b$
Maximum daily temperature (T_{max}) < T_b	$H = 0$
Mean daily temperature > T_b	$H = 0.5(T_{max}-T_b) - 0.25(T_b-T_{min})$
Mean daily temperature < T_b	$H = 0.25(T_{max}-T_b)$

Thermal time was accumulated on a daily basis. Angus *et al.* (1981) found that reducing the time step in their spring wheat temperature/photoperiod model to one hour did not increase the accuracy of the predicted date of anthesis.

The concept of base temperature is based on biological principles as well as statistical significance. Growth and development increase above T_b at roughly linear rates up to a critical temperature above which there is no further rate increase. Higher temperatures then have an adverse effect on development. The base temperature is not the temperature at which growth and development cease, but rather that which minimises the variation in the accumulated temperature required to reach a particular stage of development. In the UK the effects of super-normal temperatures are usually ignored, although it is possible to incorporate the effect as in the CERES models.

Exact values for T_b and the upper limit depend on both the environment and the development stage. Detailed experimental work has provided estimates for suitable values from a number of locations world-wide (e.g.: Nuttonson, 1957). There is some evidence that T_b alters with sowing date (Kirby, Appleyard & Fellowes, 1985a, 1985b; Sharratt *et al.*, 1989) and thus with photoperiod (Angus *et al.*, 1981; Ellis *et al.*, 1988; Roberts & Summerfield, 1987; Roberts *et al.*, 1988) over the range 0 - 5°C, but this may be due in part to seasonal variation of apical temperature with respect to air temperature (Ellis & Russell, 1984). An analysis of soil temperatures at 5cm, 10cm and 20cm over the four years 1980 - 1983 at the Bush weather station outside Edinburgh, showed that soil temperatures were highly correlated with air temperature

($r^2 > 0.97$) although the soil takes longer to warm in spring, and cool down in autumn. However, although soil temperature at sowing depth would better estimate apical temperature during the early stages of development whilst the stem apex is below soil level, from the onset of stem extension, air temperature becomes a better estimate. Following established practice, air temperatures were used throughout this analysis.

Table 5.4. Variation in base temperature with development stage

DEVELOPMENT PHASE	T_b	95% CI	DATA SETS
Sowing to emergence	3.03	2.42 - 3.64	173 x
Sowing to collar initiation	4.02	3.39 - 4.66	135
Collar initiation to MPN	2.60	0.44 - 4.76	44 xx
MPN to anthesis	10.44	7.94 - 12.95	45 xx
Anthesis to maturity	7.34	-0.06 - 14.74	13 xx

x denotes a row with X values away from the centre
xx denotes a row with very extreme X values

T_b was determined from the database for each development phase to test its stability. Development rate during the phase, measured as the reciprocal of the phase duration (Delecolle *et al.*,, 1989), was plotted against mean temperature during the phase. The intercept on the x-axis gives the least squares value for T_b (Table 5.4). T_b did not vary significantly between sowing and MPN and confirmed the value of 2.6°C (S.E. 0.28°) reported by Angus *et al.* (1980) using least squares estimation. However, the residuals from the regressions increase with temperature indicating that temperature alone cannot explain the variation in development rate.

Solar Radiation and Photoperiod

Solar radiation is not recorded at all agrometeorological stations, and in the event of missing data, values were calculated from sunshine hours at the site. The relationship between sunshine hours and solar radiation is a function of the latitude and the day of the year. The closest fit between measured and calculated ($r^2=0.966$) solar radiation for a site where both solar radiation and sunshine hours had been recorded (Edinburgh, Bush House, 1983) was obtained using the expression in McGechan (1985) based on the Ångstrom (1924) method. However, this was designed to be used with 10 day periods and errors are to be expected when daily values are used. Calculated daylengths include daylight hours plus twice civil twilight (Keisling, 1982).

ARCWHEAT uses a photo-vernal-thermal time scale for modelling phenology (Table 5.5). A photoperiod factor (P_f), ranging from 0 (severe photoperiodic limitation) to 1 (no limitation) is based on the difference between actual photoperiod (P_h) and an optimum photoperiod of 20 hours. Base photoperiod (P_b) varies with phase of development.

$$P_f = (P_h - P_b) / (20 - P_b)$$

If the value for P_b is low, then the effect of the photoperiod correction factor, P_f, is decreased (Table 5.5) and accumulated photothermal time will be increased. Photothermal times were calculated for each development stage using the suggested values for P_b and P_{opt}, however, the range of values for each stage was very large.

Table 5.5a Values of the photoperiod correction factor P_f

Popt = 20	**Pb = 0h**	**Pb = 7h**	**Pb = 12h**
8h Photoperiod	0.4	0.08	0
10h	0.5	0.23	0
12h	0.6	0.38	0
14h	0.7	0.54	0.25
Popt = 16			
8h Photoperiod	0.50	0.11	0
10h	0.63	0.33	0
12h	0.75	0.56	0
14h	0.88	0.78	0.50

Table 5.5b The timing of development in the ARCWHEAT model

DEVELOPMENT STAGE	°Cdays	Photo-Vernal-Thermal time	P_b	T_b
Emergence	120	T		1
Floral Initiation	140	PVT	0	1
Double Ridge	130	PT	0	1
Terminal Spikelet	90	PT	7	1
Beginning Ear Growth	205	PT	7	1
Anthesis	200	PT	7	1
Start Grain Fill	65	T		9
End Grain Fill	260	T		9
Maturity	40	T		9

Thermal times for 'Avalon' winter wheat, Brooms Barn (Latitude 52.3°N),
Model input data: Porter (Pers. comm.)

The cumulative degree of vernalisation affects the duration of vegetative growth prior to floral initiation. Vernalisation may occur between -4°C and 17°C, but is most effective between 3°C and 10°C. Full vernalisation for wheat cv. 'Avalon' required 33 vernalisation days (cf. 30 Thermal Development Units in CERES barley).

Base photoperiods (P_b), which minimised the variation in accumulated photoperiod required to reach a particular stage, were determined from the barley database by a similar method to T_b. P_b in the ARCWHEAT model is set at zero before double ridge stage and 7 hours after. Equivalent values for P_b from the barley database (Table 5.6) were higher than these figures and showed an increase in P_b with development. Values of P_b of 10 hours from sowing to collar initiation, 13 hours from collar initiation to MPN and 15 hours after MPN were used to calculate photothermal times for the database.

Table 5.6. Variation in base photoperiod with development stage

DEVELOPMENT STAGE	P_b	95% CI	Number of Data Sets
Sowing to			
Emergence	12.4	12.2 - 13.0	219
Collar initiation	10.4	9.5 - 11.2	175
Double Ridge	5.8	4.7 - 6.8	29
MPN	8.4	5.6 - 11.2	7
Ear Emergence	8.6	7.5 - 9.6	12
Anthesis	9.3	8.5 - 10.2	41
Maturity	10.6	10.3 - 10.9	95
Harvest	9.9	9.4 - 10.4	105
Sowing to collar initiation	10.4	9.5 - 11.2	175
Collar initiation to MPN	13.4	12.8 - 14.0	61
MPN to anthesis	16.3	15.9 - 16.7	53
Anthesis to maturity	15.8	15.5 - 16.2	95

5.2.3. SITE DESCRIPTION

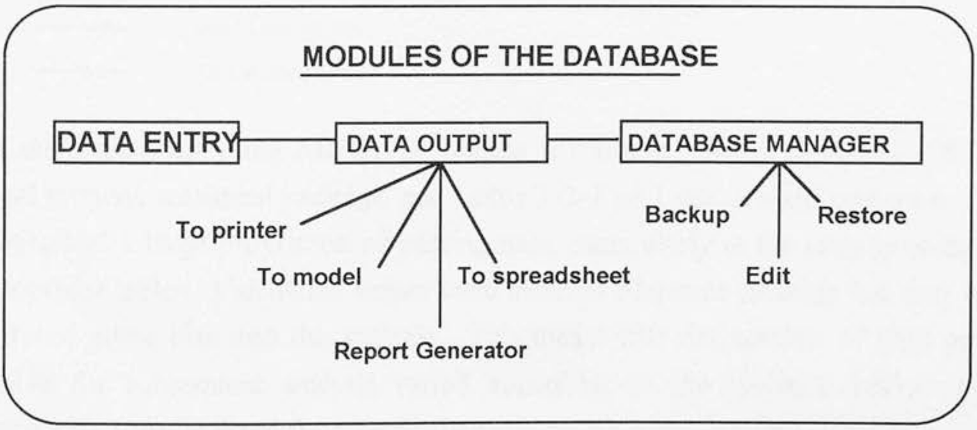
Detailed soil physical and chemical characteristics were not generally recorded for these data sets. The soil series and classification for each trial were found from Soil Survey maps (eg. Anon, 1971) and an estimate of soil depth, chemical composition (soil pH and organic matter content only) and texture obtained for input to the

SOILDATA program for each layer. Soils were further categorised according to texture and drainage (Appendix C) using the recording scheme for Co-ordinated Variety Trial sites. The database holds descriptions of 33 soils, representing the main agricultural soils of Scotland.

5.3. DATA STORAGE AND ANALYSIS

The database was stored on an IBM compatible microcomputer using the dBase III+ (Ashton Tate, 1985) relational database management software. It was developed as a series of linked modules for data entry, output and file management written in the dBase language, each dealing with a specific aspect of the system (Figure 5.2). The system was menu driven, fully integrated into one initial menu, to lead the user quickly to the required process with minimum keyboard action. A modular approach ensured that the complete system had a continuity of design and a high degree of data compatibility. dBase was chosen for its ability to relate information from up to 10 tables at once and for its sophisticated querying facilities which allowed enquiry on any field of the database. Attributes of each entity are given in Appendix C (Figure 5.3) A suite of supporting FORTRAN programs were used to calculate day number, days from sowing, accumulated temperatures and photoperiods and daily solar radiation from sunshine hours..

Figure 5.2. Inter-relationships between modules of the database.

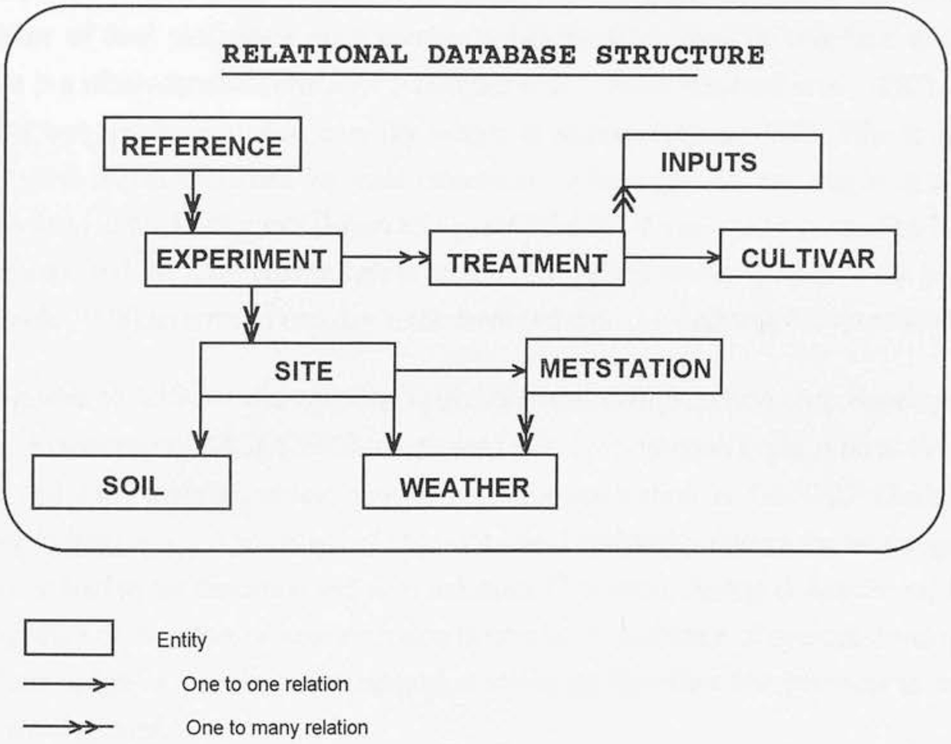


Supporting administration options included a flexible use of the printer, and easy system back-up and restore. Power faults only affect the current activity (individual record) on the screen, but in the unlikely event of file corruption, the facility to restore files from back-up was included. The ability to amend/update individual or groups of records was also included in the database manager. Further enhancements to the system can be easily accommodated into the menu system once initiated and integrated to give a standard approach.

The system does have some disadvantages:

memo fields are extravagant with storage space
access time for queries increases as the number of links between files is increased

Figure 5.3. The relational database structure



Data were analysed using MINITAB release 6.1 (Ryan, Joiner & Ryan, 1985), a general purpose statistical package, and Lotus 1-2-3 v3.1 spreadsheet software. The database had a large proportion of missing data, particularly in the crop growth and development tables. Calculated values were inserted wherever possible but may have introduced some bias into the analysis. This meant that the number of data points available for subsequent analysis varied according to the question being asked. Missing data were omitted from calculations; regression for example, used only cases where both the dependent and all independent variables were present. The database did not have an even spread of points between sites, seasons, cultivars or experimental methods, however, the relation between crop development, cultivar, temperature and photoperiod could be explored for a range of sites and sowing dates.

6. MODELLING BARLEY DEVELOPMENT

6.1. INTRODUCTION TO FACTORS AFFECTING DEVELOPMENT

Accurate prediction of the rate of development and duration of different developmental stages, and particularly of the dates of floral initiation and anthesis, is an essential part of mechanistic modelling of crop growth. Pinpointing floral initiation precisely is important since rates and duration of primordium production can vary widely between sowing dates and cultivars with differing vernalisation requirements. The date of anthesis can be a good predictor of final yield since grain number is largely determined by this time and grain weight is a relatively stable character (Gallagher *et al.,* 1976b; Shepherd *et al.*, 1987). Grain number can also be related to crop dry weight at anthesis (Dyson, 1977; Ellis & Russell, 1984) so it is also important for yield estimation. Above ground dry weight at anthesis ranges from 296 - 1275 g m^{-2} (Mean 850 g m^{-2} SE 34). If grain yield is equal to biomass at anthesis, and the crop growth rate is 36 g m^{-2} d^{-1} (cf maximum CGR 34 - 39 g m^{-2} d^{-1} Monteith, 1978) an error of one day in the predicted date can lead to a 4% error in yield.

Field guides to fertiliser and chemical application are often based on crop developmental stage. For example, BASF (1990) recommend split dose nitrogen application at the 3-leaf stage and early stem extension; growth regulator application at GS30-37 (Zadoks) to reduce lodging risk. Application of hormone-based herbicides during the late vegetative stage can lead to ear distortion and yield reduction (Thomson, Scragg & Matthews, 1984). Recognition of the onset of stem extension from reliable prediction of internal development and knowledge of its relation to external morphology therefore has practical as well as theoretical interest.

The duration of phenological stages is controlled by a complex interaction of genotype and environment including effects of temperature and photoperiod. Several hypotheses were tested using the barley database in which development stage was related to various factors:

A. Sowing date
B. Time - measured in days from sowing
C. Thermal time - °Cdays
D. Photo-thermal Time - °Cdays
E. External Morphology - Leaf Number
F. Primordium initiation rate - primordia $°\mathrm{Cdays}^{-1}$
G. The ARCWHEAT winter wheat model of photo-vernal-thermal time
H. The van Keulen spring wheat model concept of proportional thermal time

6.1.1. PHOTOPERIOD

Barley is a quantitative 'long-day' plant - the rate of development and time to flowering are faster in longer days but it will eventually flower even in short daylengths provided there are not long periods of darkness. However, short days can delay the switch from vegetative to reproductive growth (Rahman & Wilson, 1977). The implication of this is that there are dark processes which will inhibit flowering, but which are themselves inhibited at low temperatures. Since the switch takes place whilst the apical meristem is still below ground level, the leaves must therefore be the sensory organs for daylength. There is some evidence that the plant is sensitive to the direction of rate of change of daylength at emergence, and will respond differently in lengthening or shortening days (Ellis & Russell, 1984). The 'flowering hormone' will be synthesized in the leaves under conditions of long, or lengthening daylight.

Roberts *et al.* (1988) recognise an 8 to 10 day 'pre-inductive' phase after germination during which the vegetative plant does not respond to the photoperiods which normally initiate the flowering response. The duration of the phase varied little between genotypes in their experiments, provided their vernalisation requirement had been satisfied, but was extended for unvernalised winter cultivars. After this, the development rate increased linearly with mean photoperiod at any one latitude. Stewart & Dwyer (1987) conducted growth room experiments at photoperiods of 8, 12 and 16 hours and showed that the effect was non-linear; a decrease from 16 to 12 hours had little effect on development rate before anthesis, but a further decrease to 8 hours slowed the rate markedly.

The duration of each phase shows an inverse relation with mean photoperiod during the phase (Cottrell *et al.*, 1981; Thomson, 1979). For example, the rate of primordium production increases with photoperiod (Thomson & Matthews, 1982), but takes place over a shorter period resulting in the production or survival of up to 20% fewer spikelets per ear (Cottrell *et al.*, 1981; Thomson, 1979).

The response to photoperiod, measured as the slope of the regression of development rate against photoperiod, varies markedly between cultivars (in wheat, 'early Australian cultivars had Tb of 7.6h, 'late' cultivars had Tb of 9.1h: Angus *et al.*, 1981). The critical photoperiod may be modified by other factors such as nutrition, irradiance, and plant age but there is little supporting data.

Nicholls (1974) compares development in wheat, rye, barley and oats under short (12hr) and long (16hr) photoperiod controlled environment conditions at the same temperature. Development was faster in barley than wheat under long daylengths and was delayed markedly in oats in short days, but only delayed a little in the others. However, cv 'Clipper', which was used as the barley cultivar, has extreme sensitivity to photoperiod and did not reach MPN until awn appearance in the short day treatment.

The response is also temperature dependent. The influence of temperature decreases with increase in photoperiod suggesting that the photoperiodic effect is paramount (Guitard 1960). Keatinge *et al.* (1979) working with perennial ryegrass, showed that daylength largely influenced the date of initiation of reproductive growth, but subsequent growth and development towards ear emergence was mainly influenced by temperature. The final number of main stem leaves is determined before double ridge is achieved and thus the phase from double ridge to anthesis may be unaffected by photoperiod. After anthesis, the rate of development is insensitive to photoperiod (Aitken, 1974; Angus *et al.*, 1981).

Models using photoperiod to weight thermal time imply that the effect does not alter within each phase of development. Ellis *et al.* (1988) use a general equation :

$$\text{Development Rate} = a + bT + cP$$

relating development rate to mean Temperature (T) and mean Photoperiod (P) during the phase. Their results were obtained for the sowing to awn emergence phase under constant photoperiod controlled environment regimes, but they also found that certain genotypes responded to changing photoperiods prior to MPN.

The effect of sowing date

Since photoperiod is completely specified by latitude and the day of the year, sowing date has proved to be important in determining rates and durations of development phases. Several experiments have looked at the variation in development rate over a range of sowing dates (Patel, 1979; Ellis & Russell, 1984; Jones & Allen, 1986; Wright & Hughes, 1987) to investigate the combined effect of temperature and photoperiod.

The low temperatures and short days of winter slow development of autumn sown cultivars, to maintain them in a vegetative state with associated increased resistance to frost. Spring sown cultivars are sown into a period of lengthening days and increasing temperatures and develop faster. Delayed sowing of spring cultivars results in faster development and earlier attainment of all stages of development (Patel, 1979; Wright & Hughes, 1987). Knopp (1985) compared development rates in nine winter barley cultivars in Denmark and found a delay of 40 days in sowing was reduced to a difference of 6 days in the date of anthesis. The hastening of development is associated with a reduction in the number of leaves together with an increased rate of leaf production. In addition, late sowing may minimise infection, and enable plants to withstand disease by quick replacement of older diseased leaves within the canopy.

The effect of latitude

A systematic variation in photoperiod occurs with increasing latitude. At high latitudes, cultivars are selected for a high response to photoperiod to enable sowings over a wide range of dates to reach grain fill during the optimal period around the longest day of the year. Experiments to compare similar crops at sites of different latitude, (Ellis & Kirby, 1980; Cottrell *et al.*, 1985) showed that the effect of longer photoperiod at northerly sites was often offset by a reduction in temperature. However, overall yields were often higher at the northern sites, due to cooler conditions and heavier rainfall prolonging the period of grain fill and allowing heavier grains to develop. Taller plants which are heavier at anthesis have a greater ability to translocate reserves into larger primordia in cooler environments. Cool, damp weather also encourages persistence of leaf area (Biscoe & Gallagher, 1977). However, barley cultivars are generally more widely adapted to latitude than wheat cultivars (Bingham, 1976; Russell, 1990; Russell & Wilson, 1993).

Changing daylength at emergence

Including the rate of change of daylength at crop emergence (CHGDL) in a model can improve prediction of development (eg: Constable & Rose, 1988 modelling soybeans), since the direction of change may be of crucial importance. Development may be inhibited under conditions of decreasing photoperiod (negative CHGDL) and accelerated under increasing photoperiods (positive CHGDL) but the importance of CHGDL decreases at lower latitudes as daylength changes less in the tropics. Cultivars differ in their sensitivity to CHGDL (Ellis & Russell, 1984; Jones & Allen, 1986) as to photoperiod. Data from controlled environments ignore CHGDL as a potential factor controlling development (Ellis *et al.*, 1988, Roberts *et al.*, 1988*)*.

6.1.2. GENOTYPE

Several factors may cause differential development rate between cultivars. However, these differences are generally smaller than those attributable to sowing date. The erectoid and semi-prostrate dwarf types may have reduced grain size as well as height, but this is compensated for by the lower likelihood of lodging. The contribution of genotype to the variation in date of anthesis may be 80-90%, to grain weight, 50% and to grain number per unit area, 20%.

Tillering

Cultivars differ in tillering habit, ranging from uniculm cultivars which tend to produce large, heavy ears, to freely tillering cultivars producing up to 20 ears per plant. Lower tiller number reduces loss through sterile tillers and allows remaining culms to produce larger ears (Donald, 1968). A study of the early development of three winter barley cultivars showed leaf primordium formation was complete and tiller development commenced before the second leaf had fully unfolded (Appendix D), with tiller buds forming in the axils of the coleoptile and first leaf from emergence onwards. Tillering in spring barley continues until about MPN, longer than winter wheat (Kirby & Ellis, 1980; Gallagher & Biscoe, 1978a). Tillers develop faster than the main stem so that ear emergence occurs within a few days on all fertile stems. This may be partly explained by tillers producing fewer leaves, with an average of 5 leaves per ear-bearing tiller found in spring barley (Appendix D). The effect of plant population on the number of grain-bearing ears is compensated by an increase in the duration of tillering at low densities (Nerson, 1980; Kirby & Faris, 1970) and the initiation and growth of secondary and tertiary tillers at each primary tiller site.

Ear Type

Row number and floret fertility are both under genetic control. Well-adapted 2-row types produce more tillers, bearing ears with fewer grains than 6-row types. 2-rows also produce more leaves and leaf emergence can start earlier (Kirby & Riggs, 1978; Appendix D). However, this delays ear initiation and reduces the duration of spikelet initiation and pre-anthesis spike growth.

Leaf Type

Lax leaf genotypes reach canopy closure earlier, but more light can penetrate through an erect leaf canopy so lower leaves senesce more slowly, giving them a slight advantage in higher LAI during the latter part of development and prolonging the period of grain fill. Tillering is also enhanced in erectoid leaf types due to the greater light penetration (Donald, 1968) through the canopy, prolonging the pre-MPN phase.

Vernalisation requirement

Barley cultivars can be classified into winter, spring or facultative types according to their vernalisation requirement, although the classes are not distinct. Spring cultivars do not require vernalisation, but the stem apex of winter cultivars requires exposure to a period of cool temperatures, either as an imbibed seed or as a juvenile plant, before floral initiation occurs. The response may be seen in the range -5 to 16°C with an optimum in the range 0° to 8°C (Kirby, 1973). The number of days required for full vernalisation increases with temperature. This vernalisation requirement prevents floral development during winter providing additional protection for the more sensitive floral organs (Law *et al.*, 1976). The response may be conditional on cool temperatures being followed by long days. A period of short days before the cool temperatures may enhance the effect in some genotypes. The response is more effective in young leaves (Bernier *et al.*, 1981). Vernalisation is reversible if a period of warm weather occurs before it is complete. A further period of cold temperatures will re-start the vernalisation process, but once complete, the process is irreversible.

Delayed sowing of winter cultivars may result in an unsatisfied vernalisation response. Vegetative growth continues with the initiation of more leaf primordia and formation of many main-stem leaves (Pugsley, 1983; Rahman, 1980; Jones & Allen, 1986; Ellis & Russell, 1984) and ear emergence is delayed or inhibited.

Frost Tolerance

Cold hardening is greatest under conditions of long photoperiod and decreasing temperatures. A temperature below 10°C is sufficient to induce partial hardiness but not sufficient to maintain hardiness in fully acclimatised crowns. Extreme low temperatures or freeze-thaw action can weaken hardiness. Cold survival is positively correlated with water content of the crowns.

6.1.2. TEMPERATURE

The rate of apical development is largely dependent on temperature (Kirby & Appleyard, 1978). Development has been linked both to accumulated thermal time from sowing (Ritchie *et al.*, 1984) and to mean temperature during each development phase (van Keulen & Seligman, 1987). Other processes which are temperature related can therefore be used as a guide to apical development.

Leaf number

Leaves emerge at a more or less constant rate with respect to thermal time (Delecolle *et al.*, 1989; Cao & Moss, 1989a, 1989b) and variation in the rate of primordium production was found to be strongly correlated to the total leaf number, with the number of primordia at any time related to emerged leaf number (Kirby, 1993). This has led to the use of the phyllochron as a measure of apical development (Ritchie *et al.*, 1984). Kirby (1969) found a close correlation between leaf number and time to ear emergence depending on cultivar. Final leaf number has also been shown to be related to time by a sine function (Russell, 1990) and a negative exponential function (Miglietta, 1991a, 1991b).

Kirby and Appleyard (1984) suggest approximate leaf numbers for each stage of apical development, based on month of sowing. However, crops of cv 'Proctor' barley sown over a range of dates in autumn and spring produced nine mainstem leaves irrespective of sowing date (Scott & Dennis-Jones, 1976). Leaf number varies with photoperiod and thus with sowing date (Gallagher *et al.*, 1983; Jones & Allen, 1986; Miglietta, 1989), with fewer leaves produced under long photoperiods and at high densities. Varietal differences, especially between 2- and 6-row types and those with different photoperiodic sensitivity, may also account for variation in leaf number and development rate (Kirby, 1967). Jones & Allen (1986) looked at the control of leaf number by daylength, and found a relationship between daylength at emergence, the direction of change of daylength and leaf number, but found no significant temperature effect. On this basis, northern sites might be expected to have 0.5 - 1 more leaves than southern sites across the span of latitudes in this study from early autumn sowings, similar numbers from October sowings, and fewer leaves from later sowings. However, little difference in leaf number was observed between Cambridge and Edinburgh (Kirby & Ellis, 1980) with a range of 8.5-10 leaves for spring-sown cvs. 'Golden Promise' and 'Maris Mink'.

Rate of leaf emergence

Leaves emerge on the main stem at a constant rate per degree day between emergence and ear emergence, by which time all leaves are fully unfolded. The rate of leaf emergence can be expressed in thermal time as R_l - leaves °Cday^{-1} (the reciprocal of the phyllochron) and varies little between sites and seasons (Jones & Allen, 1986; Ritchie *et al.*, 1984) although some variation occurs between genotypes (Marshall & Boyd, 1985 for wheat; Naylor & Munro, 1993 for wheat and barley). Variation from 0.007 to 0.013 leaves per °Cday (phyllochron 76 to 140 °Cdays) has been reported. However, since each successive leaf has further to travel before it emerges, R_l is not the same as the rate of leaf extension (Hay, 1986).

R_l may increase with daylength (Kirby, Appleyard & Fellowes, 1982; Baker & Gallagher, 1983; Porter, 1984, 1985, Delécolle *et al.*, 1985), thus the phyllochron is reduced (Roberts *et al.*, 1988) and leaf production is increased under longer photoperiods. This was confirmed at constant temperature in controlled environment experiments by Cao & Moss (1989a). There is some support for the concept of a reducing phyllochron between successive leaves (Miglietta, 1991b).

Primordium production

The onset of reproductive growth has been equated with an acceleration in the rate of primordium production that occurs at about this time (Figure 5.1). Both leaf (R_p) and spikelet primordium initiation (R_s) are approximately linear processes with respect to thermal time, although the first few leaf primordia may well form at a slower rate within the germinating seed. There is some doubt as to whether the point of rate increase coincides with collar initiation, but it almost certainly occurs before double ridge stage is reached. The use of double ridge to approximate the switch would substantially overestimate the time when the rate changed. Kirby *et al.* (1987) found 48-82% of the final spikelet numbers of wheat were initiated by double ridge.

Delécolle *et al.*, (1989) describe a model for wheat incorporating the number of primordia in the embryo (a), sowing date, R_p, R_s, the date at which the rate changed (T_{12}), Collar Initiation (T_0) and Terminal Spikelet (cf. MPN in barley). They found that T_{12} did not coincide with T_0 for all sowings, and some spikelets were initiated at the slower rate, but no leaves were ever initiated at the faster rate. Double ridge showed no consistent relationship to any of these parameters. Variation in the number of embryonic primordia was simply expressed by varying the intercept for the model.

The model for the transition to reproductive growth may be associated with a critical apex size (Charles-Edwards *et al.*, 1979 - modelling chrysanthemums), or with biochemical systems (Williams & Cartwright, 1980), or may be genetically determined (Riggs & Kirby, 1978). Thornley & Cockshull (1980) include apical size, primordial size and plastochrons (interval between successive primordial initiations) using catastrophe theory to describe the switch. Data to test these alternative theories were not available.

The ARCWHEAT development model

Wheat has a morphologically recognisable conclusion to the phase of spikelet primordium initiation in production of the terminal spikelet. Barley has no exact equivalent, but primordium numbers increase to a plateau at MPN and then decline until anthesis. Barley also develops faster than wheat (Kirby, Appleyard & Fellowes, 1985b) so a comparison of the duration of development phases was inappropriate. Duration of development phases for a cultivar in thermal or photothermal time is read from input in the ARCWHEAT model. If these values are constants between sites and seasons for each cultivar, then the timing of development will be predicted accurately. Values for the mean photothermal times for each developmental phase were calculated for the barley database to see if they remained constant for cultivars between seasons.

Leaves grow and senesce at a rate determined by thermal time. Thermal time is also the driving variable for production and death of shoots. The rate of leaf appearance (R_l), the inverse of the phyllochron, is defined by the following equation:

$$R_l = 0.025 * CHGDL + 0.0104$$

A crop emerging on the 15th September at latitude 52°N would produce a new leaf every 129°Cdays; on the 15th December, every 98°Cdays. This equation was tested with barley data and predictions made by the CERES model.

The van Keulen spring wheat development model

Development of spring wheat is divided into pre-anthesis and post-anthesis phases, with the length of each phase determined by regression of the number of days between emergence and anthesis, or anthesis and maturity against the mean temperature during the phase. Intermediate development stages are reached after a fixed proportion of the phase has elapsed. Two questions were thus addressed using the barley database:
Is the pre-anthesis phase length linearly related to mean temperature during the phase?
Is the proportion of the phase in thermal time to reach each intermediate stage constant across sites, seasons and cultivars?

6.1.4 OTHER FACTORS

Planting density

Kirby and Faris (1970) found that increasing the density from 50 to 1600 plants m^{-2} reduced leaf number and hastened double ridge by 6 days. Stem extension began earlier and started at a lower internode in dense populations, with thinner, weaker stems as a result (Kirby 1976). The duration of the tillering phase was also reduced. R_S is not affected by density, but the duration and final spikelet number may be reduced at high densities (Kirby & Faris, 1970; Scott & Dennis-Jones, 1976).

Soil moisture level

Soil conditions, especially water status, can have a great effect, particularly in determining germination, crop emergence and the duration of the tillering phase. Raised evapo-transpiration earlier in the season in densely planted crops can lead to water stress. Moisture stress may then slow the rate of spikelet initiation (Green, 1984; Ellis & Russell, 1984), possibly due to slower transport of the hormonal floral stimulus (Bernier *et al.*, 1981). Undifferentiated tiller sites appear better able to survive periods of stress than elongated tiller shoots, such that tillering can recommence later in the season if conditions become favourable again. Late tillering may occur when heavy rainfall follows a period of water stress. This resumed vegetative growth has an adverse effect on yield, since the late tillers do not ripen at the same time as the main crop and have fewer grains. High nitrogen levels prolong the vegetative phase and reduce reproductive development (Bernier *et al.*, 1981); conversely, deficiency during the reproductive phase slows the rate of spikelet production. If nutrient levels fall, previously formed tillers continue to grow but further tiller buds do not elongate; when restored, tillering recommences.

Atmospheric conditions and solar radiation

Atmospheric carbon dioxide concentration affects development and carbon dioxide removal reduces floral initiation. Leaf canopy development is influenced by the irradiance and spectrum of the incoming radiation (Russell *et al.*, 1989): a low ratio of red to far red light promoting faster development (Friend, 1965a, 1965b).

6.2. RESULTS FROM ANALYSIS OF THE BARLEY DATABASE

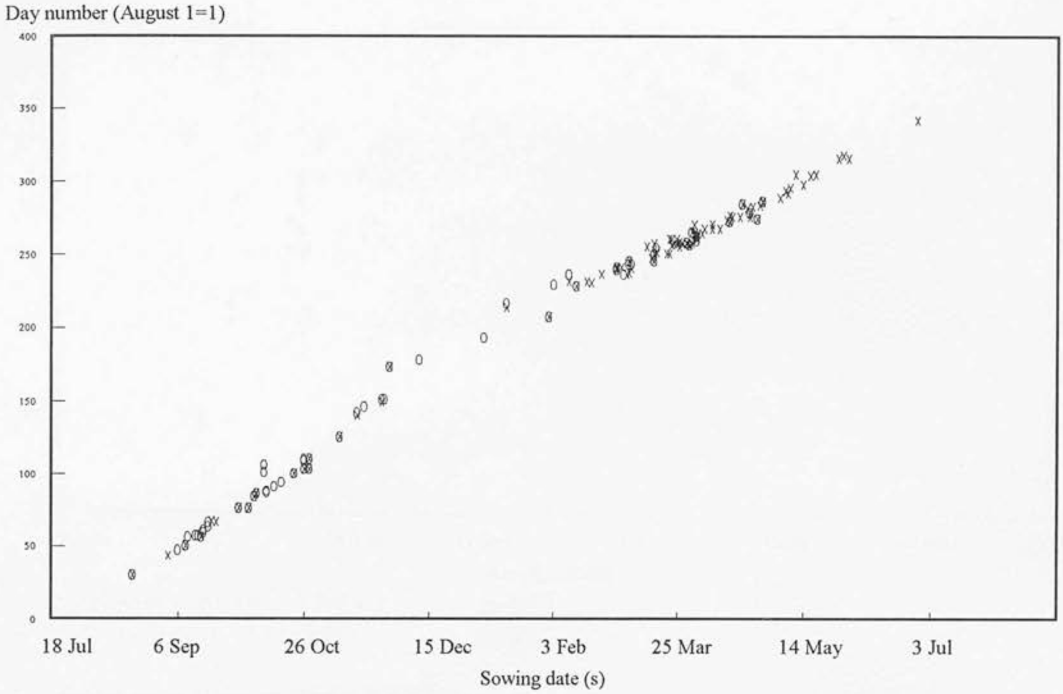
A. SOWING DATE

Crops matured between 3 July and 3 October despite a range of sowing dates which spanned the entire year (Table 6.1). The only exceptions were three sowings of winter barley in late spring and early summer, which did not mature due to an unsatisfied vernalisation requirement. The error attached to a linear regression of date of each development stage against sowing date increased as the interval from sowing increased. Sowing date gave a reasonable linear model for predicting crop emergence (r^2=99.0), but for collar initiation (r^2=90.0), double ridge (r^2=73.8), MPN (r^2=56.5), ear emergence (r^2=37.1), anthesis (r^2=57.3) and maturity (r^2=27.4) it explained progressively less of the variation (Table 6.2).

Spring cultivar development was more predictable than that of winter cultivars from sowing date alone (Table 6.2). Sowing date proved more important than the winter/spring genotype, and as the crop life cycle proceeded, the data were better described by a split line relationship with spring sowings showing a lower gradient than autumn sowings at double ridge and MPN, but a higher gradient at other stages of development. The slope of the regression for winter and spring cultivars was not significantly different at collar initiation, ear emergence or anthesis, but was at other stages of development. However, the difference between autumn-sown and spring-sown crops was significant at each stage suggesting that temperature and photoperiod effects override genotype for determining the vegetative phase duration and flowering date (Figure 6.1.).

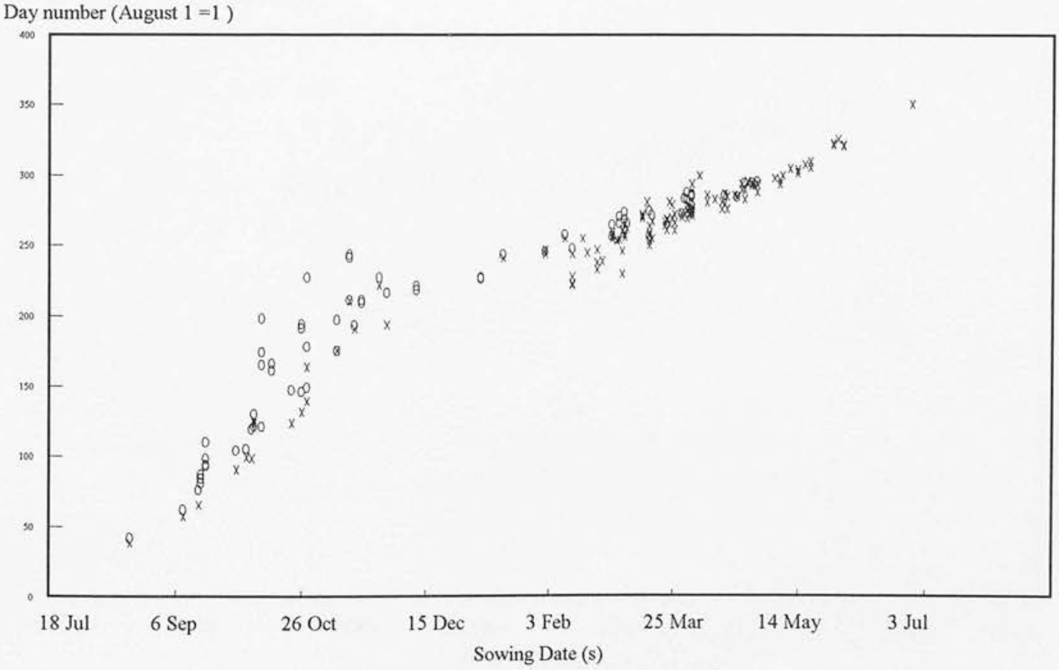
Figure 6.1. **Prediction of development stage from date of sowing. o = winter cultivars, x = spring cultivars**

a. Emergence



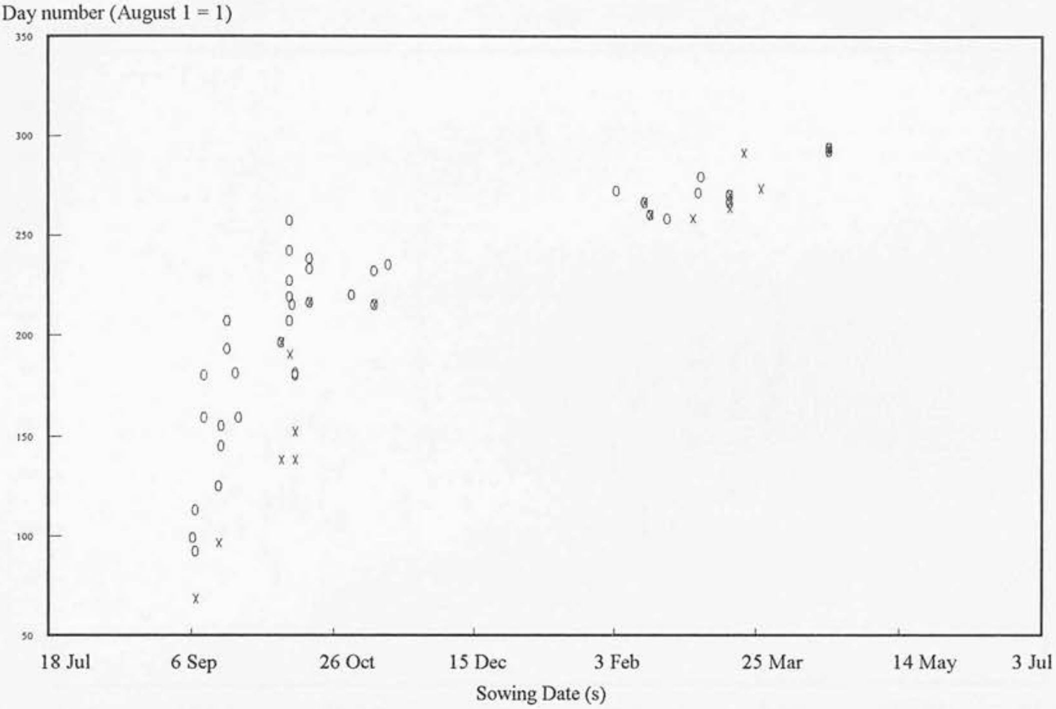
Date of Emergence = 17.47 + 0.99 s (n = 225)

b. Collar Initiation



Date of collar initiation (winter cvs) = 80.57 + 0.84 s (n=80)
Date of collar initiation (spring cvs) = 60.87 + 0.86 s (n=145)
Date of collar initiation (all cvs) = 78.04 + 0.80 s (n=225)

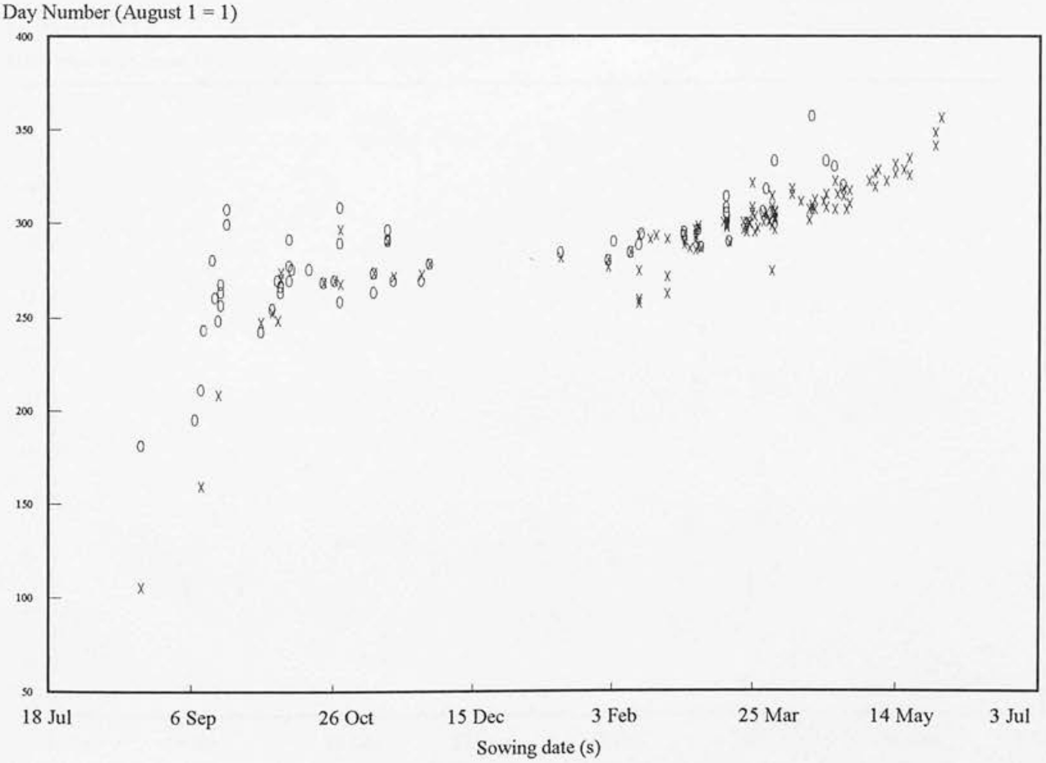
c. Double Ridge



Date of DR (winter cvs) = 146.65 + .059 s (n=47)

Date of DR (spring cvs) = 60.87 + 0.86 s (n=25)

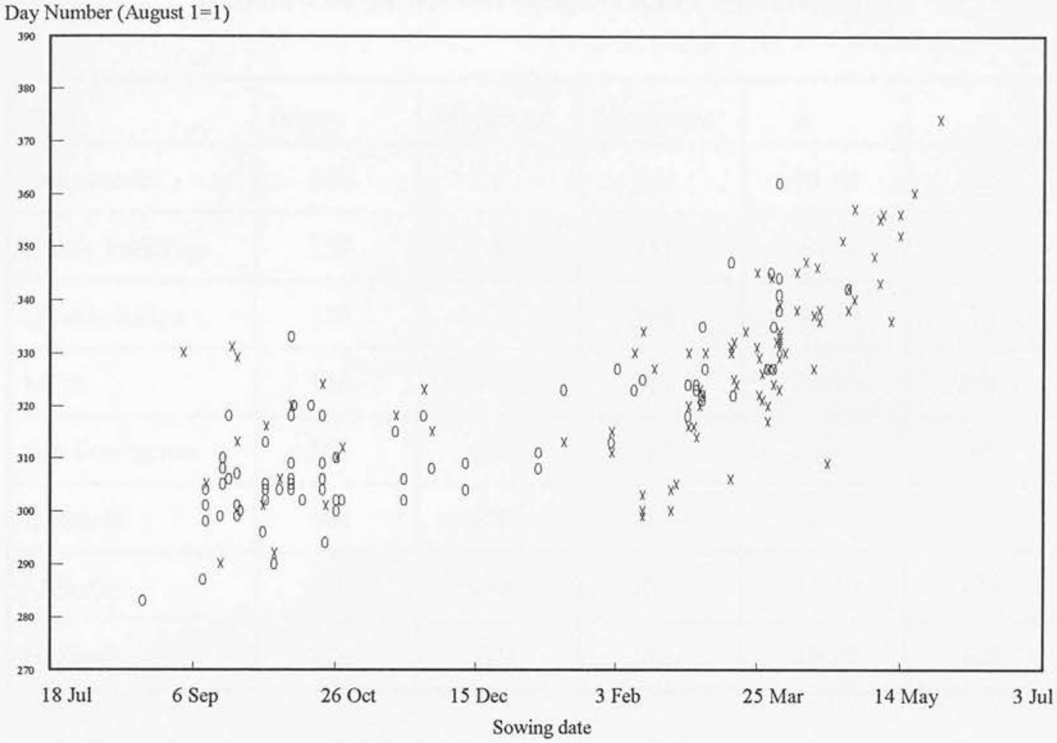
d. Maximum Primordium Number



Date of MPN (winter cvs) = 242.73 + 0.29 s (n=61)

Date of MPN (spring cvs) = 208.70 + 0.39 s (n=125)

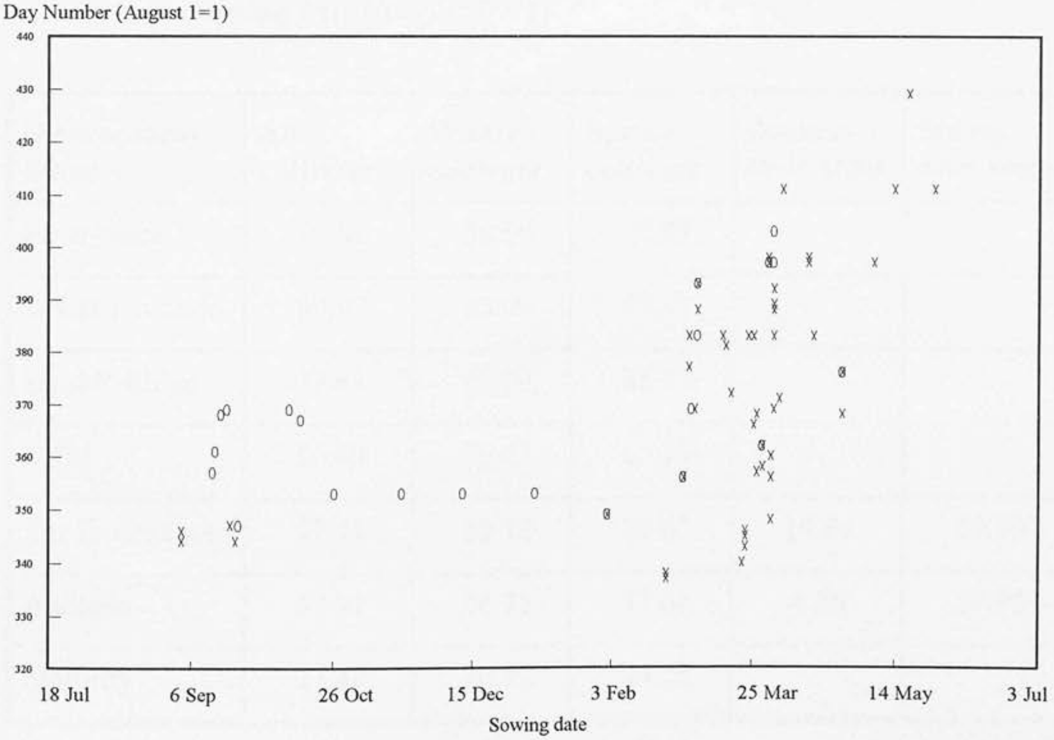
e. Anthesis



Date of anthesis (winter cultivars) 292.79 + 017 s (n=78)

Date of anthesis (spring-sown cultivars) n=116

f. Maturity



Date of maturity (winter cultivars) n=37

Date of maturity (spring cultivars) n=72

Table 6.1. Development stage related to calendar date (Jan 1st = 1). Mean, standard deviation and range of dates for each stage.

Stage	Mean	Minimum	Maximum	σ	n
Emergence	160	20	364	91.65	225
Collar Initiation	138	8	361	80.44	205
Double Ridge	124	2	364	95.83	72
MPN	140	6	317	31.93	188
Ear Emergence	166	120	201	14.97	84
Anthesis	169	130	221	16.66	190
Maturity	220	184	276	19.60	109
Harvest	221	190	276	18.97	125

Table 6.2. Sowing date as a predictor of development stage. Correlation of linear regression of date of reaching development stage against sowing date (August 1 = 1)

Development Stage	All cultivars	Winter cultivars	Spring cultivars	Autumn-sown crops	Spring-sown crops
Emergence	99.02	98.59	98.97		
Collar Initiation	89.97	85.00	93.91		
Double Ridge	73.81	69.29	86.24		
MPN	56.49	50.47	66.79		
Ear Emergence	37.14	68.72	28.67	19.84	59.89
Anthesis	57.31	66.71	37.61	4.18	58.92
Maturity	27.42	26.82	34.25		

B. TIME - MEASURED IN DAYS FROM SOWING

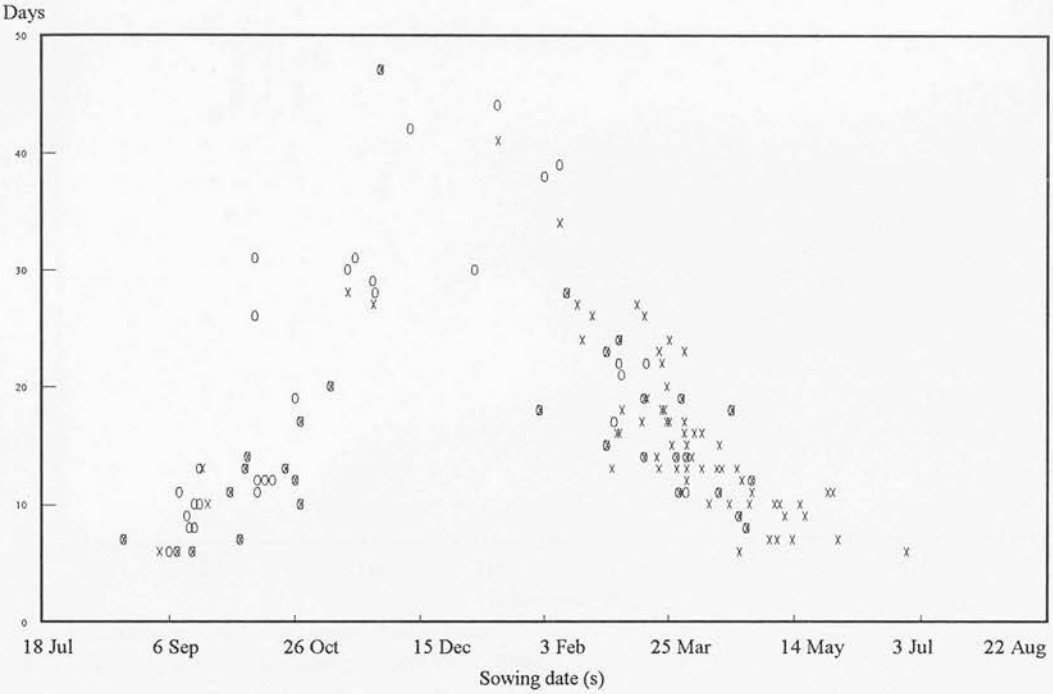
The number of days from sowing to each development stage shows a strong relationship with sowing date. The mid-winter peaks in the data (Figure 6.2) correspond with short daylengths and cool temperatures. Early autumn-sown crops reach collar initiation in a time of cool temperatures and decreasing daylength, whereas the spring-sown crops reach the same stage when temperatures and daylength are increasing (Table 6.3). However, double ridge and later stages of development are seldom reached before the winter solstice. Differences between autumn- and spring-sown crops become less important as the crop matures, with the peak in the data appearing earlier in the autumn. The data for regression of autumn- and spring- sown cultivars were separated at progressively earlier dates until MPN and as a single set thereafter. The regressions were calculated using *s* =sowing date (August 1=1). Two data points for winter cultivars sown in late spring were omitted from the regression at MPN since they showed incomplete vernalisation and did not reach anthesis. The timing of each development stage relates better to sowing date than to a particular calendar date, with interval from sowing more predictable for a given sowing date than the phase duration (Figure 6.3).

Table 6.3. Duration of phenological stages in days

Stage	Mean	SE	min	max	n
Sowing to emergence	16.18	0.53	6	47	225
Sowing to collar initiation	40.03	1.89	6	134	192
Sowing to double ridge	85.88	4.98	26	182	72
Sowing to MPN	99.24	4.46	27	254	188
Sowing to ear emergence	139.62	7.95	57	268	84
Sowing to anthesis	144.52	5.17	59	293	190
Sowing to maturity	172.95	6.60	97	317	109
Sowing to harvest	176.44	6.13	97	317	124
Collar initiation to MPN	60.75	3.92	15	209	158
Collar initiation to anthesis	92.07	2.96	42	241	137
MPN to anthesis	34.20	1.06	7	102	128
Anthesis to maturity	51.78	1.15	31	74	91

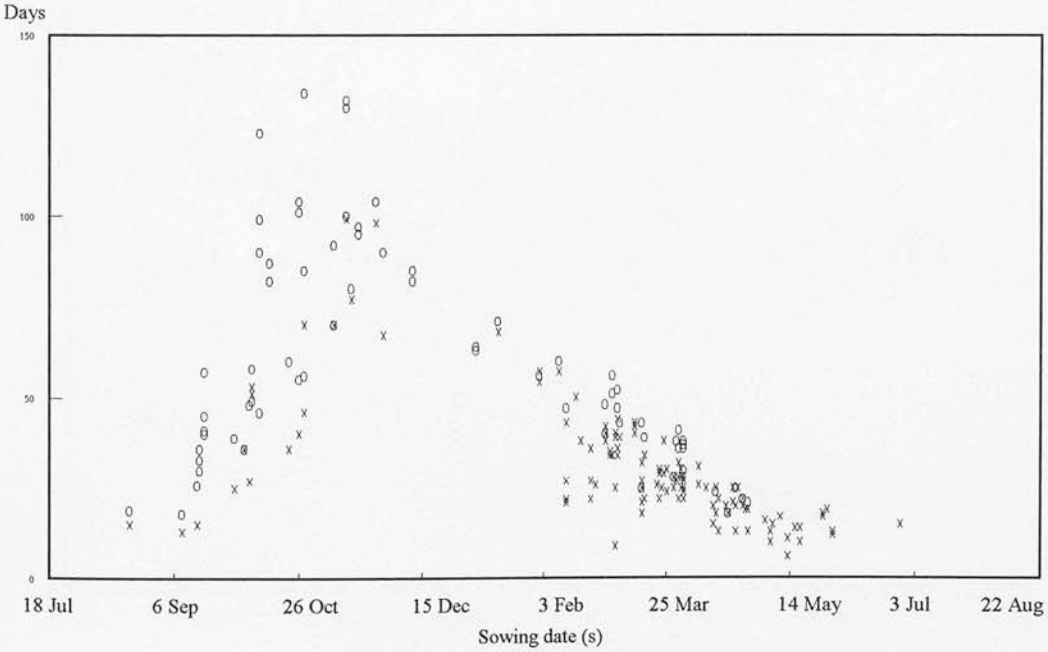
Figure 6.2. **The relationship between sowing date and the duration of development stages.**
o = winter cultivars, x = spring cultivars

a. Days from sowing to emergence



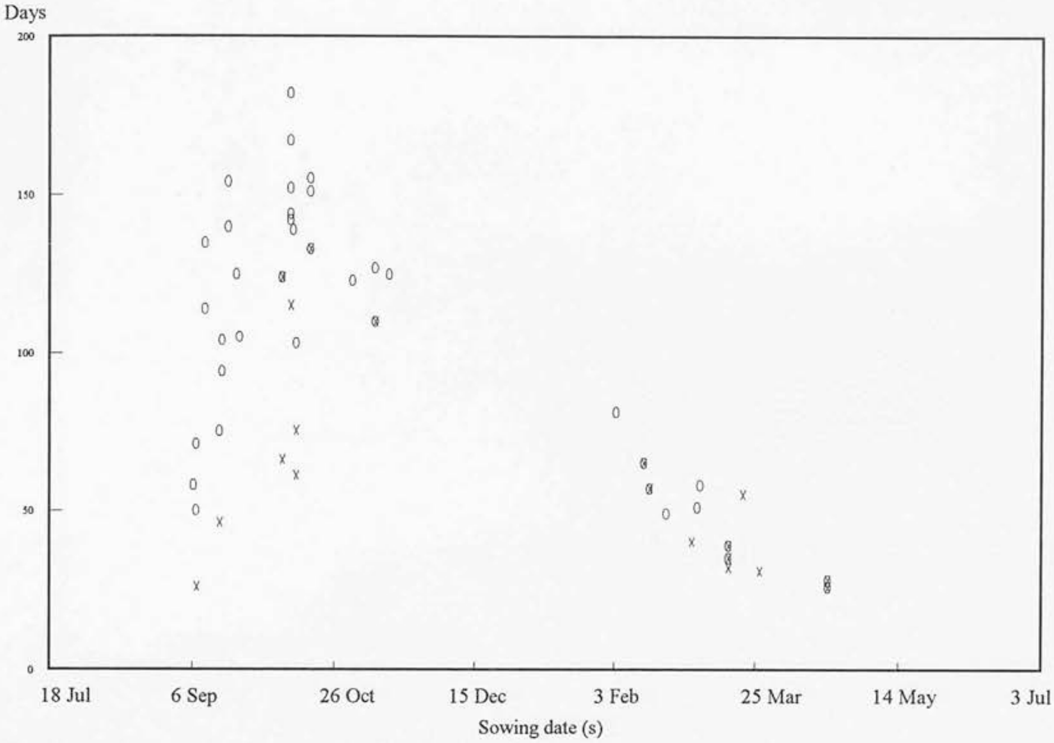
Days from sowing to emergence (autumn-sown) = -2.53 + 0.24 s (n=72)
Days from sowing to emergence (spring-sown) = 57.64 - 0.17 s (n=153)

b. Days from sowing to collar initiation



Days from sowing to collar initiation (autumn-sown) = -5.61 + 0.85 s (n=57)
Days from sowing to collar initiation (spring-sown) = 110.13 - 0.33 s (n=135)

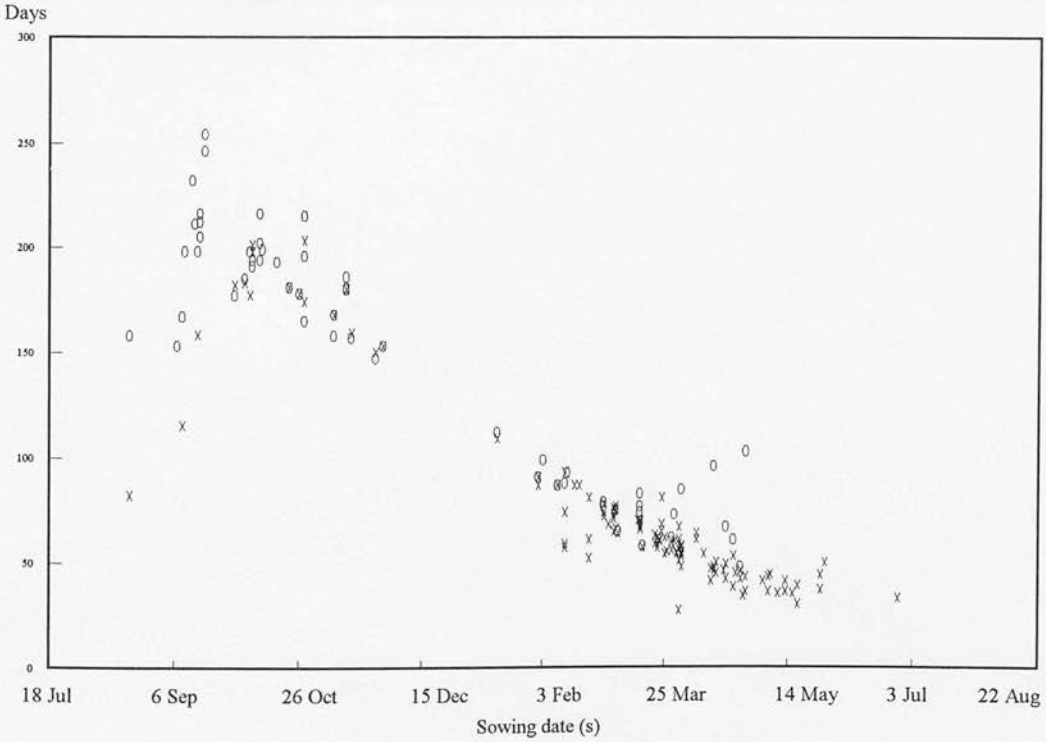
c. Days from sowing to double ridge



Days from sowing to double ridge (autumn-sown) = 66.04 + 0.7 s (n=41)

Days from sowing to double ridge (spring-sown) = 173.1 - 0.55 s (n=31)

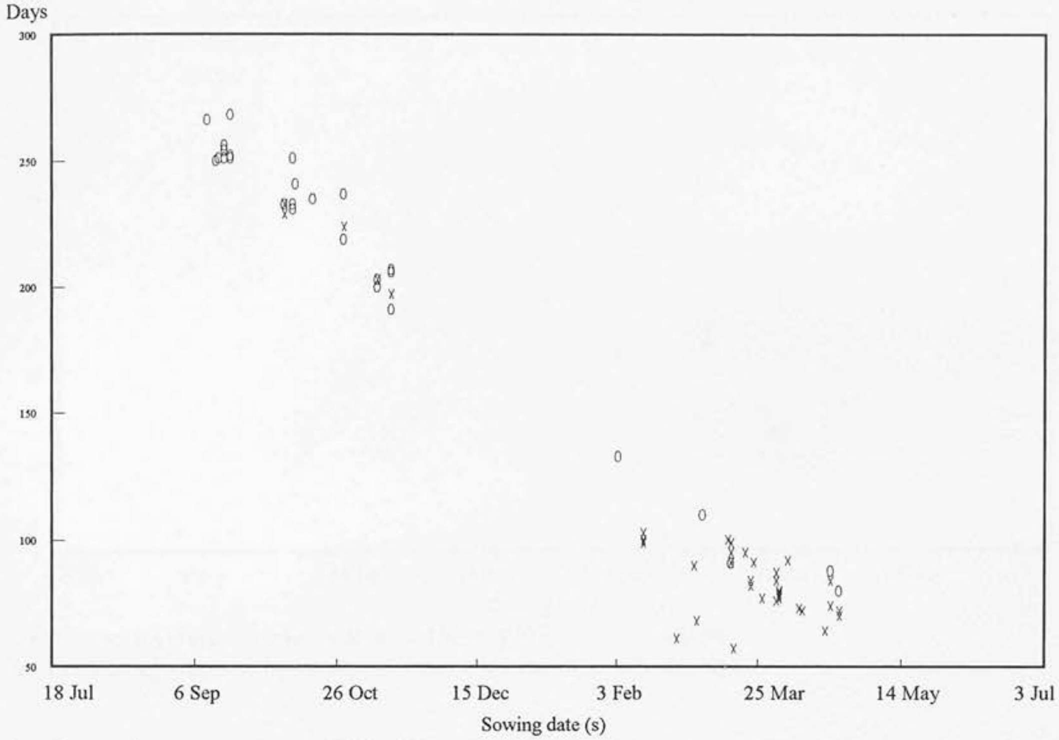
d. Days from sowing to Maximum Primordium Number



Days from sowing to MPN (sown before mid September) = 42.5 + 3.48 s (n=15)

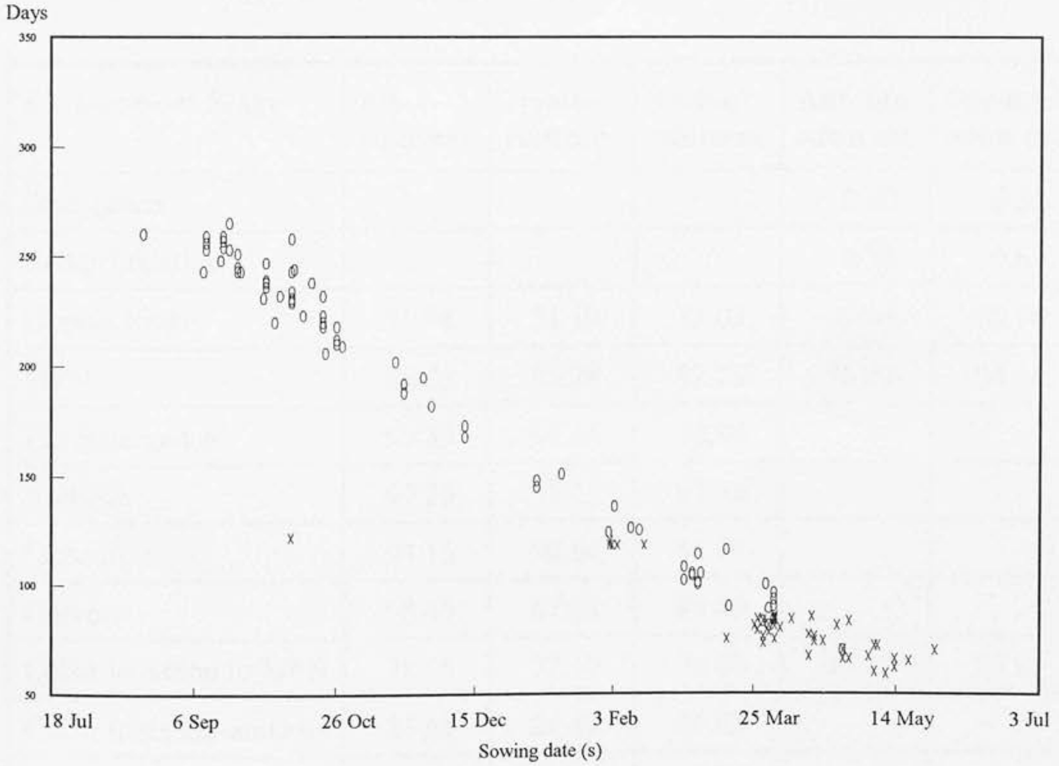
Days from sowing to MPN (sown after mid September) = 250.43 - 0.76 s (n=45)

e. Days from sowing to ear emergence



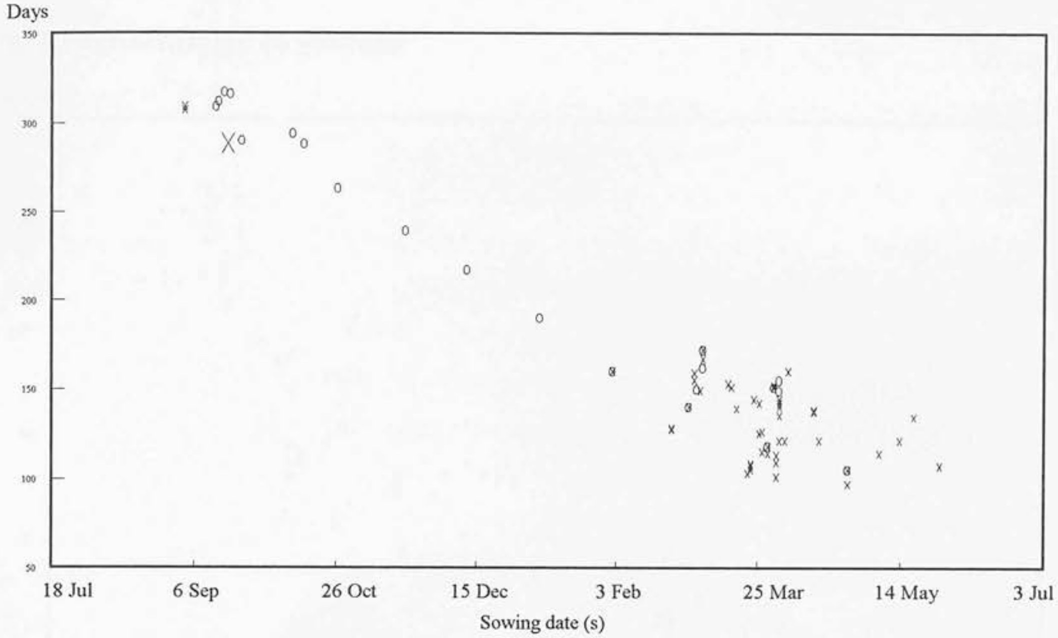
Days from sowing to ear emergence = 298.93 - 0.89 s (n=84)

f. Days from sowing to anthesis



Days from sowing to anthesis = 298.93 - 0.89 s (n=190)

g. Days from sowing to maturity



Days from sowing to maturity (winter cultivars) = 354.93 - 0.90 s (n=37)

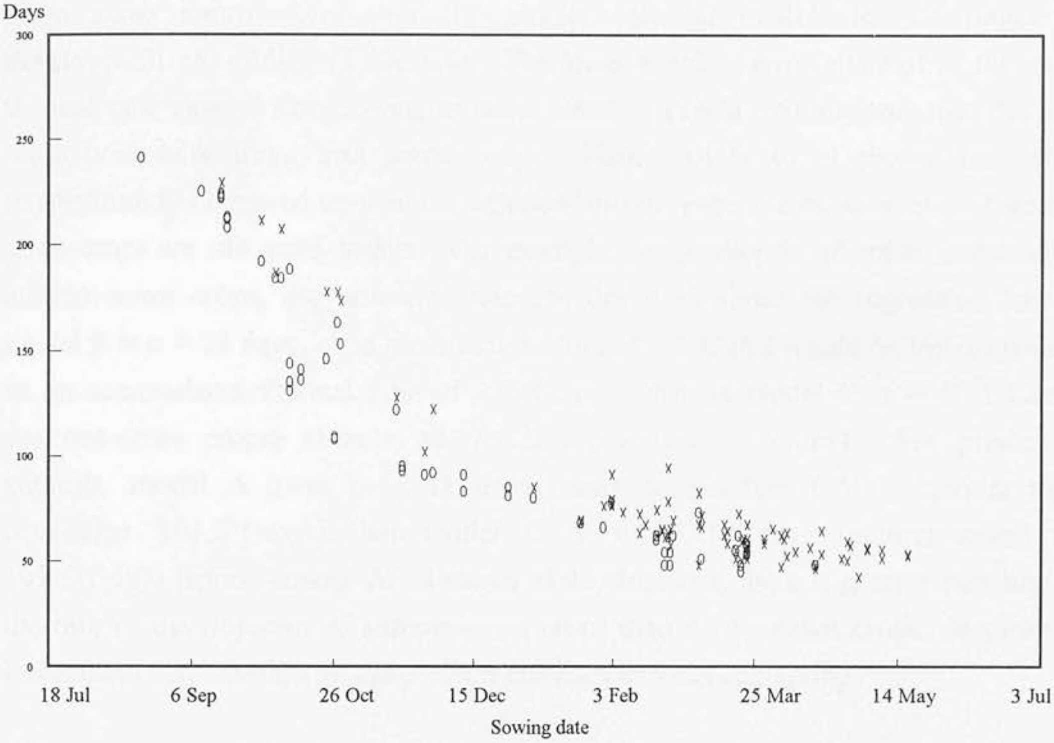
Days from sowing to maturity (spring cultivars) = 318.91 - 0.76 s (n=72)

Table 6.4. Duration of development stage from sowing related to sowing date. Correlation of linear regression of number of days to reach each development stage against sowing date (August 1 = 1)

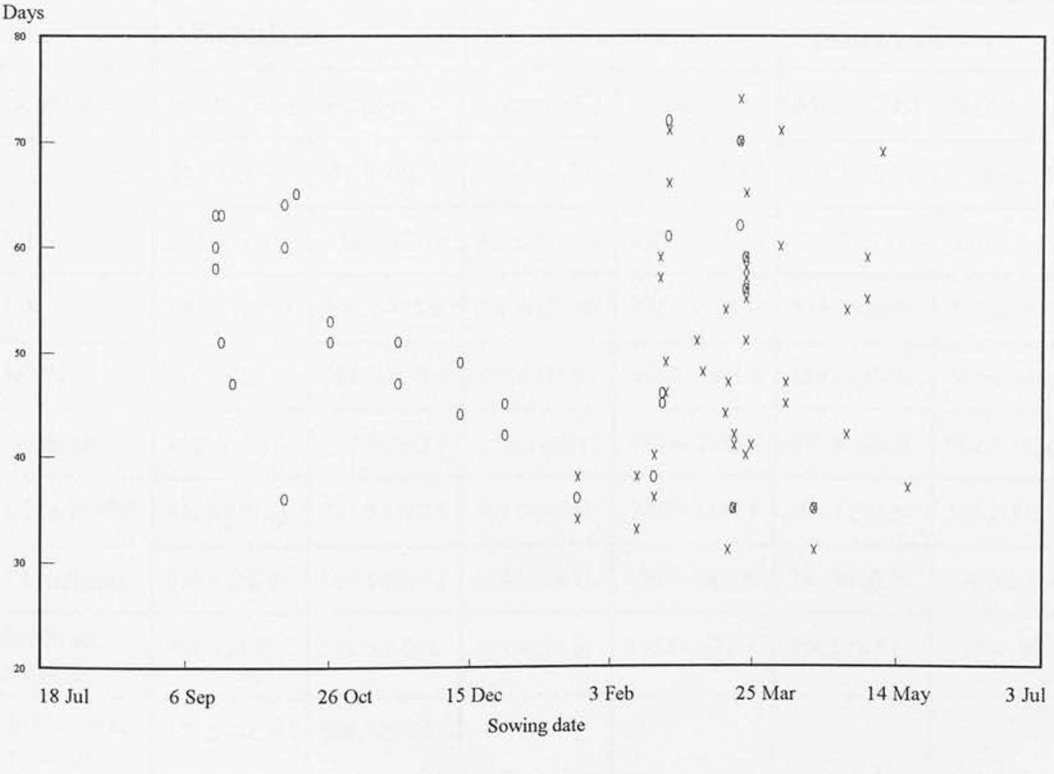
Development Stage	All cultivars	Winter cultivars	Spring cultivars	Autumn-sown cvs	Spring-sown cvs
Emergence				0.60	0.56
Collar Initiation				0.52	0.63
Double Ridge	50.98	51.19	33.03	14.05	66.80
MPN	88.83	85.28	82.23	56.01	94.26
Ear Emergence	97.34	98.14	90.96		
Anthesis	97.58	98.25	95.56		
Maturity	94.16	96.84	84.49		
Harvest	95.43	97.03	89.80		
Collar initiation to MPN	78.15	72.10	76.40	49.13	26.81
Collar initiation-anthesis	83.63	84.49	81.93		
MPN to anthesis	25.50	10.90	47.29		

Figure 6.3. Duration of development stages.

a. Collar initiation to anthesis



b. Anthesis to maturity



C. THERMAL TIME

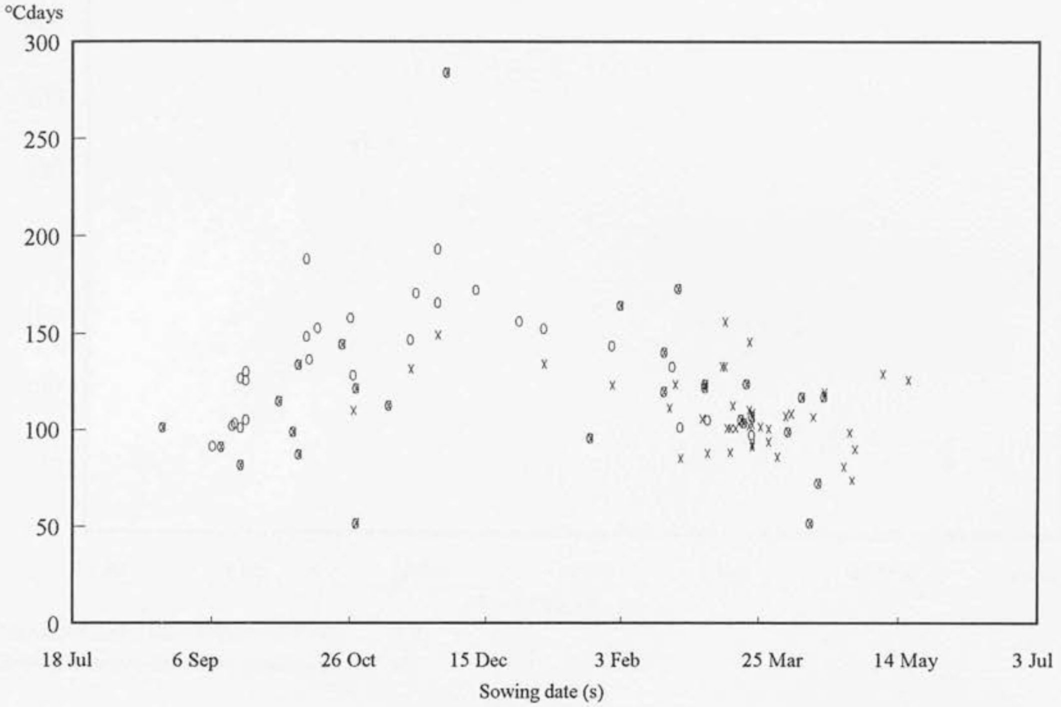
There is still unexplained variation between experiments but the thermal time model gives some improvement over the simpler calendar models for all stages of development after MPN (Table 6.6). The lower standard error attached to the mean thermal time interval from sowing to collar initiation (Table 6.5) suggests that this is a more predictable event than double ridge. Figure 6.4 (a to e) shows that whilst temperature has removed some of the variation between experiments, autumn- and spring-sown crops are still quite distinct. For example, for prediction of collar initiation in autumn-sown crops, the estimated standard deviation about the regression line of model B is $\sigma = 23$ days. At a mean temperature of 7.8°C this would be the equivalent to an accumulated thermal time of 178°Cdays, whereas model C $\sigma = 63.1$°Cdays (autumn-sown crops) or $\sigma = 42.87$°Cdays (spring-sown crops). For predicting anthesis, model A gives $\sigma = 11$ days (mean temperature 9.5°C, thermal time equivalent 101.9°Cdays), but model C $\sigma = 223.5$°Cdays (autumn-sown) or 109.3°Cdays (spring-sown). At all stages of development, there is greater variation in the rate of development of autumn-sown crops than spring-sown crops, despite the incomplete vernalisation of some winter cultivars sown in late spring.

Table 6.5. The timing of development in thermal time

Stage	**All cultivars**		**Winter cultivars**		**Spring cultivars**	
Sowing to	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
Emergence	262.9 (4.3)	51.1-283.7	125.8 (4.3)	51.1 - 283.7	109.3 (2.8)	51.4 - 283.7
CI	262.9 (7.8)	112.0-573.6	325.2 (13.6)	116.5 - 573.6	228.5 (7.4)	112.0- 449.6
DR	483.6 (20.1)	201.7-775.0	530.9 (21.8)	201.7 - 775.0	375.7 (30.6)	201.7- 630.7
MPN	716.4 (22.7)	383.3-1571.9	929.6 (35.5)	434.7- 1571.9	599.6 (21.9)	383.3-1415.5
Anthesis	1077.9 (46.5)	732.7-2343.9	1276.1 (46.5)	772.4- 2343.9	977.8 (24.3)	732.7-1924.1
CI to MPN	461.8 (19.7)	143.2-1287.1	587.7 (35.2)	170.2- 1287.1	391.4 (20.3)	143.2-1155.1
CI-anthesis	836.4 (22.4)	550.4-2059.1	924.5 (38.1)	550.4- 1811.5	787.8 (26.3)	552.3-2059.1
MPN to anthesis	381.7 (7.9)	116.5-772.0	376.9 (16.2)	116.5 - 772.0	384.1 (8.6)	179.4- 566.6
Anthesis to maturity	550.5 (41.5)	229.5-788.1				

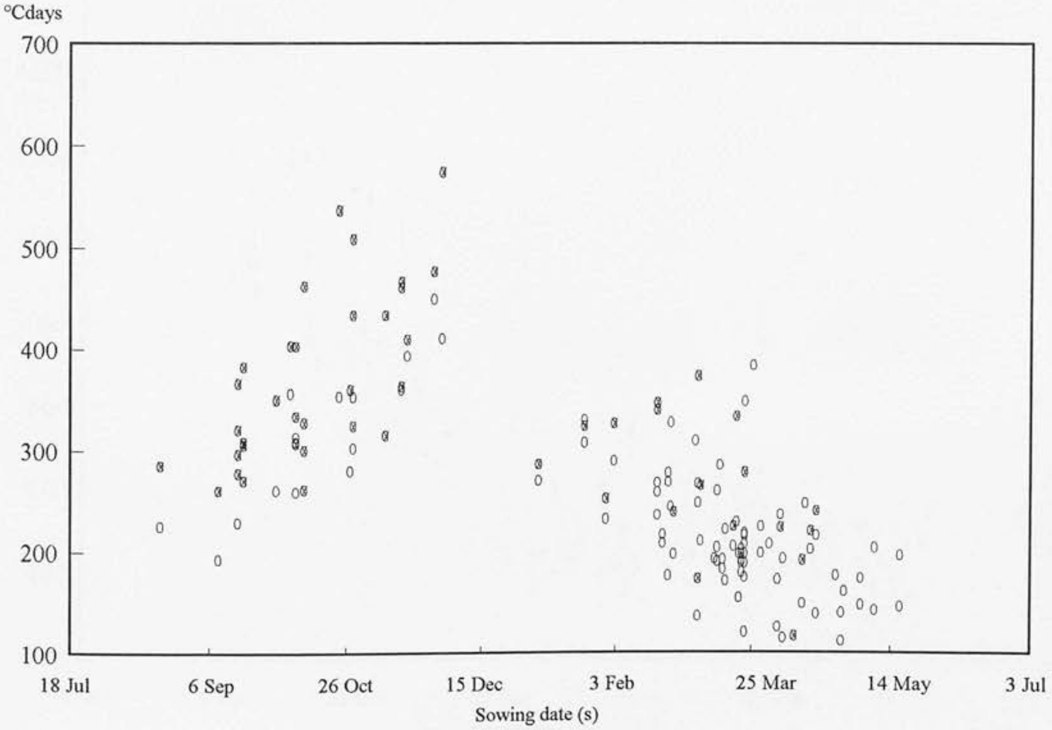
Figure 6.4. The relationship between development and sowing date expressed in thermal time. o = winter cultivars, x = spring cultivars

a. Sowing to emergence



Sowing to emergence n=180

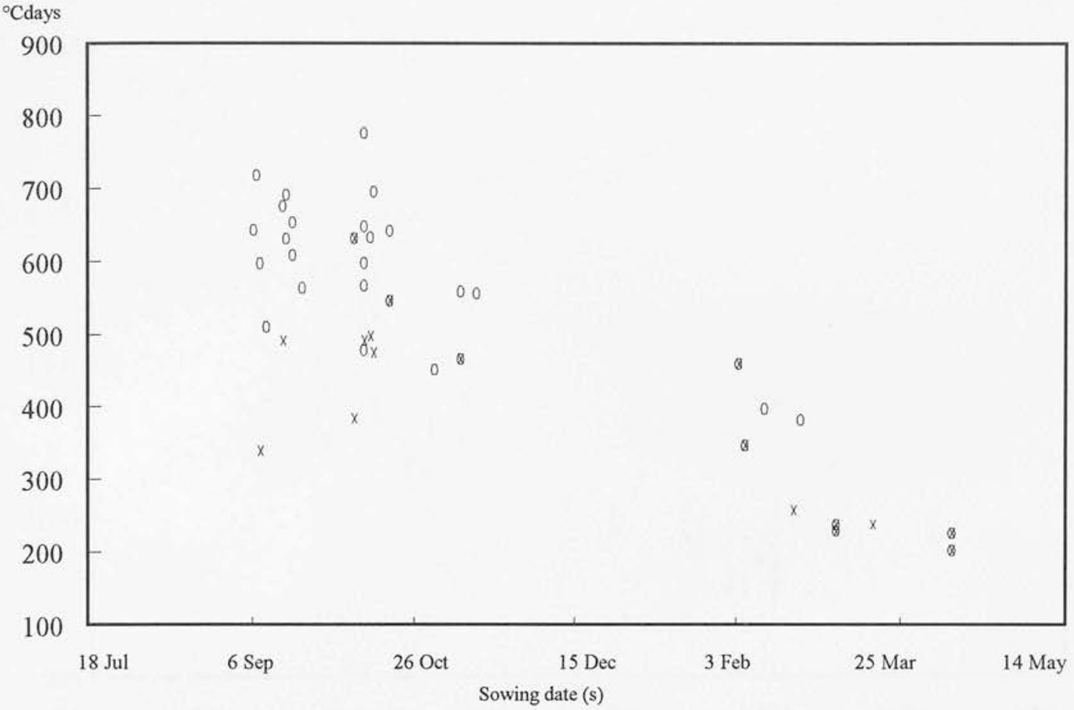
b. Sowing to collar initiation



Sowing to collar initiation (autumn-sown crops) = 187.82 + 2.05 s °Cdays (n=49)

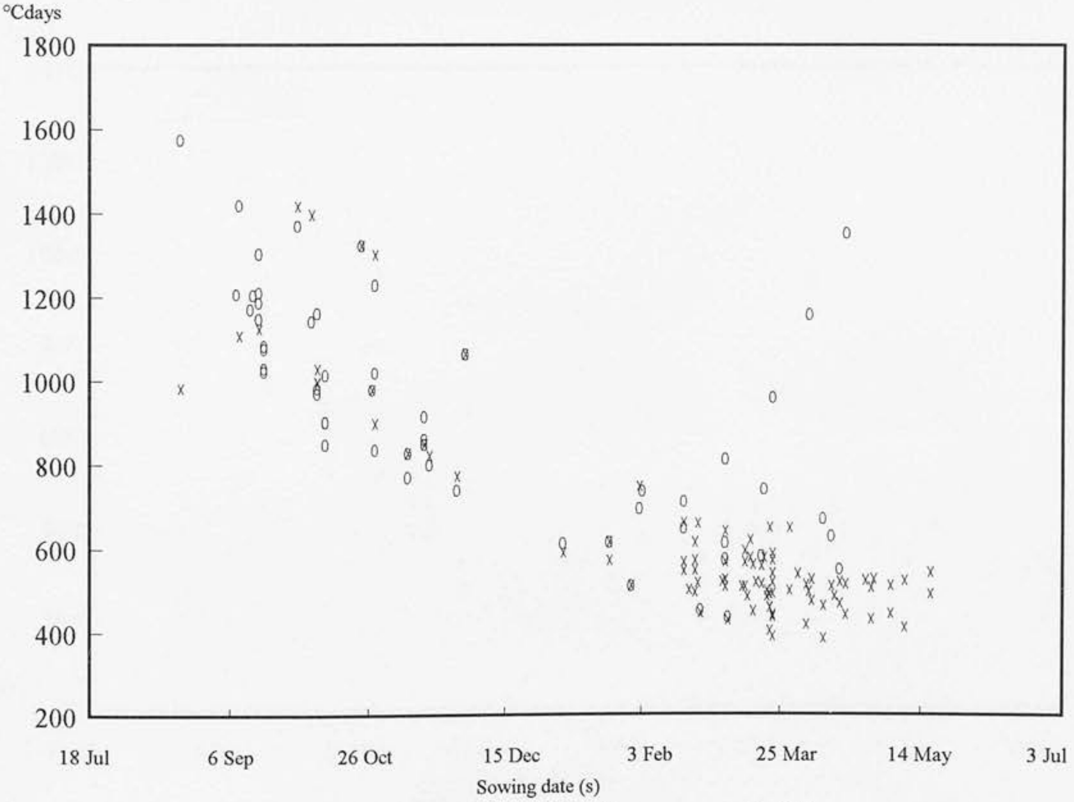
Sowing to collar initiation (spwing-sown crops) = 524.68 - 1.31 s °Cdays (n=97)

c. Sowing to double ridge



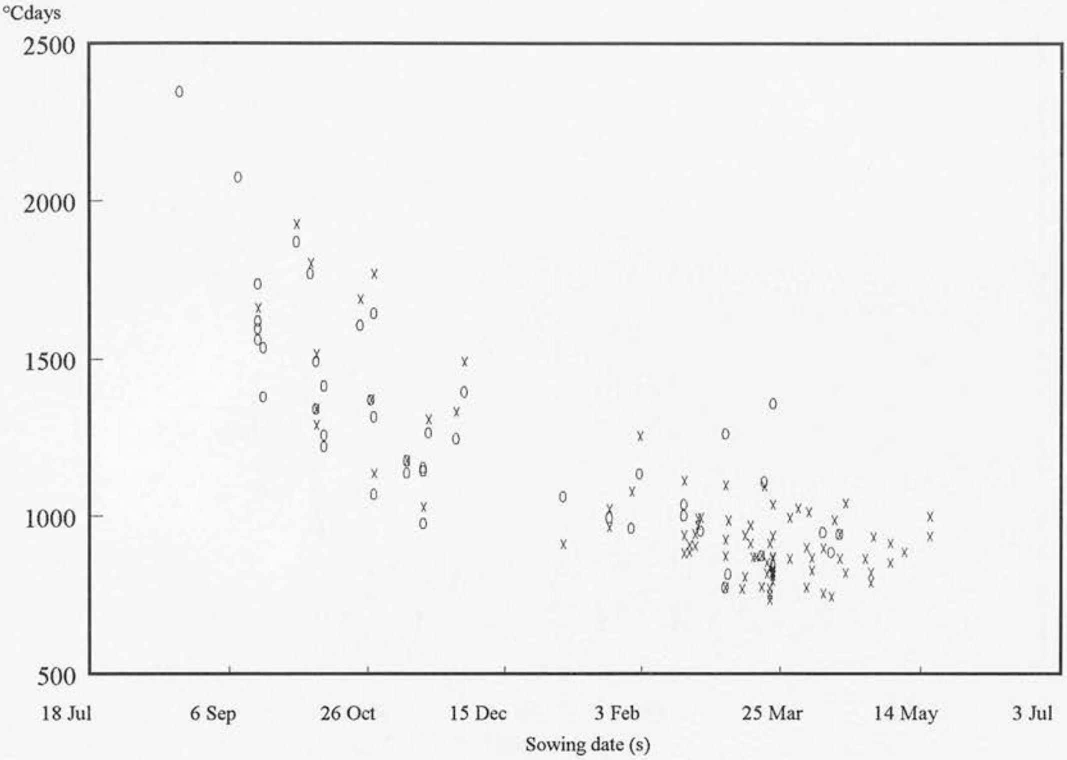
Sowing to double ridge (winter cultivars) n=41
Sowing to double ridge (spring cultivars) n=18

d. Sowing to Maximum Primordium Number



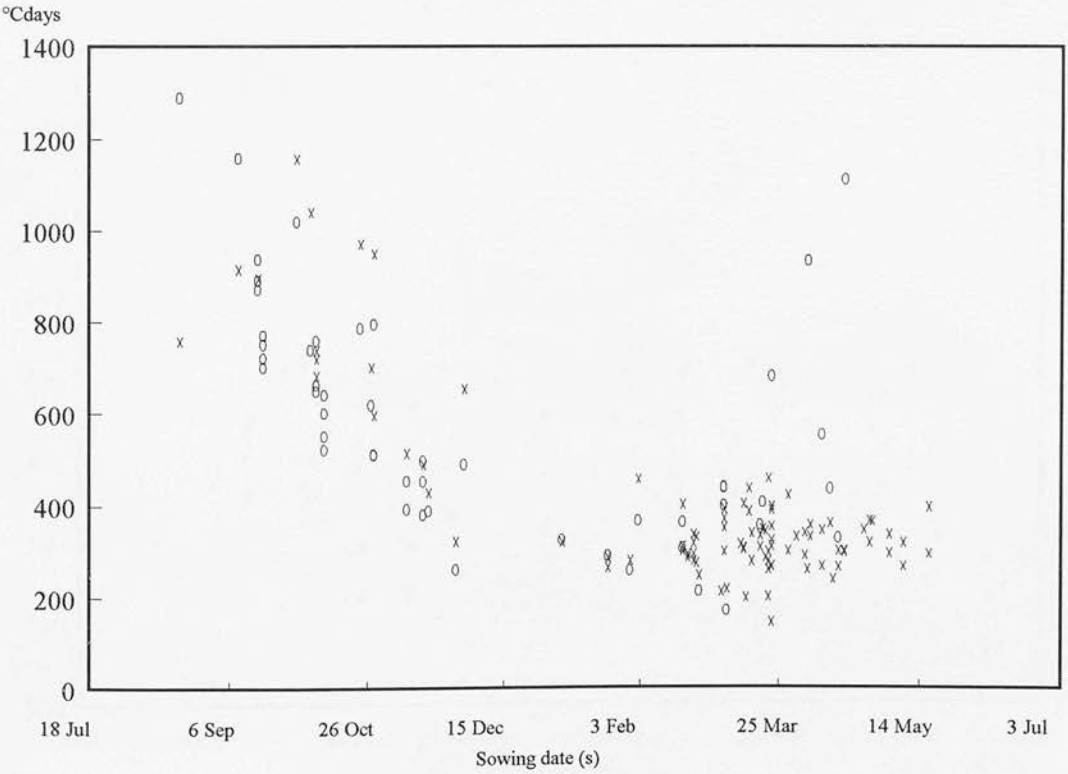
Sowing to MPN (omitting 3 exceptional data points) = 1298.83 - 3.27 s °Cdays (n=158)

e. Sowing to anthesis



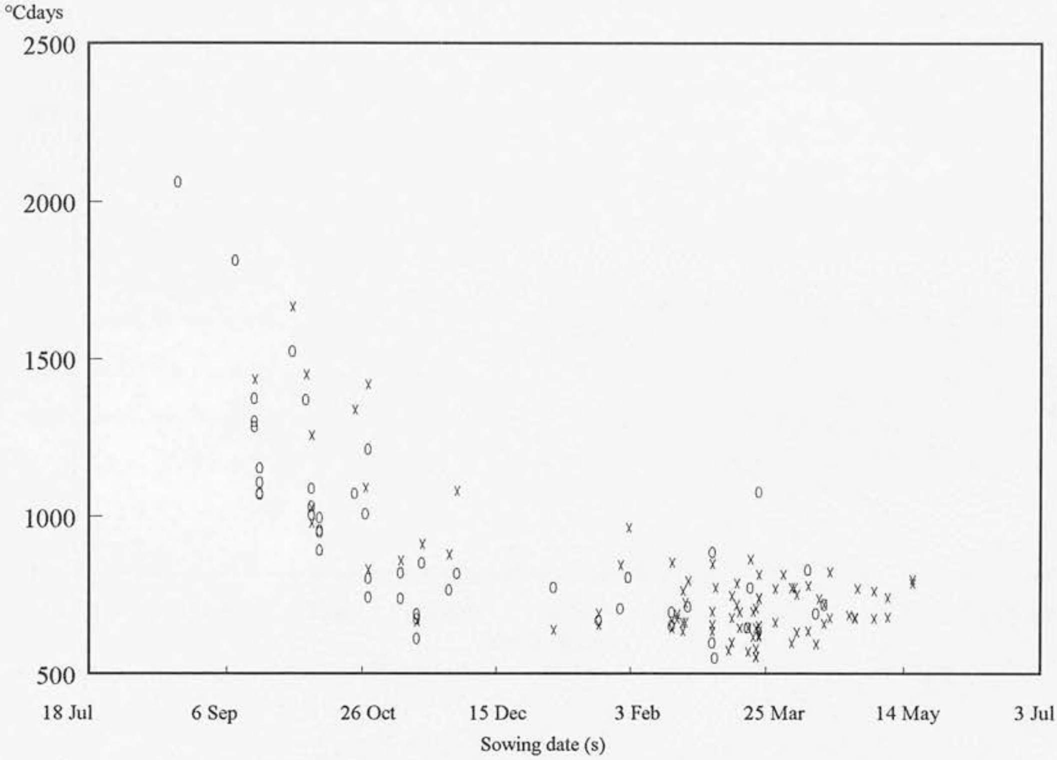
Sowing to anthesis = 1717.57 - 3.44 s °Cdays (n=149)

f. Collar initiation to MPN



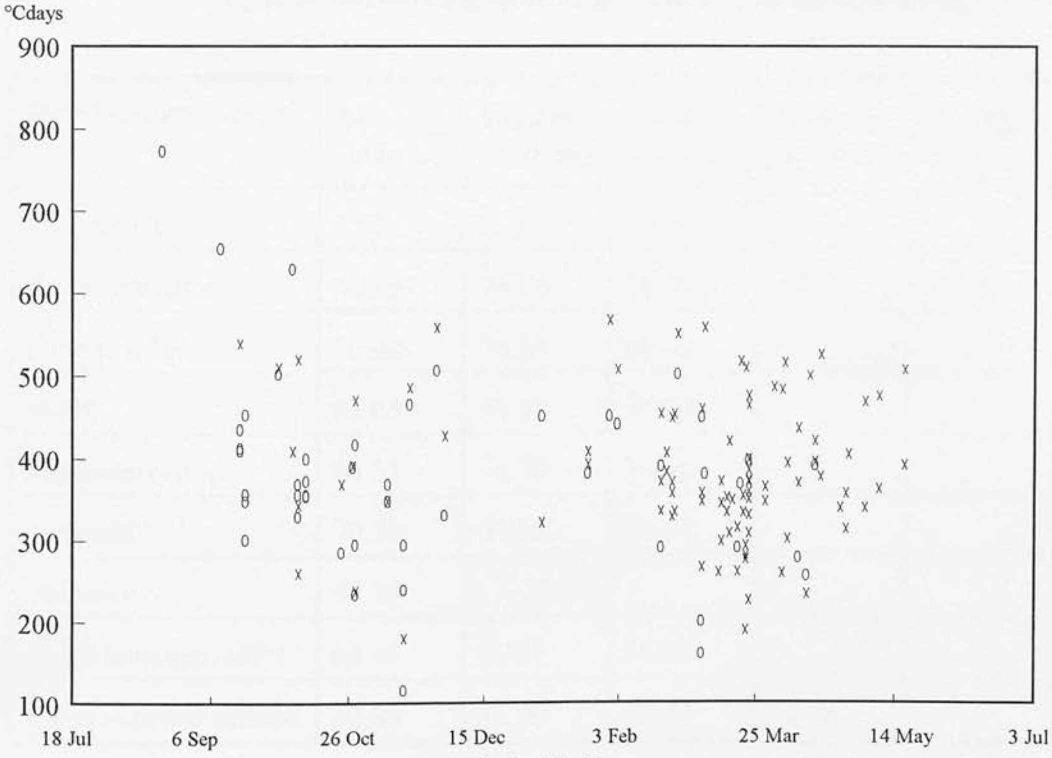
Collar initiation to MPN n=142

g. Collar initiation to anthesis



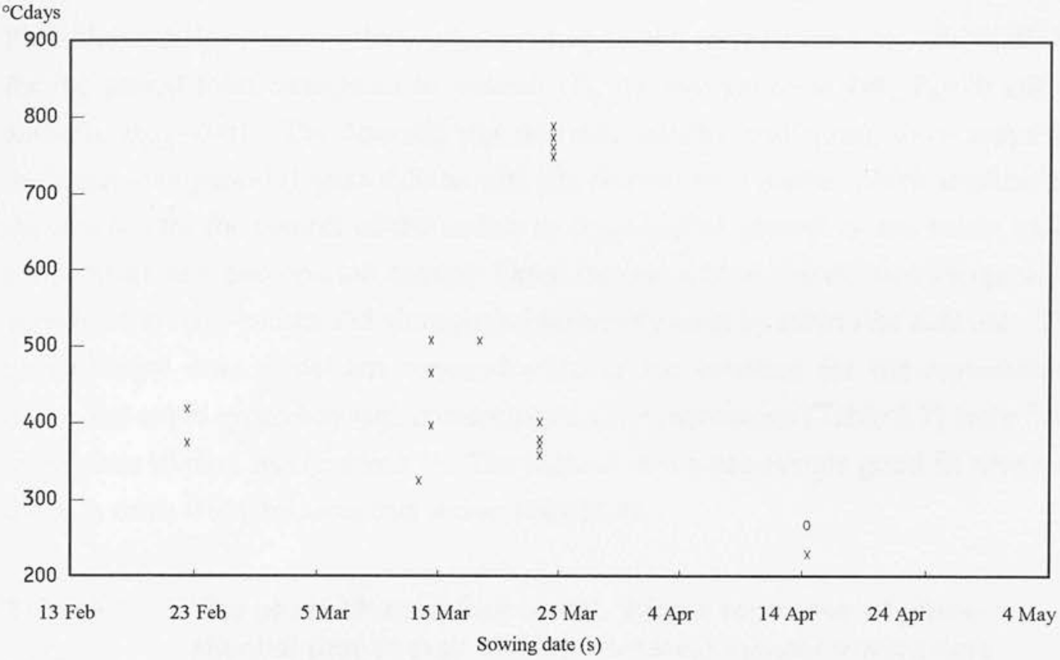
Collar initiation to anthesis (autumn-sown crops only) = 1810.85 + 8.88 s (n=47)

h. MPN to anthesis



MPN to anthesis n=149

i. Anthesis to maturity



Anthesis to maturity n=23

Table 6.6. Thermal time as a predictor of development stage. Percentage of variation explained by the linear regression of predicted thermal time to reach development stage against sowing date (Aug 1 = 1)

Development Stage	All cultivars	Winter cultivars	Spring cultivars	Autumn -sown cvs	Spring-sown cvs
Emergence	3.91	2.34	0.19		
Collar initiation	42.39	24.16	36.70	43.43	33.16
Double ridge	70.42	76.84	66.09		
MPN	81.65	71.32	77.39		
Ear Emergence	84.51	74.79	75.94		
Anthesis	70.78	57.26	68.52		
Maturity	59.19				
Collar initiation -MPN	64.45	51.87	65.06		
Collar initiation-anthesis	52.86	43.49	56.92	53.26	

D. PHOTO-THERMAL TIME

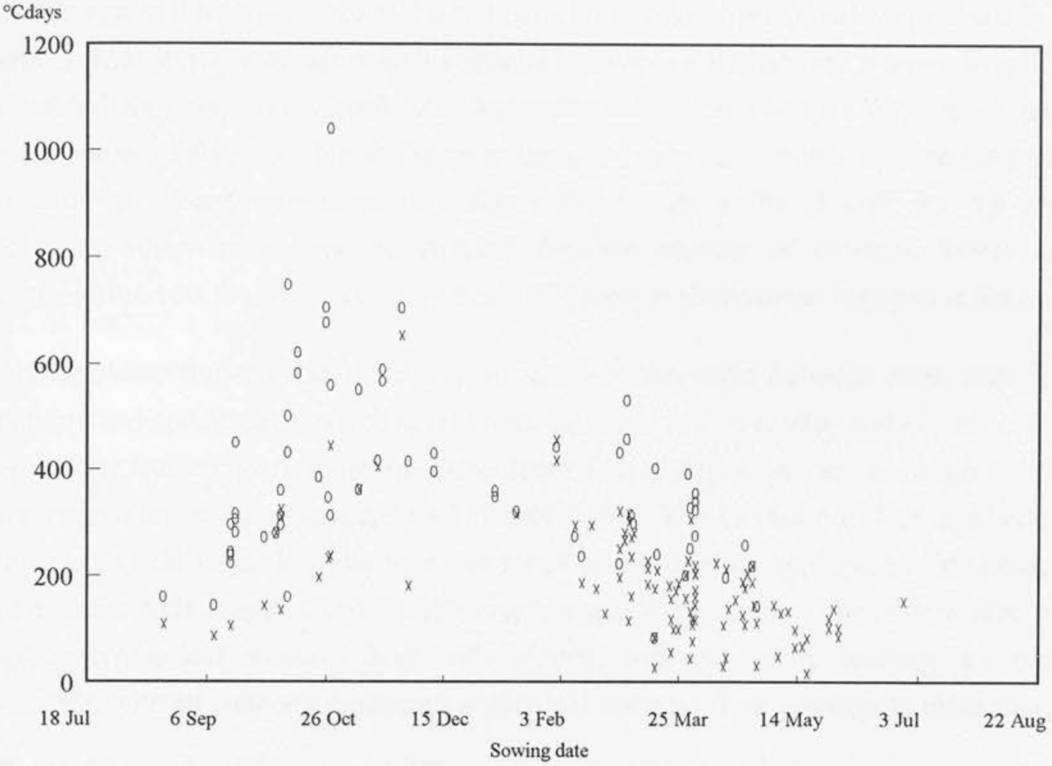
Photothermal times were calculated according to the method used in ARCWHEAT for the period from emergence to anthesis (P_b=0h emergence to DR; P_b=7h DR to anthesis; P_{opt}=20h). The data still separate into autumn- and spring-sown crops for the vegetative period (Figure 6.5) as with the thermal time model, which implies that the mechanism for control of the switch to reproductive growth is not solely under temperature and photoperiod control. Other factors such as genotypic differences in vernalisation requirement and photoperiod sensitivity must be taken into account. The photothermal time model has removed some of the variation for the reproductive phase, but some apparently high correlations for the regressions (Table 6.7) were from fewer than 10 data sets (marked *). The regression is a deceivingly good fit where all the data came from the same trial series (marked #).

Table 6.7. The photo-thermal time model. Linear regression of photo-thermal time to each development stage against sowing date (August 1st =1)

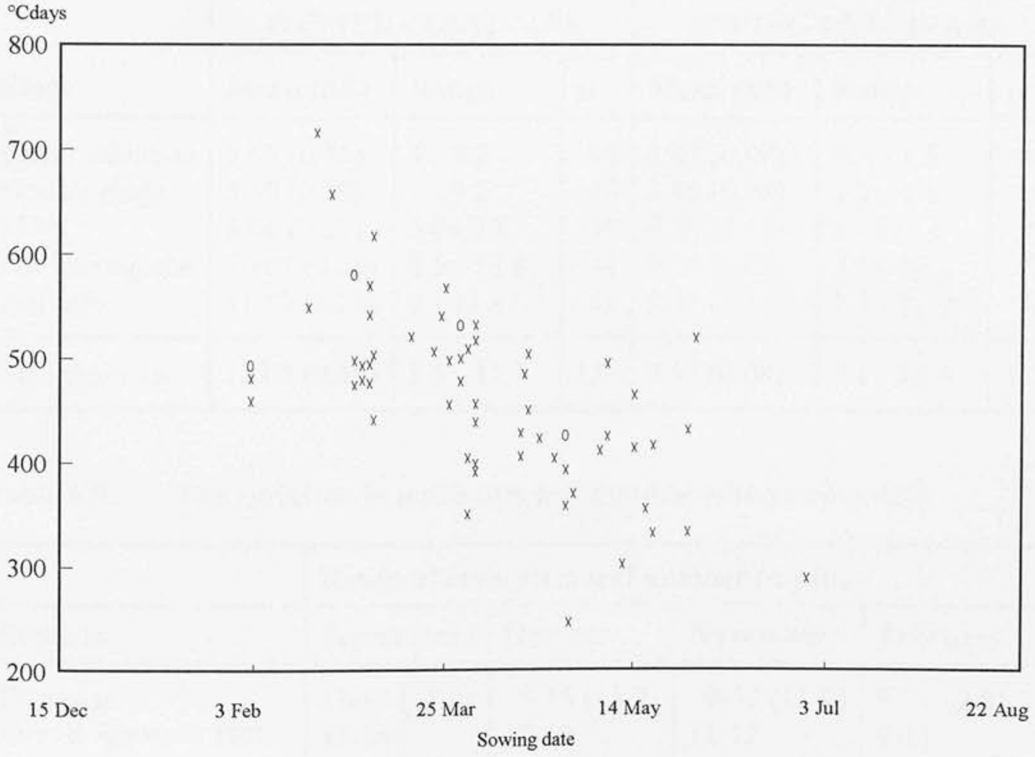
Development Stage	**Autumn -sown crops**		**Spring-sown crops**	
Sowing to	**r^2**	**SD**	**r^2**	**SD**
Collar initiation	67.8	31.20	34.8	72.39
Double ridge	4.1	38.37	84.9 #	39.66 #
MPN	*	*	56.1	62.46
Ear Emergence	88.8 #	36.5 #	58.6	120.00
Anthesis	54.8	57.13	0.0	34.12
Emergence to CI	1.8	37.9	15.1	43.97
Emergence to DR	30.2	26.38	87.1 * #	6.48
CI to DR	64.4	10.62	71.6 * #	7.80
CI to MPN	*	*	65.2 * #	37.04

Figure 6.5. The relationship between development stage and photo-thermal time. o = winter cultivars, x = spring cultivars

a. Emergence to Collar Initiation



b. Collar Initiation to MPN



E. EXTERNAL MORPHOLOGY - LEAF NUMBER

The difference in leaf number between winter and spring cultivars was significant at each stage of development (Table 6.8, Figures 6.7, 6.8). Spring barleys produce 9-11 leaves from spring sowings: winter cultivars behave in a similar way if sown in spring, provided they are fully vernalised. Autumn-sown winter cultivars form more main stem leaves (Table 6.9), but the number does not vary consistently with sowing date or cultivar. Early autumn-sown spring cultivars may suffer if they are not cold tolerant, otherwise a linear relationship between number of emerged leaves and temperature was found with no significant variation in phyllochron between cultivars.

The database showed that there was no simple relationship between main stem leaf number and apical stage, which agrees with the work of Hay (1986) and Grant (1984). However, leaf numbers at intermediate development stages do vary in proportion to the maximum leaf number produced (Table 6.10). The variation in leaf numbers at different apical stages is wider than that reported by Kirby & Appleyard (1984) due in part to the wide range of sowing dates represented in this study. For both winter and spring types, leaf numbers from early autumn and late spring sowings are most variable, with all cultivars producing similar leaf numbers from sowings at other times.

Table 6.8. Leaf number at different stages of development

	WINTER CULTIVARS			**SPRING CULTIVARS**		
Stage	**Mean (SE)**	**Range**	**n**	**Mean (SE)**	**Range**	**n**
Collar initiation	2.67 (0.13)	1 - 5.6	65	1.47 (0.08)	0.2 - 3.5	85
Double ridge	5.59 (0.29)	2 - 9.2	40	2.96 (0.24)	1.2 - 5.3	29
MPN	8.96 (0.22)	5.6 - 13	70	6.66 (0.15)	3 - 11	92
Ear Emergence	10.81 (0.28)	8.5 - 13.8	34	9.24 (0.09)	7.1 - 11	78
Anthesis	11.52 (0.28)	9 - 13.8	41	9.35 (0.11)	7.1 - 11.2	70
Maximum no.	12.04 (0.16)	8.5 - 17.7	125	9.57 (0.08)	7.1 - 12.4	133

Table 6.9. The variation in maximum leaf number with sowing date

	Range of main stem leaf number (mean)			
Sown in	**September**	**October**	**November**	**February**
Database	11-16 (13.6)	8-15 (11.9)	9-13 (11.0)	8-11 (9.8)
Kirby & Appleyard 1984	11-16	12-13	11-12	9-11

Table 6.10. The relationship between maximum leaf number and leaf number during development

Maximum Leaf Number	**18**	**16**	**15**	**14**	**13**	**12**	**11**	**10**	**9**	**8**
Double ridge Database	*	*	8	7	6	7	5	3	3	2
Kirby & Appleyard 1984	*	8	8	7	7	6	6	5	4/5	*
MPN Database	13	11	11	11	9	10	8	7	6	5
Kirby & Appleyard 1984	*	13	12	11	11	10	9	8	7/8	*

There was no significant difference in maximum or intermediate leaf number of spring or winter cultivars across the range of latitude studied, although the mechanism controlling leaf number appeared sensitive to lengthening or shortening daylength. The influence of the rate of change of daylength at emergence decreases with latitude, as daylength changes more slowly at lower latitudes. This is apparent even over the narrow range of latitude in this study (Figure 6.6). When the effects of daylength and the direction of change of daylength at crop emergence are combined with the simple leaf number/temperature relationship (Figure 6.9c), Jones & Allen's (1986) conclusion is confirmed, that autumn- and spring-emerging winter cultivars follow different lines.

Figure 6.6. Variation in the rate of change of daylength at emergence with latitude for the trials in the barley database. The variation decreases with latitude.

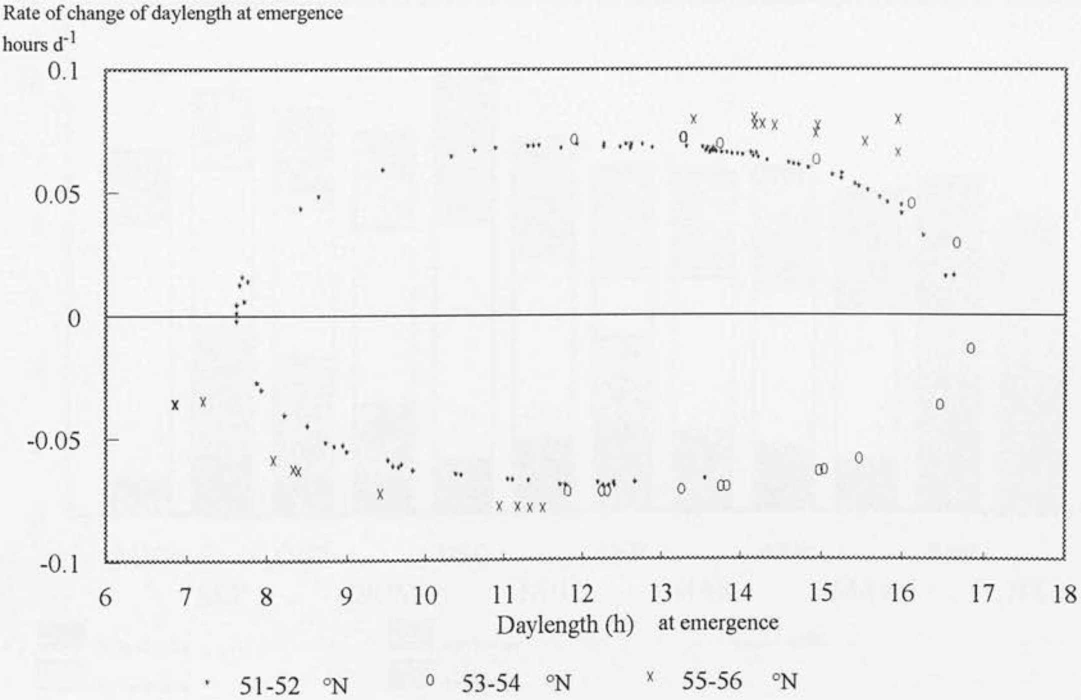
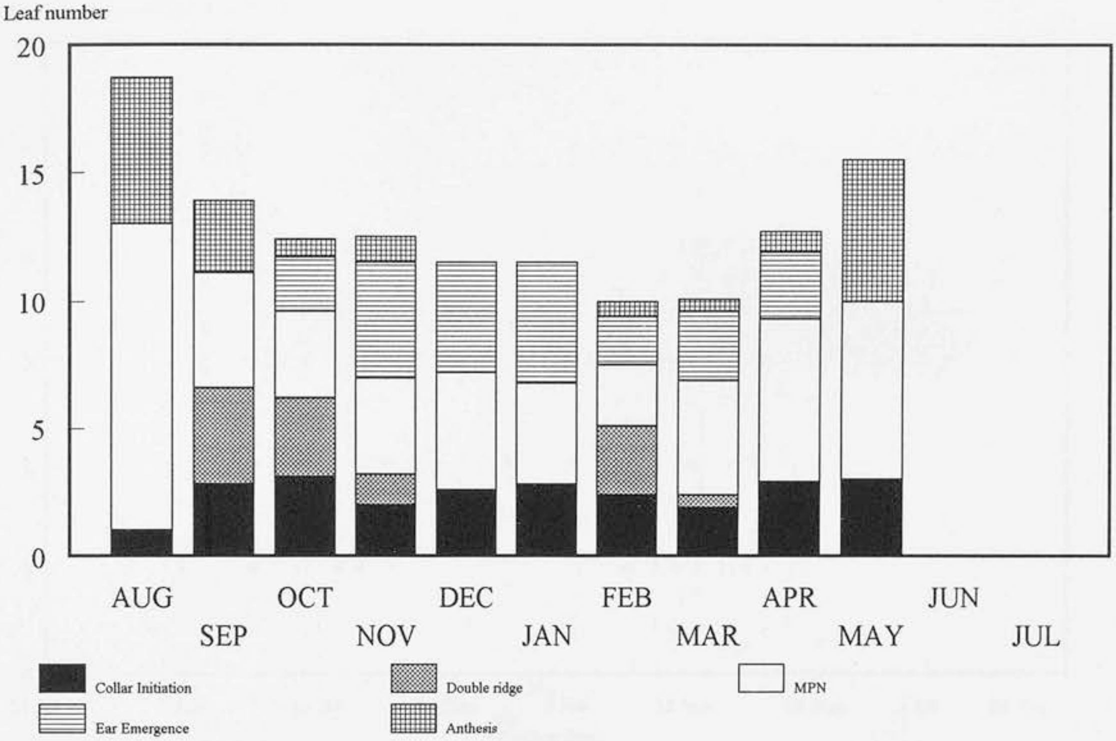


Figure 6.7. Variation in leaf number at each apical development stage with sowing date

a. Winter cultivars



b. Spring cultivars

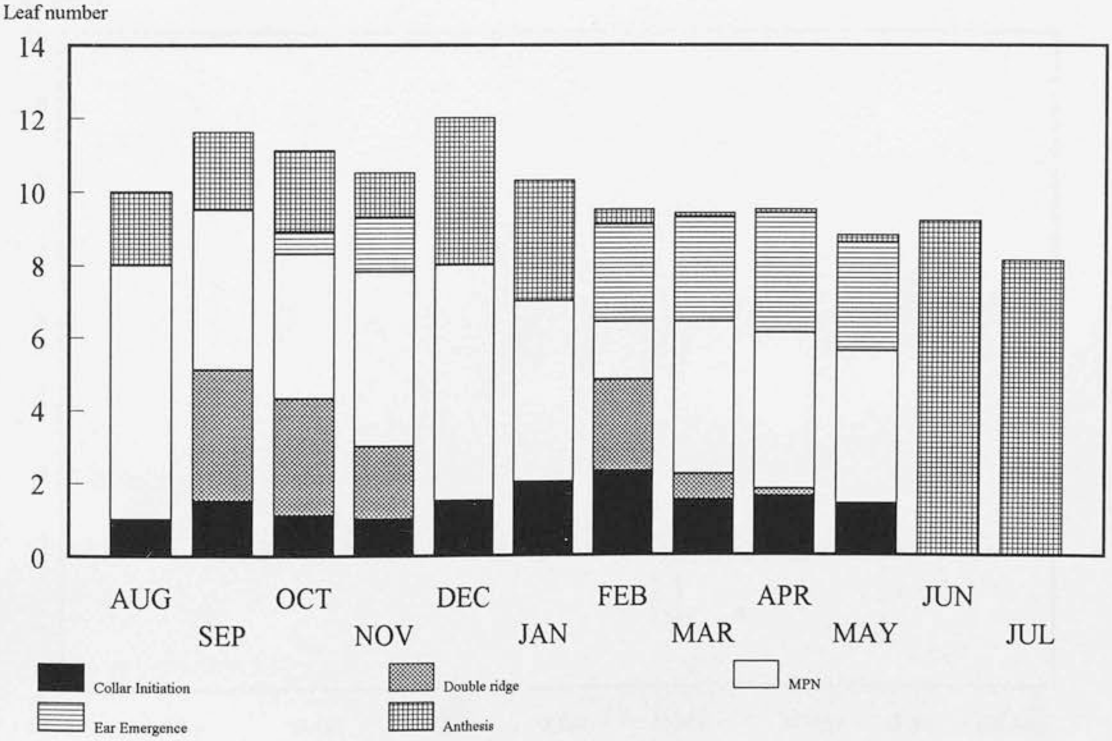
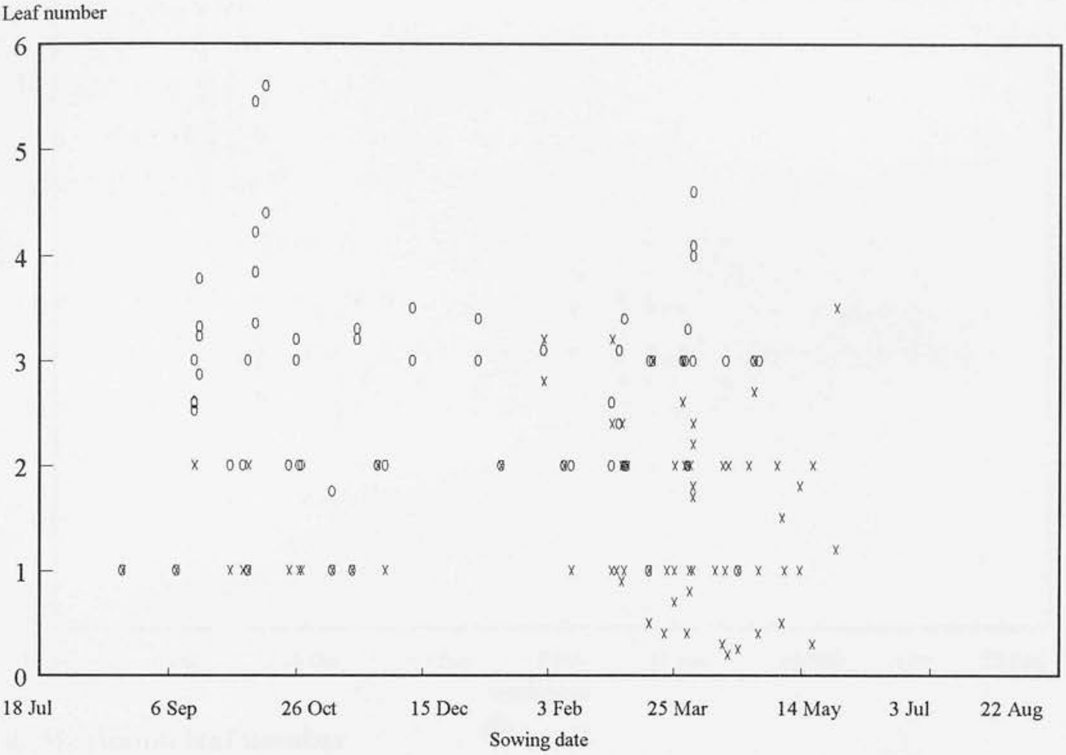
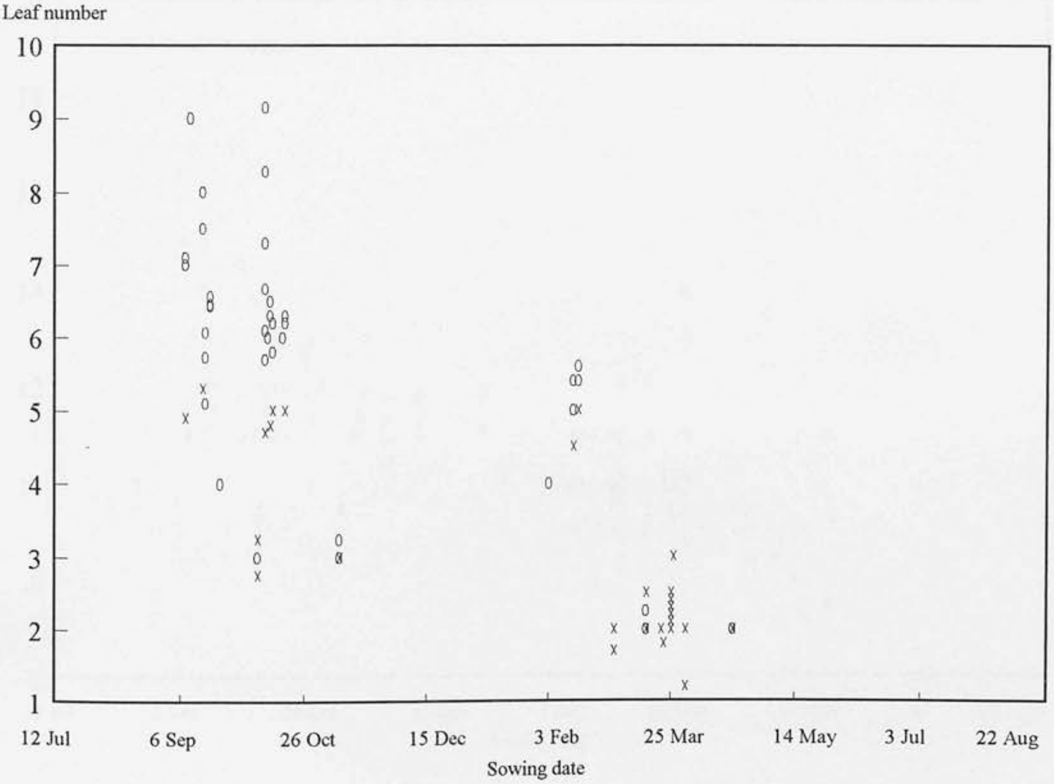


Figure 6.8. **The variation of leaf number at each development stage with sowing date. o = winter cultivars, x = spring cultivars**

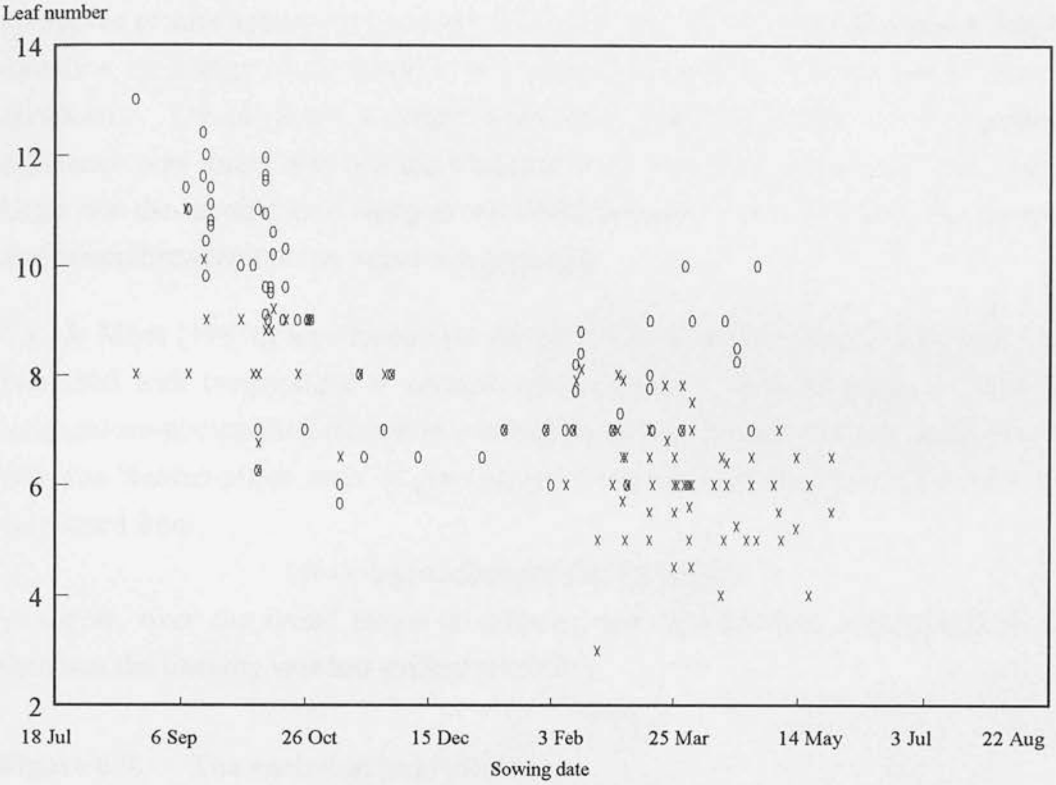
a. Collar initiation



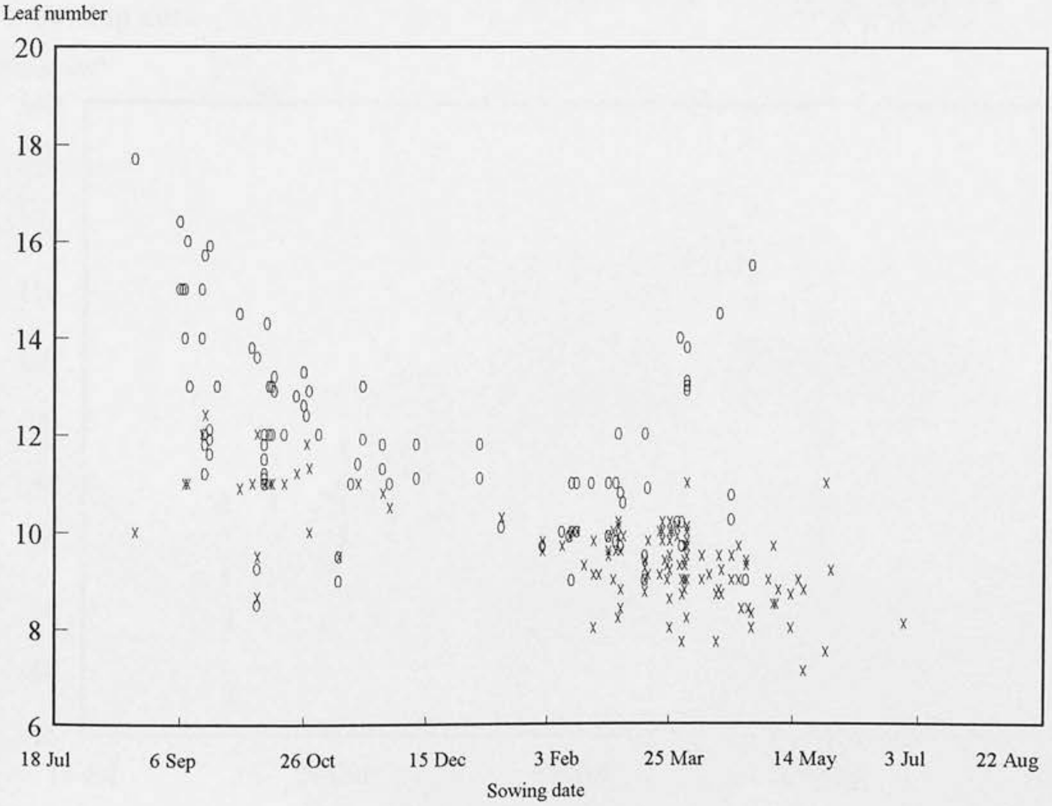
b. Double ridge



c. Maximum Primordium Number



d. Maximum leaf number



The phyllochron decreases for autumn sowings as the sowing date is delayed, but in spring the picture appears to be reversed (Figure 6.9a, b). This would suggest that the direction of change of daylength is important (Figure 6.9c), but the results are not conclusive. The phyllochron ranged from 44 to 128 °Cdays leaf^{-1}. No significant difference was found between the phyllochron of winter and spring cultivars, which bears out the modification made to the CERES barley model in which the previous distinction between the two types was removed.

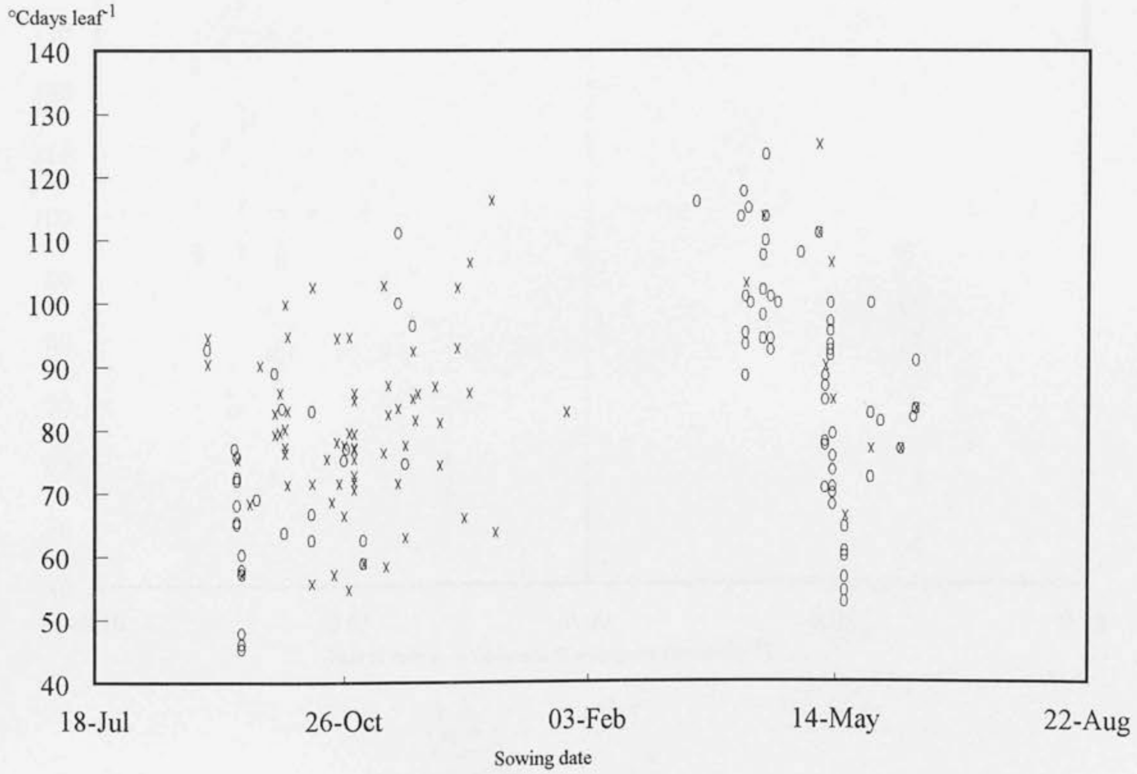
Cao & Moss (1989b) also found that the phyllochron is temperature dependent, and increased with temperature at constant photoperiods. They proposed a combined temperature-photoperiod models in which phyllochron showed a strong linear relation with the 'thermo-photo ratio' at planting (r^2=0.94) for four cultivars. The ratio was calculated from:

Mean degree-days per day/daylength

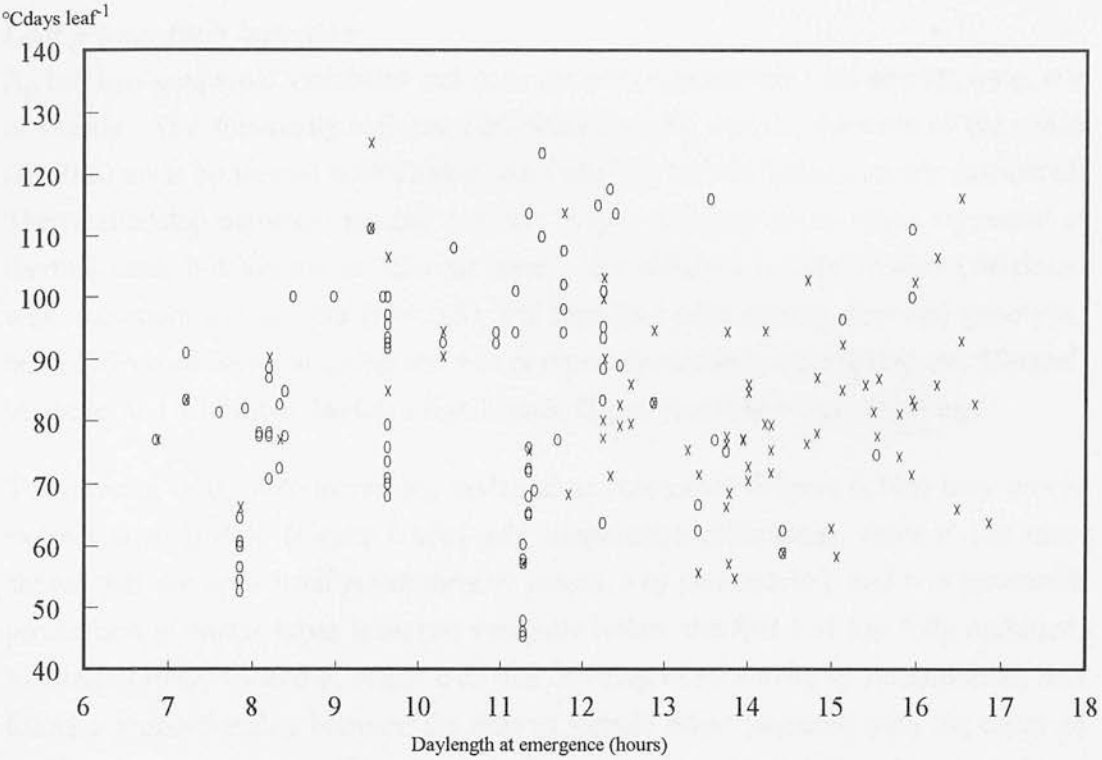
However, over the broad range of cultivars and environments represented in the database the linearity was less evident (r^2=0.32).

Figure 6.9. The variation in phyllochron
x = winter cultivars, o = spring cultivars

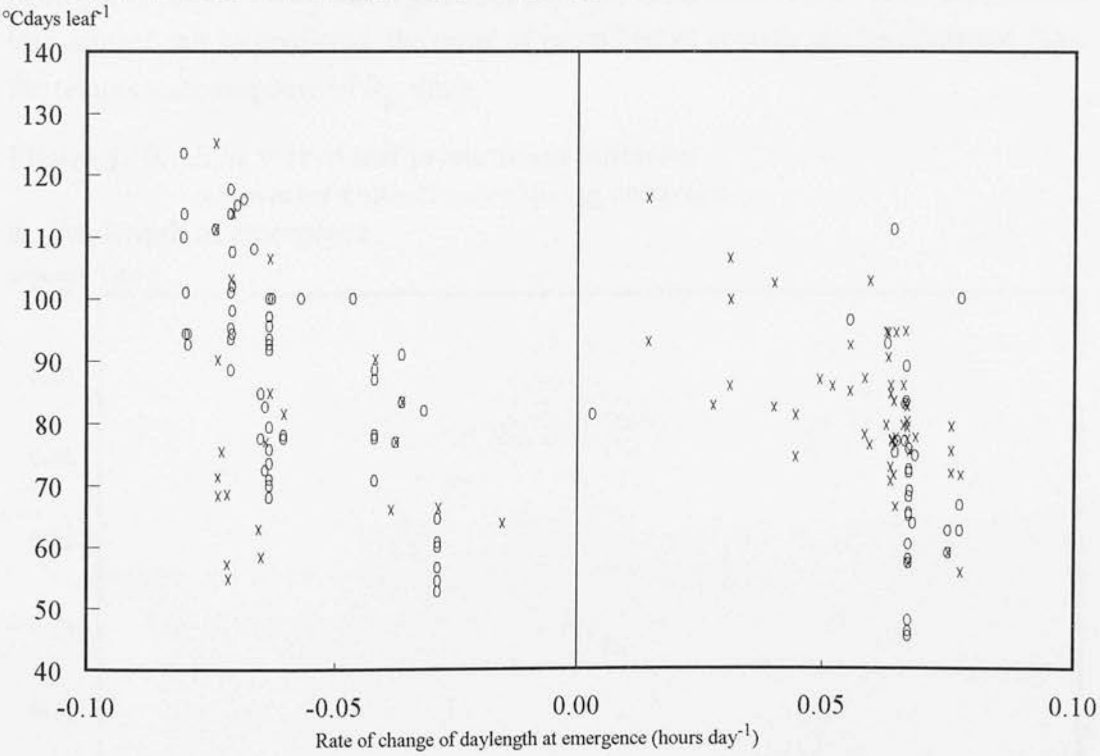
a. Sowing date



b. Daylength at emergence



c. Rate of change of daylength at emergence



F. PRIMORDIUM INITIATION RATE

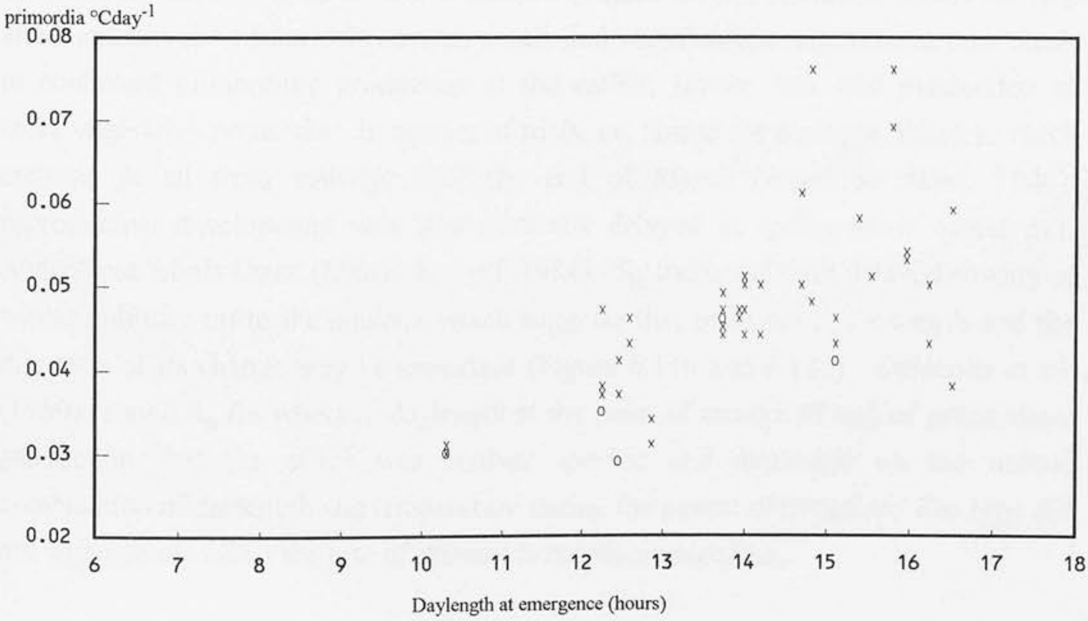
Leaf primordium initiation

R_p has low genotypic variability and does not vary consistently with sowing date, site or season. The apparently high correlation between R_p and the duration of the phase (r^2=-0.8) must be viewed with caution since the two are not independently calculated. The relationship between rate and duration is approximately linear when expressed in thermal time, but logistic in calendar time. The duration is only weakly correlated with maximum leaf number (r^2 = 0.5), and therefore with sowing date and genotype, but a difference between spring and winter types was evident, with spring cvs 'Hassan', 'Armelle' and 'Clermont' having a significantly higher rate than winter cv 'Sonja'.

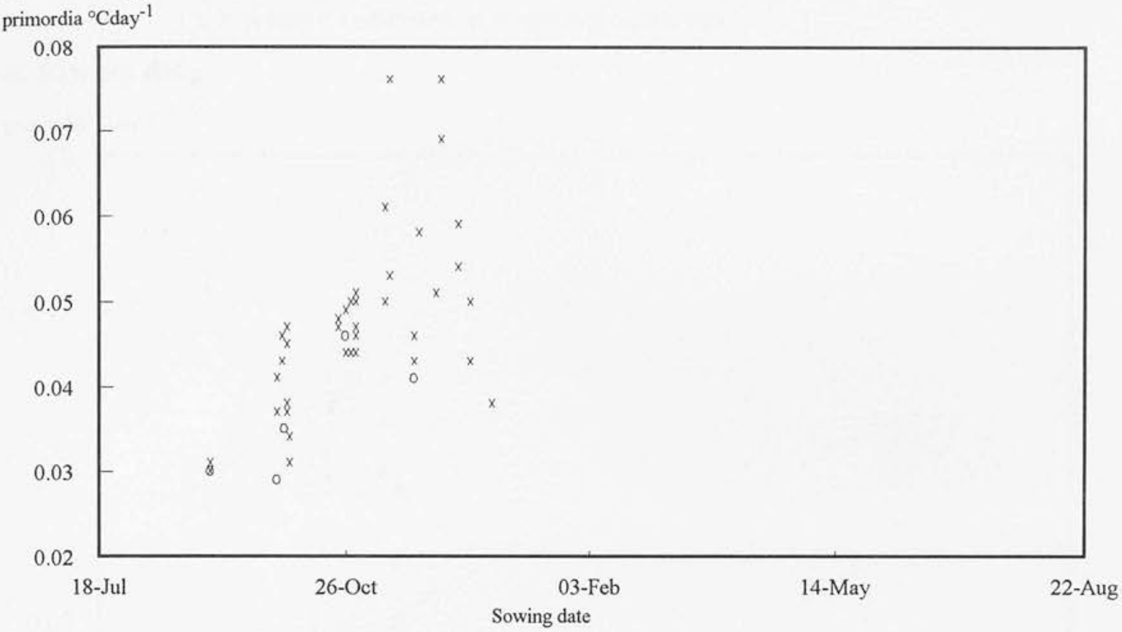
The increase in R_p with increasing daylength at emergence (Figure 6.10a) may simply express sowing date (Figure 6.10b) and temperature differences, since it has been shown that the apex itself is not directly sensitive to photoperiod, and leaf primordia production in winter types is almost complete before the first leaf has fully unfolded. Miglietta (1989) looked at wheat cultivars differing in sensitivity to photoperiod, and found a proportionality between the time to 'double ridge' (equated with the onset of reproductive growth) and maximum leaf number that showed the absence of any photoperiod effect on R_p under different photoperiodic treatments. Thus if maximum leaf number can be predicted, the onset of reproductive growth can be predicted from the temperature response of R_p alone.

Figure 6.10. The rate of leaf primordium initiation
x = winter cultivars, o = spring cultivars

a. Daylength at emergence



b. Sowing date



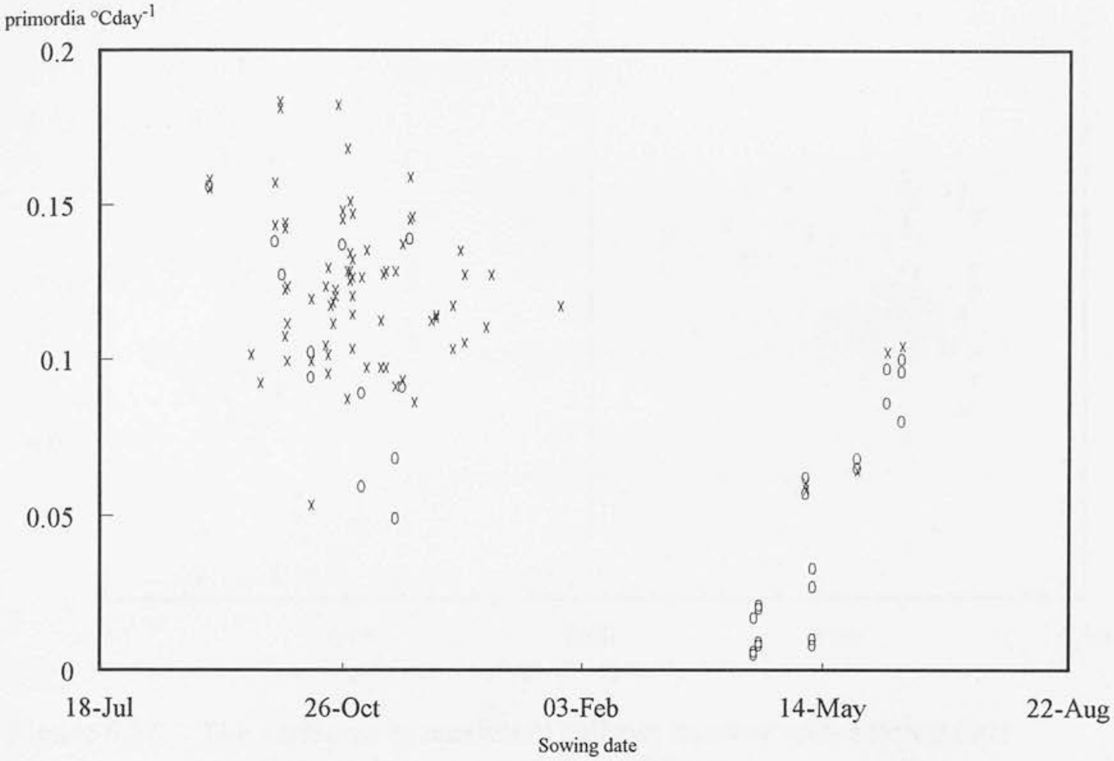
The data divide into autumn- and spring-emerging experiments, consistent with the work of Jones & Allen (1986) and Delécolle *et al.*, (1989 - for wheat) who found that R_p was more sensitive to the direction of change of daylength than the absolute value. Cultivar variation in this study may be due to differing vernalisation requirements.

Spikelet Primordia Initiation

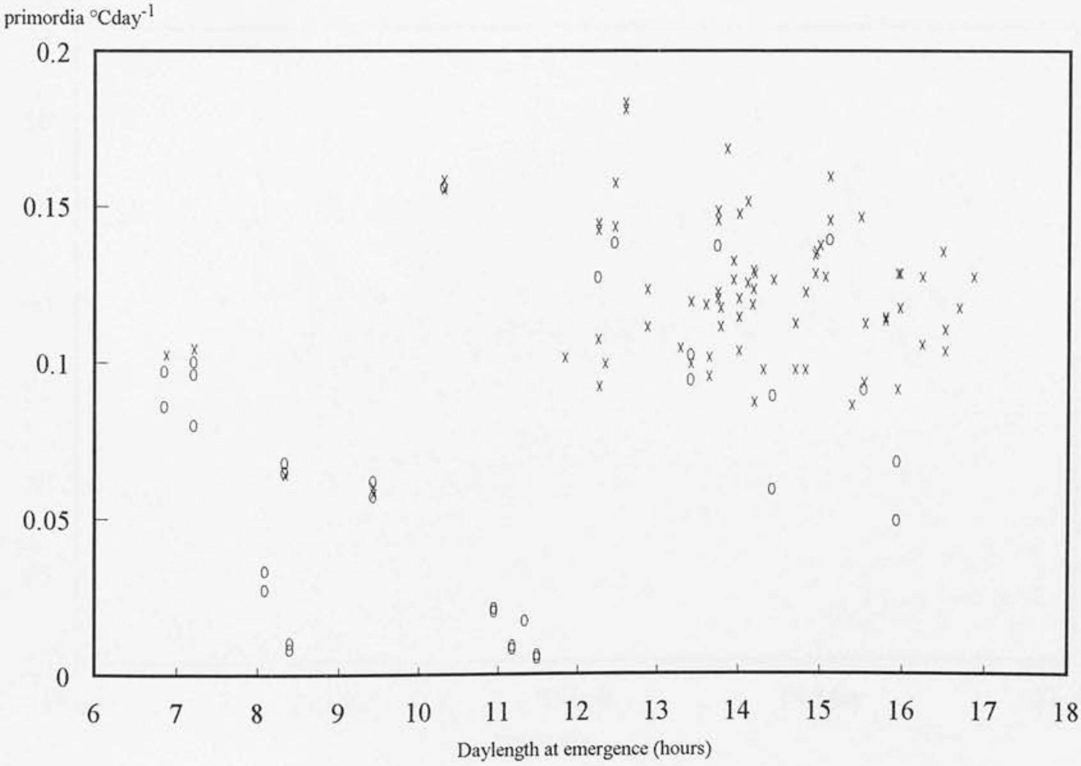
The rate of initiation of primordia increases after collar initiation but varies significantly between sowing dates and cultivars. R_s shows greater variation with site and season then R_l confirming the findings of Jones & Allen (1986). Spring cultivars show an increase in R_s as sowing is delayed (Figure 6.11a), however, whilst the rate also increases for winter cultivars, an unsatisfied vernalisation requirement may result in continued primordium production at the earlier, slower rate, and production of more vegetative primordia. In one set of trials, cv. 'Sonja' for example, failed to reach anthesis at all from sowings after the end of March (Jones & Allen, 1986): reproductive development was also markedly delayed in spring-sown winter cvs. 'Video' and 'Maris Otter' (Ellis & Russell, 1984). R_s increased with delayed sowing of winter cultivars up to the equinox which suggests that once again, daylength and the direction of its change may be important (Figure 6.11b and 6.11c). Delécolle *et al.* (1989) related R_s for wheat to daylength at the point of change of rate of primordium production, but the effect was cultivar specific and depended on the unique combination of daylength and temperature during the period of initiation. Ear type did not significantly affect the rate of spikelet primordium initiation.

Figure 6.11. Rate of spikelet primordium initiation
x = winter cultivars, o = spring cultivars

a. Sowing date



b. Daylength at emergence



c. Rate of change of daylength at emergence

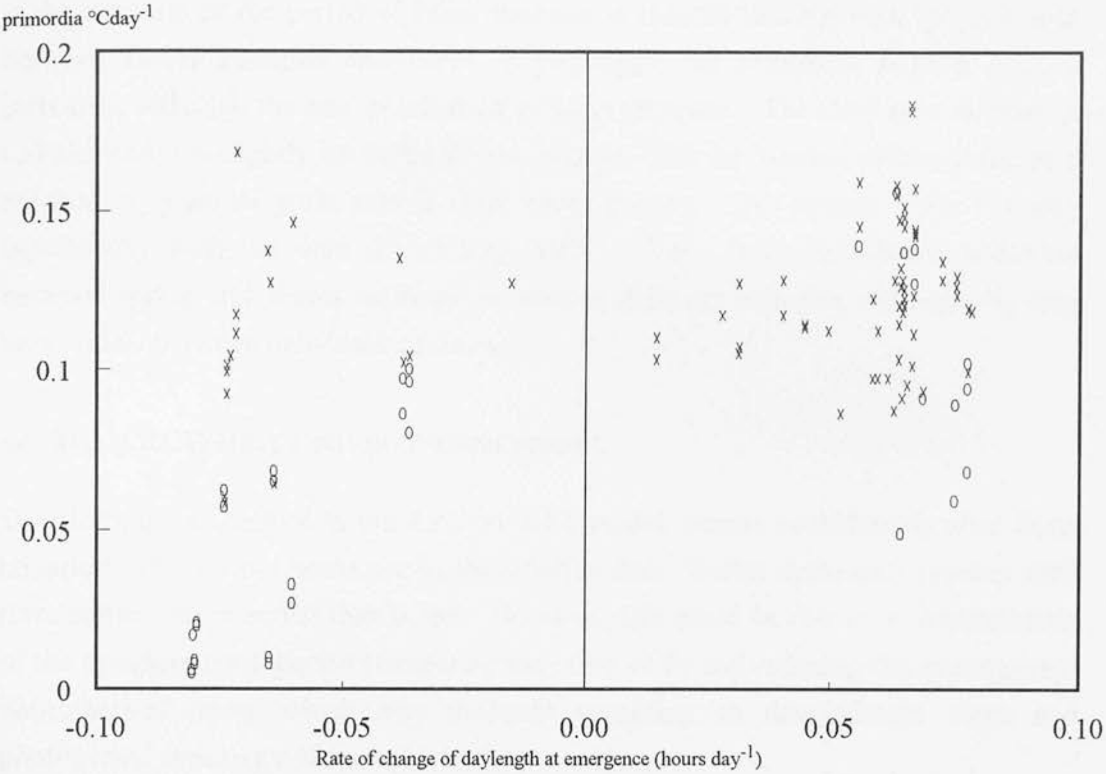
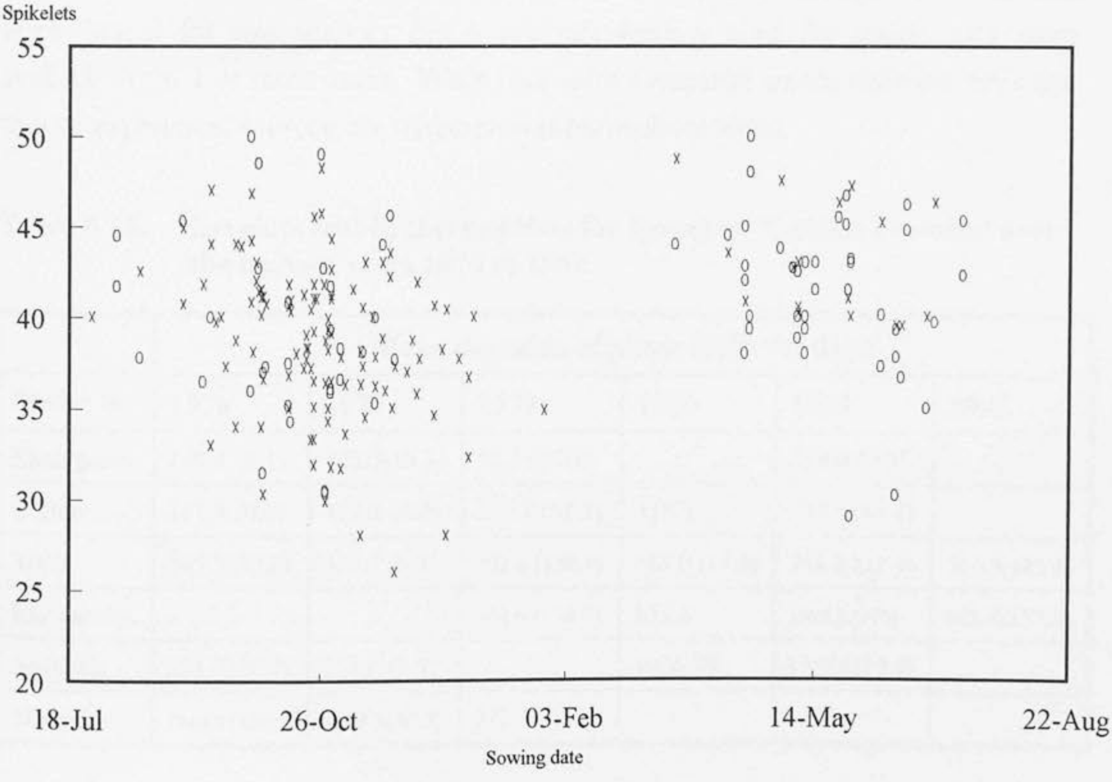


Figure 6.12. The variation in maximum spikelet number with sowing date x = winter cultivars, o = spring cultivars



Maximum Spikelet Number

If the duration of the period of linear increase in spikelet number with thermal time, between Collar Initiation and MPN, is prolonged, the maximum number (N_S) is increased, although the rate of initiation remains the same. The maximum number of spikelet nodes is slightly lower for 6-row cultivars than for 2-rows, although the final number of potential grain sites is three times greater. The number does not vary significantly with the date of reaching MPN. There is no significant difference between spring and winter cultivars, or sites at different latitudes, although N_S may vary widely between individual cultivars.

G. THE ARCWHEAT DEVELOPMENT MODEL

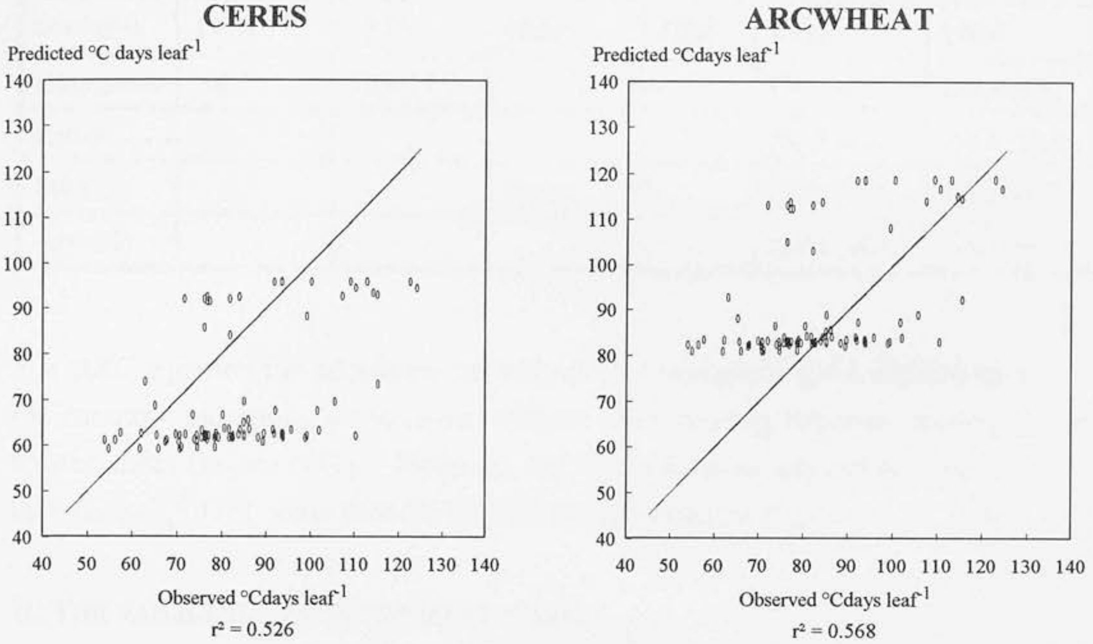
Double ridge, as defined in the ARCWHEAT model, occurs considerably after floral initiation, which is not borne out by these barley data. Barley apparently reaches each development stage earlier than wheat. However, this could be due to an overestimate of the optimum photoperiod (increasing the effect of P_f and reducing the accumulated photothermal time), which may fluctuate according to development stage and photoperiod sensitivity of the cultivar.

The duration of development stages in thermal or photothermal time for any one cultivar was not found to be constant between seasons (Tables 6.11, 6.12). The data were limited for this analysis, but 5 cultivars were studied for which data were available from 4 or more years. When data were compared across different sites and trial or experiment sources, the variation was particularly broad.

Table 6.11. Development in thermal time for spring cv 'Golden Promise' over the harvest years 1976 to 1982

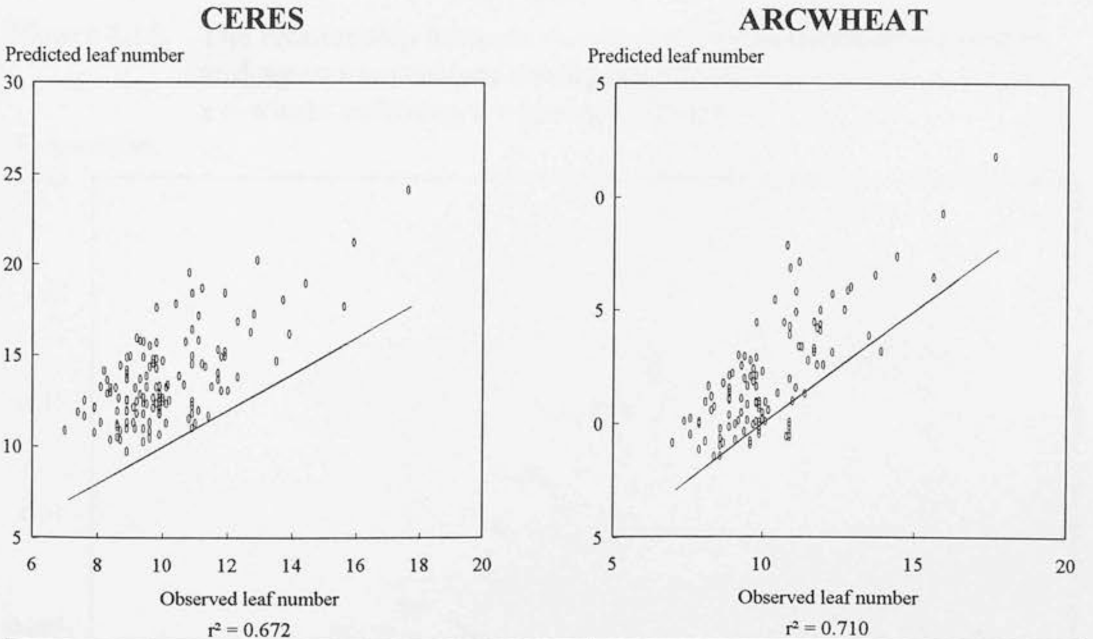
	Mean duration of phase (SE) °C days					
Sowing to	**1976**	**1977**	**1979**	**1980**	**1981**	**1982**
Emergence	144.1 (8.1)	123.5(15.3)	51.4 (0.05)		109.8 (6.9)	
Collar	191.4 (0.9)	188.3 (6.2)	225.7 (54.2)	359.7	218.9(46.4)	
MPN	549.3(30.2)	456.7 (0.1)	702.6 (136.7)	683.2(115.9)	744.2(121.9)	714.3(185.9)
Ear emerg.			938.0 (138.1)	851.8	1094.3 (177)	982.8(157.8)
Anthesis	851.7(59.9)	741.0 (5.9)		1026.38	996.0(118.4)	
Maturity	1246.6 (109)	1104.8(10.3)	972.3			

Figure 6.13. Correlation of observed and predicted values for phyllochron using the equations from the CERES model and the ARCWHEAT model


CERES

ARCWHEAT

Figure 6.14. Correlation of observed and predicted values for maximum leaf number using the equations from the CERES model and the ARCWHEAT model


CERES

ARCWHEAT

	CERES model (r^2)	ARCWHEAT model (r^2)
Leaf number	0.672	0.710
Phyllochron	0.526	0.568

Table 6.12. Development in thermal time for winter cv 'Igri'

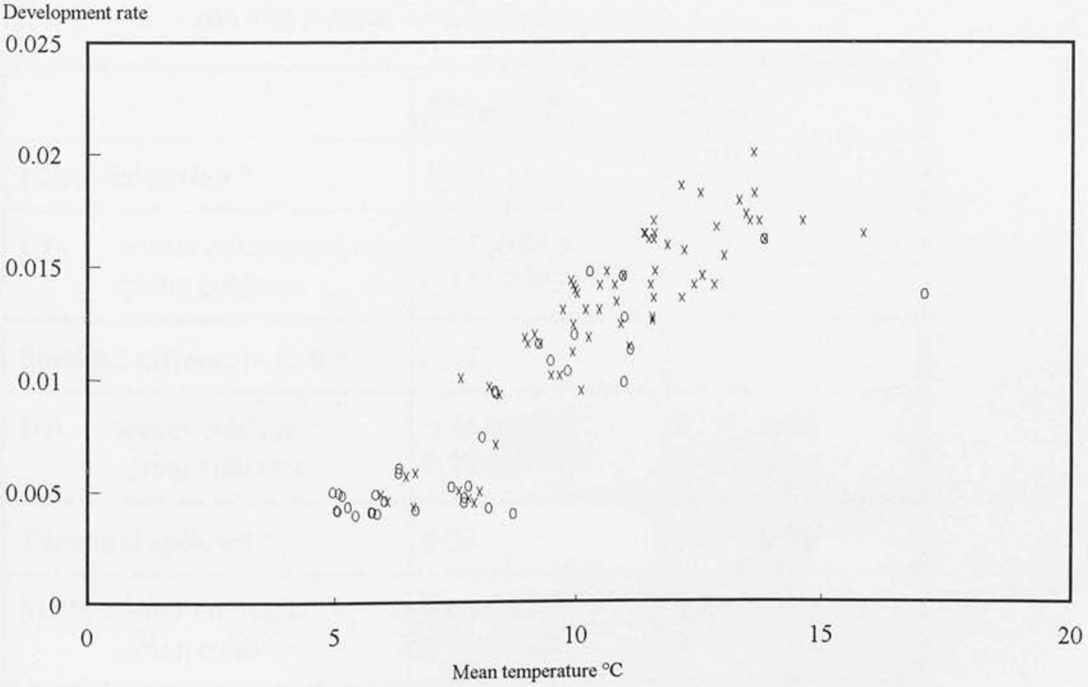
	Mean duration of phase (SE) °C days					
Sowing to	**1978**	**1979**	**1980**	**1981**	**1982**	**1984**
Emergence	106.5	51.1			126.3 (15.3)	128.5 (8.6)
Collar					265.5 (3.2)	339.4 (26.1)
MPN			1206.1		960.5 (42.1)	775.6 (98.6)
Anthesis					1315.5 (42.8)	1209.3 (92.4)

The ARC equation for calculating the rate of leaf emergence gave clusters of values for autumn- and spring-sown crops, without distinguishing between genotypes and sowing dates (Figure 6.12). However, the final maximum leaf number predicted by this method proved better than the CERES model equations (Figures 6.13, 6.14).

H. THE VAN KEULEN SPRING WHEAT MODEL

The overall duration of the pre-anthesis phase for spring wheat was related to mean temperature during the phase by regression (Figure 6.15).

Figure 6.15. The relationship between duration of pre-anthesis development and mean temperature during the phase.
x = winter cultivars, o = spring cultivars



Spring wheat: 70 data points from 22 authors (r^2=0.84) (van Keulen & Seligman, 1987):

```
1/daean = 0.00094 mtean + 0.49
```

Barley: 118 data points (r^2=0.795):

```
1/daean = 0.00158 mtean - 0.00449
```

daean = days from emergence to anthesis
mtean = mean temperature from emergence to anthesis (T_b = 0°C)
1/daean = development rate

The intercept from this regression of 0.00158 indicates a base temperature of 0°C can be used for pre-anthesis development. The database shows greater residual variability than van Keulen found for wheat (Figure 6.15). This may be due to the fact that both spring and winter cultivars and extreme sowing dates were used in the barley analysis. Thermal times to each development stage were expressed as a proportion of thermal time from emergence to anthesis (Table 6.13). Data sets which recorded ear emergence but not anthesis were not used.

Van Keulen defines floral initiation as the first appearance of double ridges. Double ridge occurred at a similar time in spring wheat and barley, but the date was more variable in spring barley since late sown crops may reach collar initiation before, or simulataneously with seedling emergence giving S_{fi} = 0. Van Keulen observed delayed floral initiation when mean temperatures increased (S_{fi} = 0.113 + 0.0065T, r^2 = 0.48). This was not apparent for barley (S_{fi} = 0.202 - 0.00718T, r^2 = 0.10).

Table 6.13. Duration of development phases as a proportion of the thermal time from seedling emergence to anthesis. * indicates data from the van Keulen and Seligman model.

	Mean (SE)	Range
Floral initiation *	0.22	0.18 - 0.24
CI winter cultivars spring cultivars	0.17 (0.010) 0.12 (0.007)	0 - 0.360 0 - 0.255
Spikelet differentiation *	0.24	
DR winter cultivars spring cultivars	0.34 (0.026) 0.22 (0.031)	0.10 - 0.50 0.14 - 0.44
Terminal spikelet *	0.52	0.43 - 0.51
MPN winter cultivars spring cultivars	0.66 (0.013) 0.54 (0.009)	0.41 - 0.81 0.36 - 0.78

Van Keulen obtained values for S_{fi} ranging from 0.18 to 0.24, and uses a value of $S_{fi}=0.21$ in his model. The database gives values from 0 to 0.36 (Mean 0.14, S.E.0.006) with significantly higher values for winter cultivars (Table 6.13). The stage of spikelet initiation begins at $S_{si}=0.24$ in the van Keulen model. Barley reached double ridge stage between 0.1 to 0.5 (mean 0.3 S.E. 0.023), with some difference between spring and winter cultivars. As the duration of the pre-anthesis phase increases, so does the proportion of that time before double ridge stage. This is due to the fact that autumn sown crops reach double ridge stage after a relatively long vegetative stage, but the length of the vegetative phase decreases as sowing is delayed. The value for S_{ts} chosen for the model is a constant 0.47 (range 0.43-0.51). S_{mp} from the database is 0.58 (S.E. 0.009) from a range of 0.36 to 0.81, with some difference between spring and winter cultivars.

6.3 SUMMARY AND DISCUSSION OF RESULTS

Analysis of the reference data set supports the use of a thermal time model for predicting emergence and the onset of reproductive growth since the greater the duration of the period from sowing to each development stage, the less reliable date of sowing alone is as a predictor of development. The thermal time from sowing to collar initiation is more predictable than the period to double ridge, due in part to the inevitable lack of confidence in the data for pinpointing the onset of double ridge. Double ridge takes place over a period of time, whereas collar initiation occurs on a unique date. MPN can then be predicted directly from collar initiation, without the need to predict the intermediate stage, overestimating the mean thermal time value from sowing to MPN by 17°Cdays instead of 135.7°Cdays.

Direct prediction of MPN was least reliable from the thermal time model. The rate and duration of spikelet initiation can be used to predict MPN given the point of change of rate of primordium initiation at the apex. Since the mechanisms for controlling development are still unclear, there are three possible approaches:

1. To equate this point of change with collar initiation predicted from thermal time,
2. To equate the onset of double ridge stage with the transition,
3. To predict collar initiation from final leaf number and rate of leaf primordium initiation.

Option 1 is favoured if collar initiation is a more predictable event than double ridge AND the rate and duration of spikelet initiation can be predicted more accurately from then than from double ridge. Option 1 has the theoretical advantage, in that the increase in rate of primordium initiation occurs at about this time. Option 2 has the practical advantage in that it can be verified by dissection. Option 3 has not been explored in existing models, and offers a novel approach.

R_p can be predicted from sowing date alone by:
Autumn-sown $R_p = 0.0588 - 0.000307*S$ $(\sigma=0.007015, r^2=48.8)$
Spring-sown $R_p = -0.00827 + 0.000232\ S$ $(\sigma=0.01143, r^2=36.1)$

Maximum leaf number can be predicted from the daylength at emergence (DAY), modified again by the direction of change of daylength:
Autumn-sown leaf number = $9.03 + 0.292\ DAY$ $(\sigma=2.04, r^2=5.0)$
Spring-sown leaf number = $13.1 - 0.239\ DAY$ $(\sigma=1.268, r^2=12.3)$

$$\text{Thermal time to collar initiation} = \frac{\text{Predicted Leaf number}}{\text{Predicted } R_p}$$

$(r^2=81.2$ spring-emerging crops, $r^2=49.6$ autumn-emerging crops)

The predicted duration of the phase from sowing to collar initiation then falls within $\sigma=47.33$°Cdays of the observed values (autumn) or $\sigma=50.88$°Cdays (spring). This can be compared with direct prediction of $\sigma=22.26$ days from the calendar model, $\sigma=63.41$°Cdays (autumn) or $\sigma=46.87$°Cdays (spring) from the thermal time model.

Each of the methods outlined in this chapter had its advantages (Table 6.14, however no one method stood out as a model blueprint which could be used reliably across all development stages. Each of the temperature-controlled methods (B, C and D) was built into the resulting simulation model as these gave consistently better results than prediction of development stage based on calendar time or phase duration alone.

Table 6.14. Summary of results. Standard deviation of the predicted duration of each development phase according to the various models tested.

Results are separated into winter and spring cultivars, or autumn- and spring-sown crops where the difference between the slope of the regression lines is significant.

	r^2 (SE of y est)				
Development Stage **Sowing to**	**A** **Sowing date** **d**	**B** **Duration** **d**	**C** **Thermal time** **°Cdays**	**D** **Photothermal time°Cdays**	**E** **Leaf number** **°Cdays**
Emergence			3.9 (131.9)		
autumn-sown	98.6 (9.8)	60.1 (7.1)	26.0 (39.5)	31.7 (63.5)	
spring-sown	99.0 (6.7)	56.2 (4.0)	23.2 (22.2)	47.3 (55.7)	
Collar initiation	90.0 (20.9)		42.4 (72.0)		
autumn-sown		51.6 (22.8)	43.4 (63.4)	47.7 (100.4)	49.6 (47.3)
spring-sown		63.4 (8.1)	33.2 (51.7)	45.8 (187.6)	81.2 (50.9)

Table 6.14. contd.

Sowing to	**A**	**B**	**C**	**D**	**E**
Double ridge			70.4 (85.3)		
winter cvs		51.2 (29.4)	76.8 (68.8)		
spring cvs			66.1 (80.1)		
autumn-sown	69.3 (29.3)			37.0 (133.9)	
spring-sown	86.2 (25.6)	66.8 (8.7)	69.8 (58.3)	8.3 (283.5)	
MPN		88.3 (21.0)	81.6 (122.0)	89.0 (112.1)	
winter cvs		85.3 (23.5)			
spring cvs					
autumn-sown	50.5 (23.4)				
spring-sown	66.8 (17.1)	94.3 (12.8)			
Ear emergence		97.3 (12.0)	84.5 (107.8)	58.3 (409.1)	
winter cvs	68.7 (8.4)				
spring cvs			75.9 (67.2)		
spring-sown	59.9 (9.9)				
Anthesis		97.8 (10.7)	70.8 (167.6)	92.6 (156.0)	
spring cvs					
autumn-sown	4.4 (10.1)		68.5 (136.8)		
spring-sown	58.9 (9.1)				
Maturity		94.2 (16.8)	63.5 (224.1)	86.4 (240.0)	
winter cvs		96.8 (13.1)			
spring cvs		83.5 (17.3)			
autumn-sown	26.8 (13.3)				
spring-sown	34.3 (17.3)				
Harvest		95.4 (14.7)	59.2 (246.3)	85.0 (242.4)	
winter cvs		97.0 (12.7)			
spring cvs	34.9 (12.8)	898 (15.0)			
autumn-sown	42.2 (15.1)				
Collar init. to MPN		78.2 (23.2)	64.5 (137.7)	39.4 (66.9)	
winter cvs		72.1 (31.3)			
spring cvs		76.4 (17.1)	65.1 (116.7)		
MPN to anthesis		25.5 (10.5)		28.1 (85.7)	
winter cvs			10.1 (110.9)		
spring cvs		47.3 (6.7)			
Collar initiation to anthesis		83.6 (22.1)	52.9 (182.1)		
winter cvs		84.5 (25.2)	56.9 (164.8)		
Anthesis to maturity		2.3 (11.0)			

7. GROWTH AND PRODUCTION OF DRY MATTER

7.1. INTRODUCTION

Leaf area development and the production and survival of tillers are central processes in this module. Grain yield is largely determined by anthesis (Dyson, 1977), since the number of ear-bearing shoots and the number of grains per ear have already been determined by this time. This chapter continues the analysis of data in the barley database (Chapter 5) and investigates the relationship between leaf area and dry matter increase and the factors determining the final number and weight of grains.

Partitioning of dry matter between roots, leaves, stem and grain is central to modelling, but the data to investigate how the fraction of assimilate to each 'sink' varies as the crop develops was not available through the database.

The time course of leaf area development was not generally available for the data sets in the barley database. Results from a field experiment at the Bush Estate, Edinburgh in 1989 (Appendix D) to study canopy development are presented in this chapter.

7.2. CANOPY DEVELOPMENT.

The leaf area at any given time is determined by the date of crop emergence, the rate of leaf emergence, the rate of leaf extension, the rate of tillering and the rate of leaf senescence, each of which can be under genetic, environmental or agronomic control.

The appropriate measure of photosynthetic tissue is difficult to ascertain. Leaf, sheath, stem and ear green areas must all be taken into account, but not all green tissue photosynthesises at the same rate (e.g. leaf blades faster than stem tissue). Green Area Index (GAI) gives a more accurate index of performance and is determined by:

$$GAI=(L+S)/A$$

L	leaf lamina surface area
S	leaf sheath green area
A	ground area

Senescing foliage is generally only significant above GAI of 3.0. However, the proportion of light interception increases with leaf area, so inaccuracies after GAI of 3.0 become less important for calculating interception. Grain yield shows a high positive correlation with GAI at anthesis and Leaf Area Duration (LAD) (Borojevic & Williams, 1982; Thomson,

1979) so if this method of prediction is used, senescence assumes greater importance. GAI at anthesis may be positively correlated with time from sowing to anthesis (ie. LAD) and LAD is correlated with the accumulated absorbed radiation.

Spring wheat and barley crops generally reach a GAI of 1.0 about 8 weeks after sowing (Kirby, 1973). GAI increases rapidly to GAI 3.0, then passes through a linear phase to a maximum (Figure 7.1; Russell, 1990) about 200°C days before anthesis (Russell & Ellis, 1988). Maximum values may approach $10m^2\ m^{-2}$, depending on location and genotype. The theoretical upper limit is set by the level of irradiance reaching lower leaves. Leaves senesce if the level of irradiance falls below a certain critical level: at UK levels of irradiance, this is equivalent to 4 leaf layers (Monteith & Elston, 1983). Lower latitudes with higher radiation levels do not necessarily support denser canopies, since water stress may be more pronounced (Russell, 1990). High temperature, disease, water and nutrient stress also cause rapid senescence after leaf production has ceased. Leaf area, lamina and sheath weights and LAD show strong genotypic variation.

The net assimilation rate increases with PAR up to an asymptote which corresponds with light saturation: any further increase in PAR has little effect on the assimilation rate as the canopy is unable to intercept all the available radiation. The proportion of intercepted PAR increases with GAI up to a GAI of 3, and at values above this there is a tendency for older, shaded leaves to reach their light compensation point and contribute little more to crop growth rate. Below the optimum GAI, growth rate is therefore dependent on GAI and light interception is incomplete; above the optimum, the net assimilation rate is depressed by increased respiratory losses.

Light penetration will be higher through erect-leaved crops, and senescence of lower leaf layers may be slower than in lax-leaved genotypes. This leads to an increase in crop growth rate and improved photosynthetic efficiency. Above the optimum GAI, interception will be reduced towards saturation point with no loss in efficiency and PAR which is not intercepted at the top of the canopy will be available to lower leaves. However, leaf area projected on a horizontal plane will not be affected. Leaf angle is included in models of absorbed radiation by incorporating an extinction coefficient, k. Thus the maximum crop growth rate depends strongly on both GAI and k at irradiances below canopy light saturation point. Measurements of GAI were taken in the field (Appendix D), but the measurement of k requires stratified measurements of irradiance, leaf area and angle through the canopy at various stages of development under a range of agronomic conditions. The value of $k = 0.5$ to 0.75 for temperate cereals (Hay & Walker, 1989) could not be confirmed.

There are three alternative approaches to calculation of GAI in the model:

1. Integrate leaf number and size (as in the ARCWHEAT model)
2. Convert leaf mass to area using the Specific Leaf Area (SLA) (as in van Keulen & Seligman, 1987, and CERES models)
3. Relate GAI to thermal time (Russell, 1990).

Leaf number and size

Leaves emerge at a linear rate with respect to temperature which can be used to predict leaf numbers (Chapter 6). Leaf extension is also a linear function of temperature, decreasing with water or nitrogen stress (Biscoe & Gallagher, 1978), but continues slowly even when the temperature is close to freezing. However, the proportion of a single leaf area that has emerged, does not show a linear relation with temperature (Appendix D).

It is estimated that barley awns contribute an additional 0.5 GAI (Scott & Dennis-Jones, 1976) after ear emergence, but this figure has not been confirmed. Awn Area Index is calculated from:

$$\text{ears m}^{-2} \times \text{mean ear (length} \times \text{breadth)}$$

Specific Leaf Area

SLA, the leaf area per unit leaf weight, varies with development and the environment. Van Keulen & Seligman (1987) use a default value of SLA = 250 cm^2g^{-1} for spring wheat. The CERES model uses SLA = 127.5 cm^2g^{-1} after MPN, when LAI is nearing its maximum, which is consistent with their definition of LAI as leaf lamina area only.

Canopy development in thermal time

Leaf emergence and extension rates are dependent on temperature. Changes in partitioning of assimilate between leaf, stem and ear are tied to crop development, also under temperature control. There have been few experiments where barley canopy development has been measured in detail in the field, and results from controlled environments reflect unrealistic conditions imposed on the plants, particularly as a consequence of low radiation levels in growth cabinets (Fletcher & Dale, 1977). Nitrogen status, population density and water supply also affect leaf size and longevity, and one of the chief affects of foliar diseases such as mildew is the effective reduction of GAI through more rapid crop senescence. Russell (1990) attempted to model GAI, expressed as a proportion of maximum GAI, as a function of thermal time, but attributed the wide variation to the range of growing conditions considered. This range was also described by Hay & Walker (1989). Maximum GAI varies with cultivar and sowing date, but irradiance, water and nutrient levels can also affect it since it can be both temperature and assimilate limited.

7.3. TILLERING

Tiller numbers and size affect both leaf area and biomass as well as the final number and size of grains. The number of elongating tillers is linearly related to the number of grains per ear, with the slope a function of the nutrient supply.

Tillers appear in a regular pattern. Kirby and Riggs (1978) saw Tiller 1 (T_1) at 3.6 leaves. Kirby & Ellis (1980) note the appearance of T_1 when there are between 3.2 and 4.1 leaves on the main shoot, and T_2 at between 3.9 and 5.1 leaves. Gallagher & Biscoe (1978b) record the appearance of the coleoptile tiller, T_c, when the third leaf is unfolding, T_1 at the fourth leaf, T_2 at the fifth leaf etc. Faivre & Masle (1988), working with wheat, note the appearance of T_1 at the appearance of leaf 4, T_2 with leaf 5, T_3 with leaf 6 etc. Secondary tillers also form in a regular sequence (T_{1p}, T_{2p}, T_{3p} forming in the axils of T_1, T_2, T_3 etc). A tiller bud may be associated with the leaf above the subtending one, since rapid elongation of T_1 and T_2 buds occurs at the time when the first and second leaves are fully elongated (Cannell, 1969a).

Tiller numbers

In a February or March sown crop in the UK, tiller numbers increase until mid May, decline to 60-70% of the maximum towards anthesis and are maintained at this level until harvest. At typical plant densities, spring barley will produce 5 tillers per plant, winter wheat 6 (Gallagher & Biscoe, 1978a).

Higher tillering genotypes have more T_c, T_3 and T_{1p} tillers (Simmons *et al.*, 1982). The number of tillers also increases with abundant nutrient supply, low temperatures and high irradiance (Aspinall, 1961; Friend, 1965b; Cannell, 1969b; Scott & Dennis-Jones, 1976). Narrow rows cause higher tiller mortality, due to competition for light, water and nutrients.

Tiller size and weight

The initial weight of a wheat tiller was found to be constant over the first four primary tillers produced (Faivre & Masle, 1988). Tillers compete with the main stem for assimilate until they are 40 - 100 mm long, and extend beyond the subtending leaf sheath, at the same time as the plant is initiating spikelet primordia. Friend (1965a) estimated that for wheat, a tiller could survive if it had produced three leaves, and barley is presumably no different.

Additional tillers add to the dry matter of the crop but do not significantly increase grain yield, since competition for light, water and nutrients reduces the size and potential yield of other developing shoots and the harvest index falls (Jones & Kirby 1977). A 160-fold increase in winter wheat density from 100 to 1600 plants m^{-2} in the Netherlands resulted in only a 3-fold yield increase (Darwinkel, 1978). Whilst tiller bud initiation is little affected by planting density, the development of tiller buds into shoots is curtailed at high density (Kirby & Faris, 1972). At densities of over 600 plants m^{-2}, only the main stems will produce ears (Kirby, 1976). Low densities not only allow tillering to continue for a longer period (Nerson, 1980, Kirby & Faris, 1970), but more of the tillers are fertile. Experiments in which tillers are selectively removed, show that growth and size of the main shoot are enhanced by tiller removal (Kirby & Jones, 1977). Removal of tiller buds allows more spikelets to be initiated and a higher proportion to survive. Early removal of tillers led to increased rate of leaf emergence, larger leaves and a greater leaf number (Kirby & Jones, 1977; Austin & Jones, 1974). Grain number and kernel weight of the remaining stems are both increased.

GAI and thus assimilation also are directly affected by leaf number in the ARCWHEAT model. As with the CERES model, growth is calculated on a m^2 basis, but the model of canopy development simulates growth of individual leaves and tiller cohorts, with survival depending on cohort age and shoot population density. Each leaf grows to maximum size in an interval of 1.8 phyllochrons and spends a fixed proportion of its life at that size (given by model input). A tiller site only remains active during a single leaf appearance interval, with a 7.5mg increase in dry matter needed to initiate each shoot. Tillering ceases at double ridge, so neither model can predict a late burst of tillering.

High levels of irradiance increase tillering. A late burst of tillering can be associated with lodged crops as light is able to penetrate to the base of the plant; these contribute little to the yield of the crop. Late formed tillers are adapted to grow rapidly into the upper layers of the canopy, with increased elongation of sheaths and internodes. Poor ear production occurs from late formed tillers at all sowing densities, and the reproductive development of higher order tillers is decreased at higher densities with fewer grains formed per ear.

The database contained planting density, final population density, tiller number and ear numbers for a range of field experiments. These data were examined to see if tiller number could be confidently predicted from the leaf number, rate of leaf emergence and the duration of tillering period from emergence to MPN. If tiller formation occurs with the same regularity in thermal time as leaf emergence between seedling emergence and MPN, but with a time lag equivalent to 4 phyllochrons (T_1 forms at the same time as leaf 5, T_2 with leaf 6 etc), the maximum number can be found from:

$$\text{Maximum tiller number} = TT_{emp} \times R_l - 4$$

TTemp Thermal time from emergence to MPN
R_l Rate of leaf emergence °Cdays^{-1}

Final stem number will then be one greater than the tiller number to include the main stem.

7.4. COMPONENTS OF YIELD

Grain yield is the product of ear number, grains per ear and grain weight. Where final yield is known, any one of these can be calculated directly from the other two. Confidence in the accuracy of the data held on the barley database was reduced when the means of derivation of the components of yield was not known.

Delayed sowing results in a linear decrease in total dry matter (Green & Ivins, 1985) and maximum grain yield for both barley and wheat (Beech & Norman, 1971) with values measured of 0.43% (winter barley cv. 'Igri'), and 0.35% (winter wheat cvs. 'Norman', 'Armada' and 'Avocet') for every day sowing was delayed after early September (Green *et al.*, 1985). However, it does not follow that a very early sowing increases yield further despite a longer period for assimilation, since the crop is at greater risk from disease.

GRAIN NUMBER

Grain number was calculated by three methods using the data in the barley database.

1. Grain number has been related to the dry weight of the plant at anthesis (Dyson, 1977; Shepherd *et al.*, 1987; Russell & Ellis, 1988) with considerable variation between genotypes. Dyson (1977) found that over a range of sites and seasons, the grain yield of spring barley was proportional to, and almost equal to the total dry weight of the crop at ear emergence ($r^2 = 0.962$) but the correlation with total dry weight accumulated after ear emergence was weaker ($r^2 = 0.795$). The weight of a single tiller at anthesis was highly correlated with its grain yield ($r^2 = 0.997$), but data

to test this was not available. A total grain number of 17.1 grains g^{-1} dry matter at anthesis (range 9.7 - 51.2) was measured (Russell & Ellis, 1988) and this figure was compared with other data in the barley database. Factors which affect shoot weight at anthesis therefore have a bearing on the final yield. Cultivar differences must also be taken into account since large-grained cultivars may produce fewer grains.

2. The rate and duration of spikelet primordium initiation in thermal time are used to determine maximum spikelet number. This can then be modified by a spikelet survival rate dependent on sowing date and density to give fertile spikelet number. Ear type (2- or 6-row) must be taken into account. Total grain number is then calculated by the product of fertile spikelet number and stem number at anthesis.

3. Total grain yield divided by mean kernel weight will also give grain number per unit area. This method is preferable since grain weight is a relatively stable character, and the process of tillering, which caused such problems in the CERES model, need not be included in the model. However, grain yield must be reliably predicted.

GRAIN WEIGHT

The rate of grain growth increases with temperature, but the duration of the period from anthesis to maturity is reduced. Therefore the net effect is that mean grain weight remains fairly constant (Biscoe & Gallagher, 1977) over a range of temperatures. At temperatures above 30°C the increase in growth rate is not compensated for by the shortened duration and the grain weight is reduced.

Increased population density may cause a decrease individual grain weight as shown by Kirby (1967) using cv 'Proctor', but later studies using cultivars less prone to lodging have not confirmed this finding. The pattern of tillering is also of importance, since mainstem ears tend to produce heavier grains than tillers. These two effects have a compensatory effect on grain weight, since increased population density reduces tillering and thus increases the relative contribution of mainstem ears. Similarly, there is a compensatory effect of fertilisation, since tillering will be promoted in highly fertilised crops which thus produce more ear-bearing stems, but nitrogen may also significantly increase grain size.

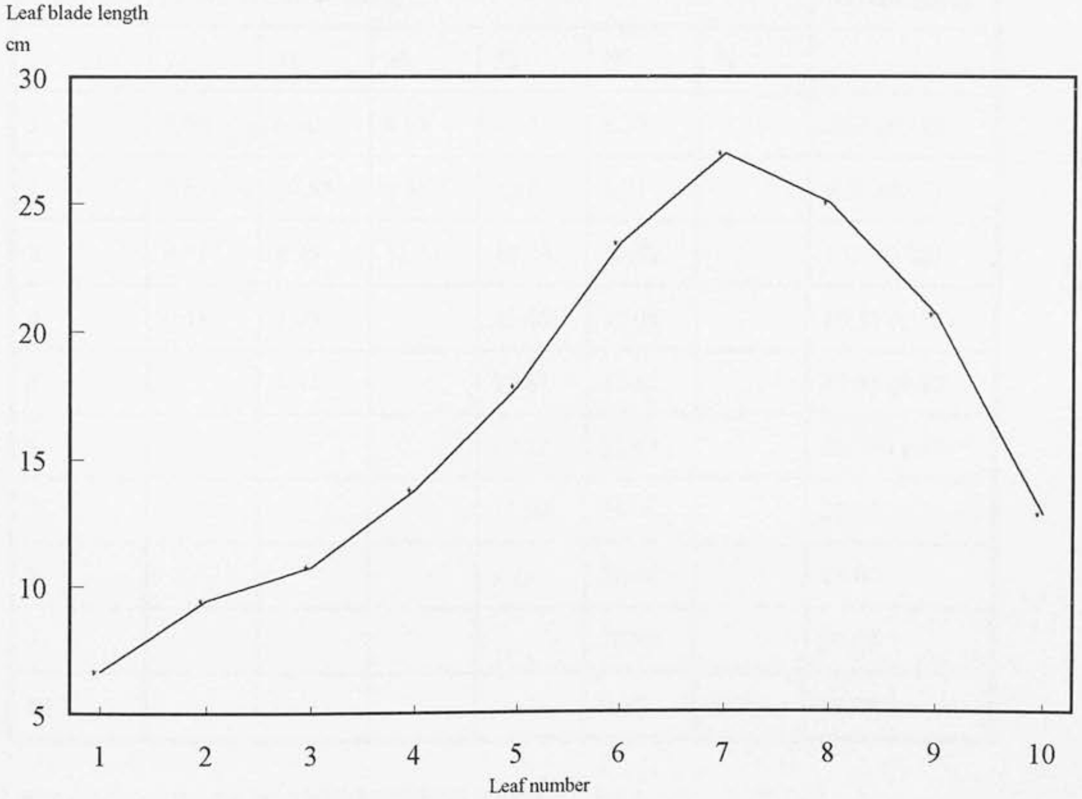
There are three main methods for modelling grain weight:

1. Calculation from total grain yield and grain number (CERES method) - (option only available if grain number is not calculated by method 3 above, to avoid circularity)

2. The mechanistic approach in which the rate of grain growth is modelled on a daily basis, varying with temperature (ARCWHEAT method), with compensation from stored reserves meeting any shortfall in assimilate. Net assimilation exceeds the storage capacity of the developing grain for the first 15 - 25 days after anthesis during the period of endosperm cell division such that excess carbohydrate accumulates in the stem and leaf sheaths. After this time, the net assimilation rate decreases as the canopy senesces and these stored reserves maintain the translocation of assimilate to the grain. Minimum and maximum values may be required in the model to restrict grain weight within a sensible range (20 to 75 mg) depending on genotype. Grain growth rate could not be calculated directly from the database.

3. Grain yield can also be determined from total biomass x harvest index (Russell, 1990). Harvest Index has improved over the years with selective breeding for high yielding, short strawed cultivars. However, the database also includes data from older, tall cultivars such as cv 'Proctor' giving rise to a larger variation in HI than would be the case for all new cultivars.

Figure 7.1. The relationship between leaf blade length and leaf number in spring barley



Data: Bush House, Edinburgh, 1988. Mean of 10 spring cultivars. Appendix D.

7.5. RESULTS

CANOPY DEVELOPMENT

Leaf number and size

Lamina length increases for the first few leaves (2 or 3 leaves: Kirby, 1973; 5 or 6 leaves: Figure 7.1) and then decreases. Lamina width of individual leaves also increases with leaf number, but is reduced at high densities. Sheath length increases with density, and tiller order. Kirby, Appleyard & Fellowes (1982) showed that there could be considerable variation in leaf dimensions at any given node, which was confirmed by the large standard errors attached to the mean leaf blade length (Table 7.1) of 10 spring barley cultivars. However, the data confirm the summary of Hay & Walker (1989) that there is a rapid phase of elongation up to the full emergence of each leaf followed by a pronounced decline in the rate of leaf expansion.

Table 7.1. The length (in cm) of successive leaf blades of ten spring barley cultivars.

Leaf no	**Days from sowing**						**Mean (SE)**
	24	**31**	**38**	**52**	**59**	**74**	
1	7.04	6.90	6.69	6.33	6.27		6.65 (0.14)
2	*9.87*	10.57	9.64	8.82	8.71		9.52 (0.37)
3	*4.69*	*8.39*	11.41	10.24	10.61		9.07 (0.28)
4	*0.58*	*3.39*		13.46	14.08		10.31 (0.22)
5		*0.83*		17.87	17.82		17.85 (0.12
6				*19.31*	23.42		21.37 (1.45)
7				*17.80*	26.94		22.37
8				*9.19*	*25.00*		25.00
9					*20.60*		20.60
10					*9.92*	12.78	12.78

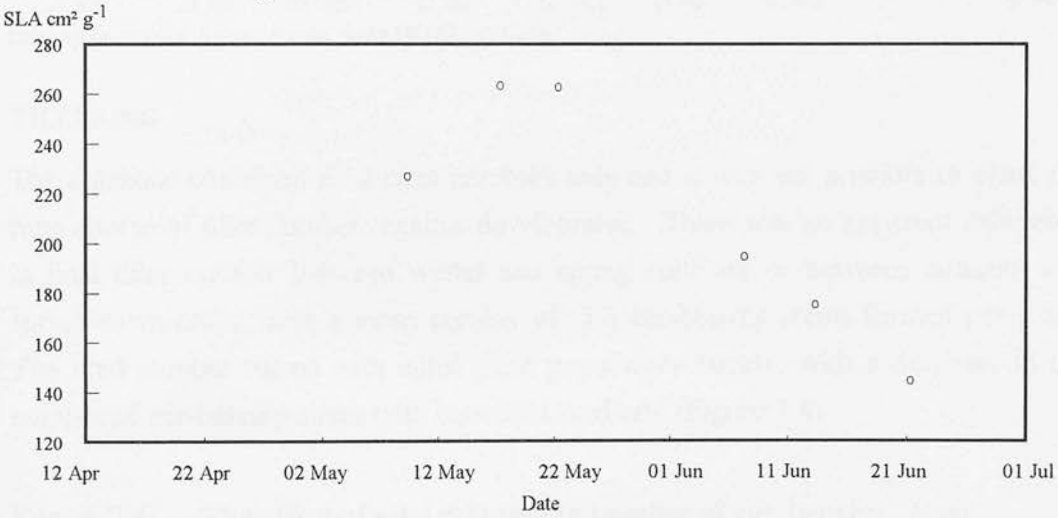
Figures in italic type represent leaves which have not fully unfolded

Data: Bush House, Edinburgh, 1988. Mean of 10 spring cultivars. Appendix D.

Specific Leaf Area

The first few leaves produced on the main stem are generally thinner and areas can be measured fairly accurately: as the leaf sheath contribution increases, the error attached to field leaf area measurement increases. SLA reaches a maximum at about the 3 leaf stage (Figure 7.2), followed by a decrease which may be exponential in form with thermal time (Baret, 1986). Experimental results suggest that the use of a constant for SLA is an oversimplification (Figure 7.2), but there are too few data sets to define the relationship between SLA and time (or thermal time) precisely. A mean value of 25 cm² g⁻¹ (used in ARCWHEAT) is higher than these data suggest, but the discrepancy may be partly ascribed to morphological differences between wheat and barley leaves.

Figure 7.2. The time course of Specific Leaf Area in spring barley from emergence to anthesis

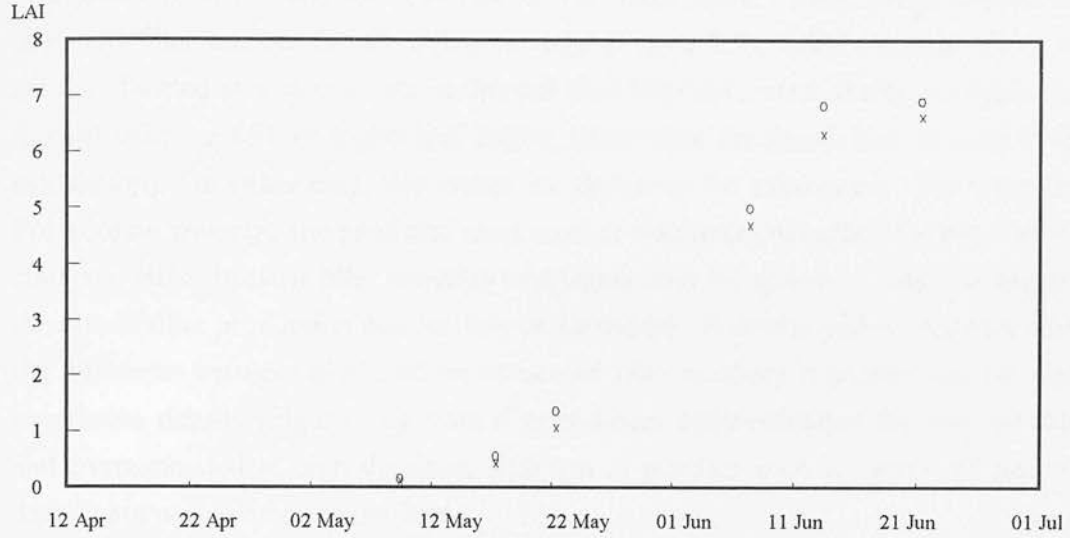


Data: Appendix D. cv. Golden Promise. Sown 19.4.89, Edinburgh.

The development of GAI

GAI was measured from dissected plants using a Leaf Area Meter (Appendix D). There was a curivlinear relationship between GAI and time from sowing (Figure 7.3) which did not differ significantly between row crops grown at narrow or wide spacing despite the potentially greater irradiance reaching the lower leaves of widely spaced crops. GAI increased with time from sowing as each successive leaf formed was larger than the last, but the rate of increase slowed towards flag leaf emergence, since the flag leaf was found to be smaller than the previous leaf in cv 'Golden Promise'. This pattern but may not be universally true for all cultivars. GAI then fell as leaves senesced, until it had reached zero by plant maturity.

Figure 7.3. The time course of leaf area development in spring barley x = narrow rows (15 cm), o = wide rows (25 cm)

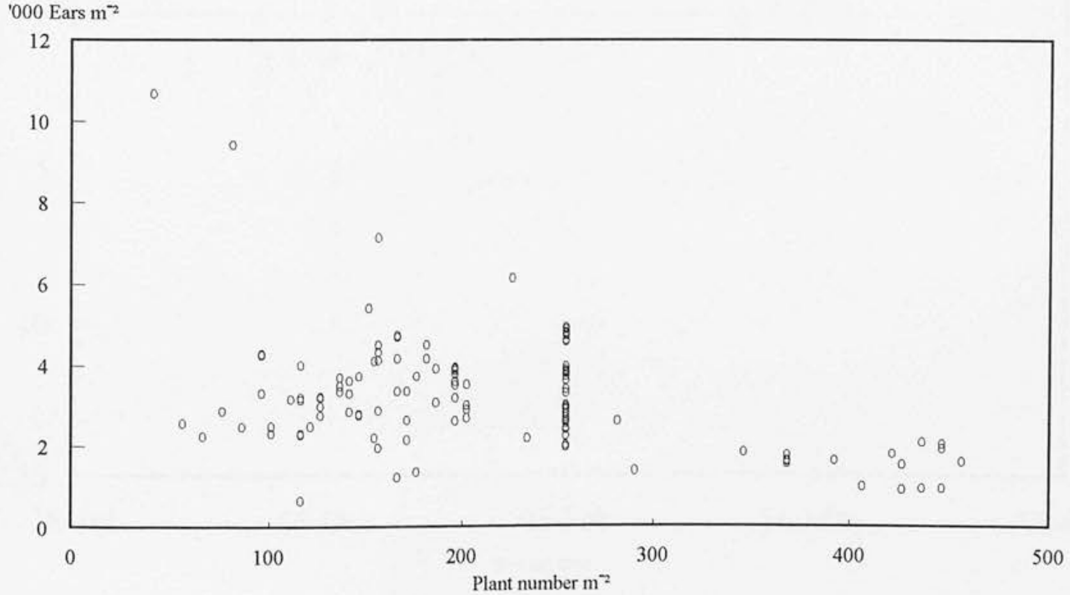


Data: Appendix D. cv. Golden Promise. Sown 19.4.89, Edinburgh.

TILLERING

The database contained final stem numbers only and it was not possible to chart the time course of tiller numbers against development. There was no apparent difference in final tiller number between winter and spring cultivars or between autumn- and spring-sown crops, with a mean number of 3.3 ear-bearing stems formed per plant. The final number varied with initial plant population density, with a decrease in the number of ear-bearing stems with increased seed rate (Figure 7.4).

Figure 7.4. The effect of seed rate on the number of ear-bearing stems



Maximum stem number was calculated from the thermal time from seedling emergence to MPN and and the rate of leaf emergence. This overestimated the observed tiller number for all spring sowings (Figure 7.5), either because tillers are actually formed at a slower rate in thermal time than main stem leaves, or each tiller formed with the fifth or higher leaf below, rather than the fourth leaf as used in the calculations. In either case, this makes no allowance for subsequent tiller mortality. For autumn sowings, the predicted stem number was underestimated for most winter cultivars, either because tiller mortality was higher than for spring sowings, or because the rate of tiller production was too low in the model. A similar pattern appears when the difference between predicted and observed tiller numbers is plotted against plant population density (Figure 7.6), with tiller numbers underestimated for low densities and overestimated at high densities, although in practice such extremes of planting density are not common in the field.

Figure 7.5. The variation between predicted and observed stem numbers with sowing date.
x = winter cultivars, o = spring cultivars

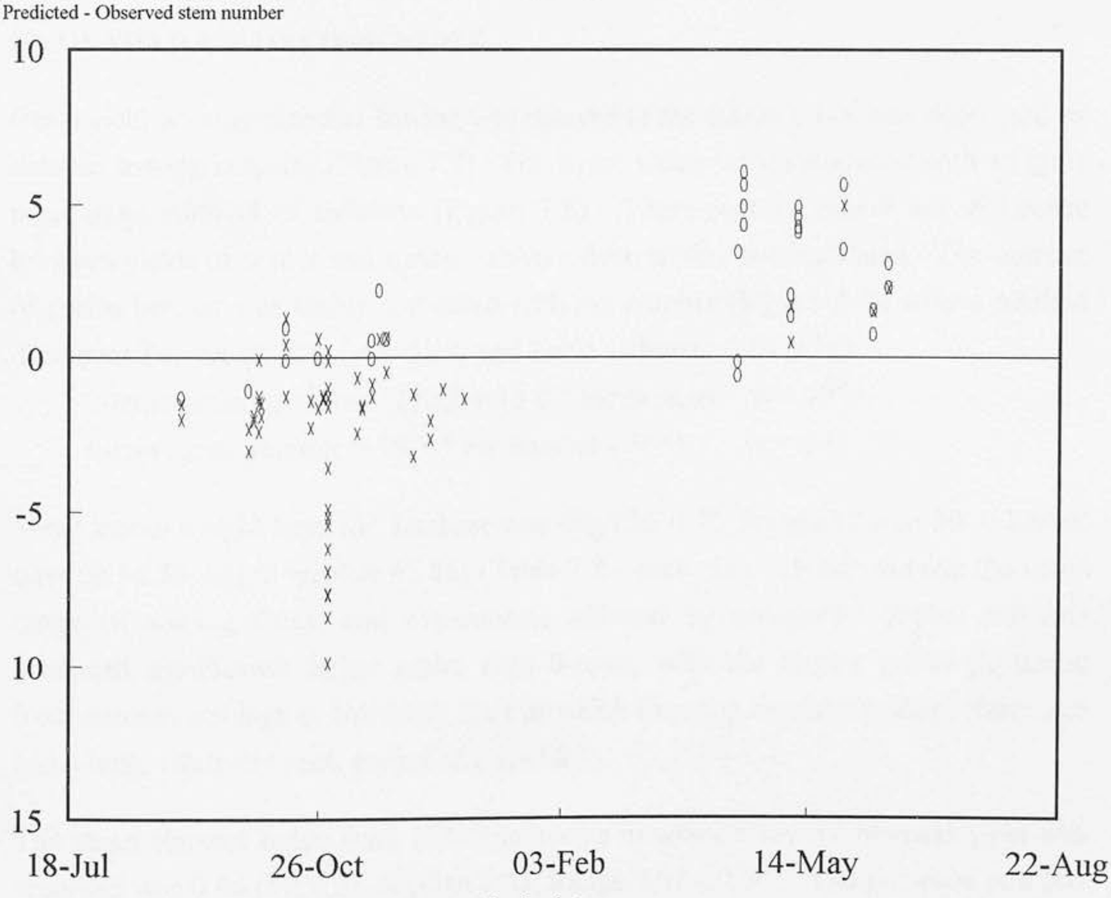
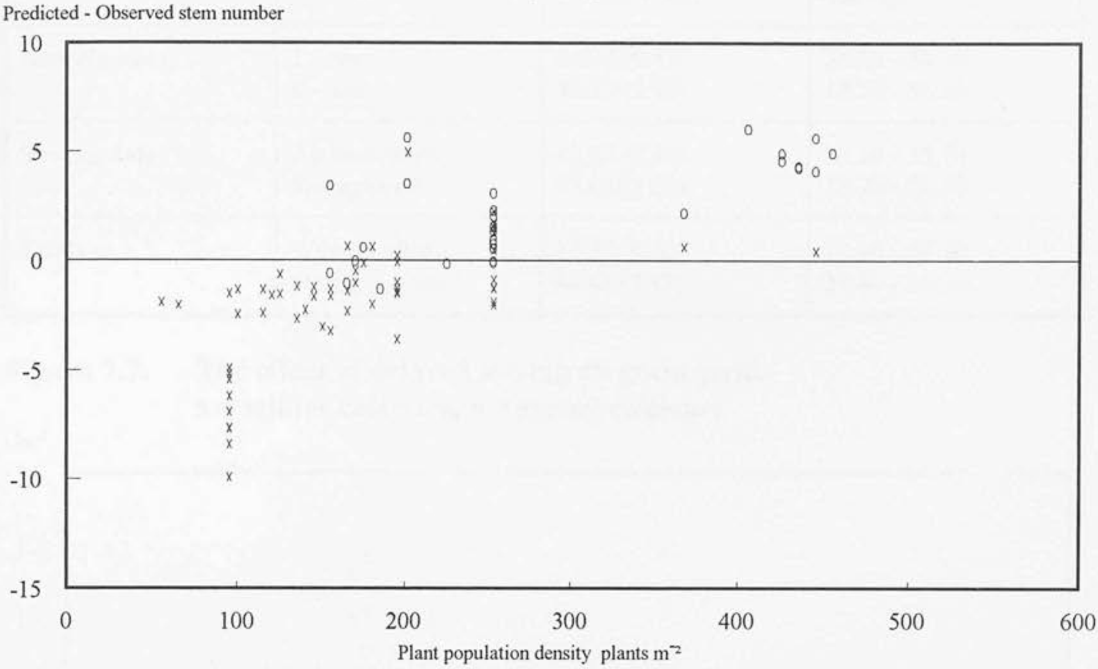


Figure 7.6. The variation between predicted and observed stem numbers with planting density
x = winter cultivars, o = spring cultivars



GRAIN YIELD AND ITS COMPONENTS

Grain yield was increased as sowing was delayed in the autumn, but was decreased by delayed sowing in spring (Figure 7.7). The larger yields were associated with a higher percentage survival of spikelets (Figure 7.8). There was no significant difference between yields of winter and spring cultivars from similar sowing dates. The number of grains per ear was highly correlated with ear number (Figure 7.9), with a marked difference between 6-row ($r^2 = 0.84$) and 2-row cultivars ($r^2 = 0.78$).

2-row: grain number = 1220.8 + 18.4 * ear number (n = 107)
6-row: grain number = 59.8 * ear number - 5641.1 (n = 24)

Mean kernel weight from the database was 40g (SE 0.72, Range 12.9 to 59.3, Lower quartile 34.55, upper quartile 45.85) (Table 7.2 - excluding sowings outside the usual range of sowing dates, and experiments affected by drought). 2-row cultivars produced significantly larger grains than 6-rows, with the largest grains produced from autumn sowings at Northerly sites in which the crop reached anthesis early and had a long, relatively cool, period of grain fill.

The mean Harvest Index from 120 experiments in which straw or biomass yield was recorded was 0.46 (SE 0.01, Median 0.48, Range 0.02 - 0.63). The presence of a few extreme values in these data should be noted.

Table 7.2. The stability of grain weight

		Mean (SE)	Range
Row Number	2 - row 6 - row	41.07 (0.85) 37.56 (1.78)	24.20 - 59.30 12.90 - 53.20
Sowing date	Autumn-sown Spring-sown	43.22 (1.19) 38.94 (0.86)	33.10 - 55.90 12.90 - 59.30
Cultivar	Winter cultivar Spring cultivar	37.35 (0.80) 44.48 (1.17)	12.90 - 51.30 23.80 - 59.30

Figure 7.7. The effect of delayed sowing on grain yield.
x = winter cultivars, o = spring cultivars

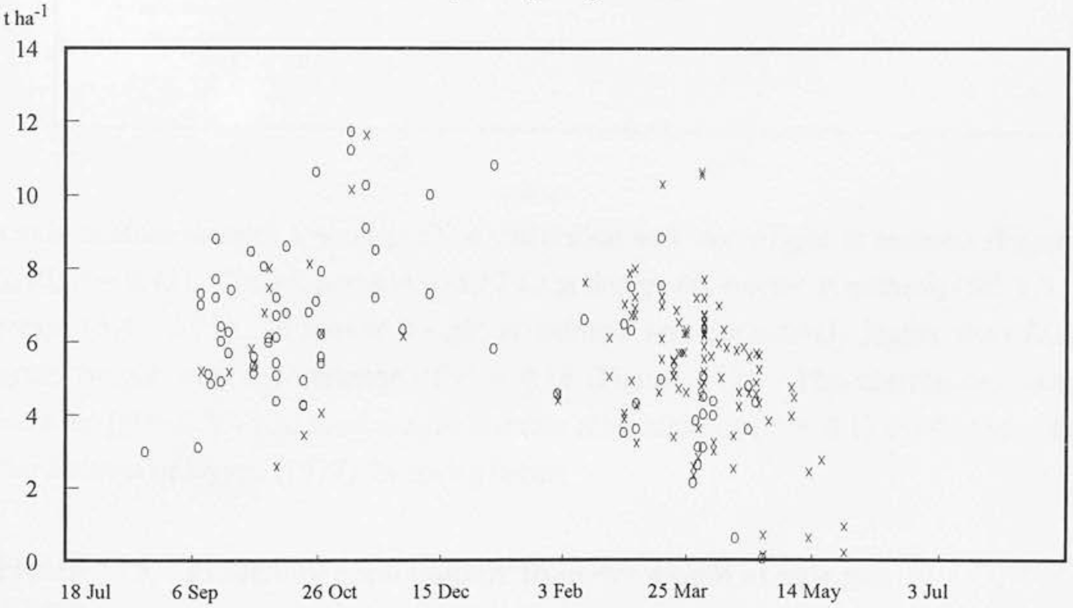


Figure 7.8. The variation in spikelet survival after anthesis with sowing date.

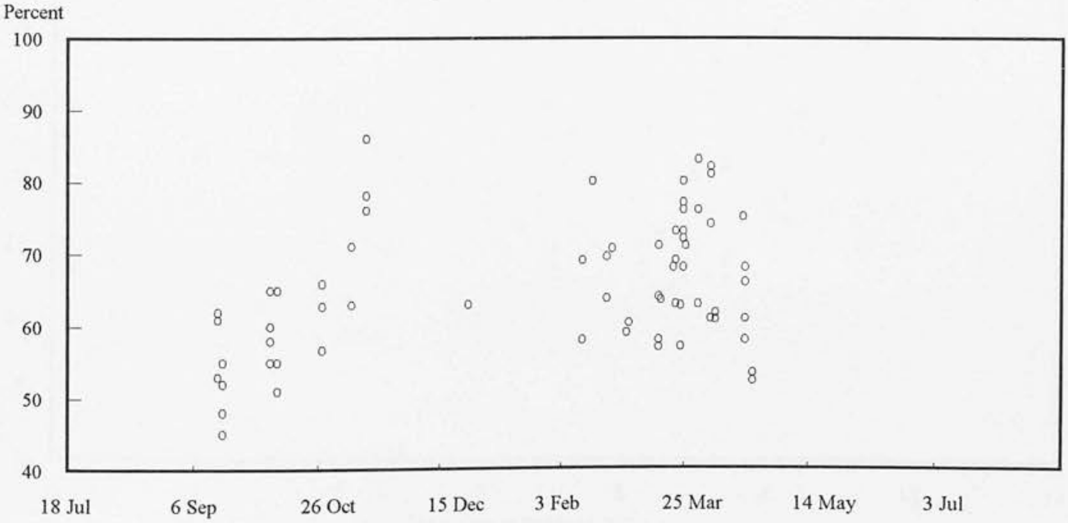
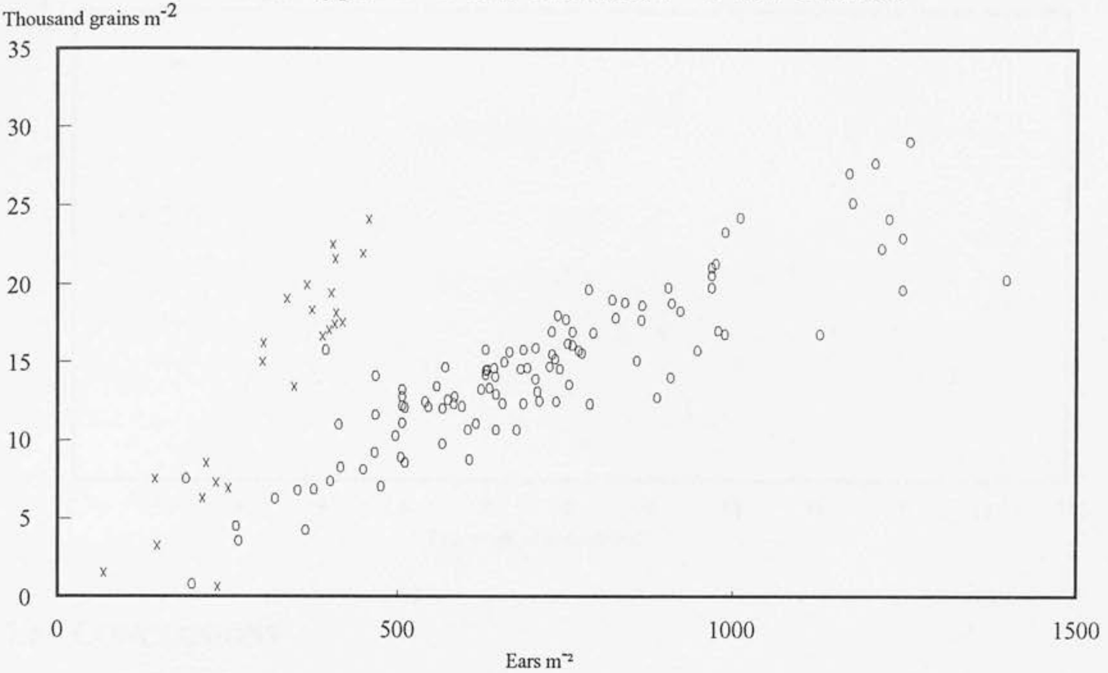


Figure 7.9. The relationship between grains per ear and ear number varies with ear type. x = 2-row cultivars, o = 6-row cultivars



Grain number showed a weak positive correlation with dry weight at anthesis (Figure 7.10, $r^2 = 0.42$). The mean value was 17.89 grains g^{-1} dry matter at anthesis (SE 1.27, range 15.4 - 35.9). However, weight at anthesis was consistently higher than final grain weight with a correlation of $r^2 = 0.18$ (Figure 7.11). The correlations with biomass ($r^2 = 0.23$) and total weight increase after anthesis ($r^2 = 0.1$) conflicted with the findings of Dyson (1977) for spring barley.

Figure 7.10. Predicting grain number from dry weight at anthesis

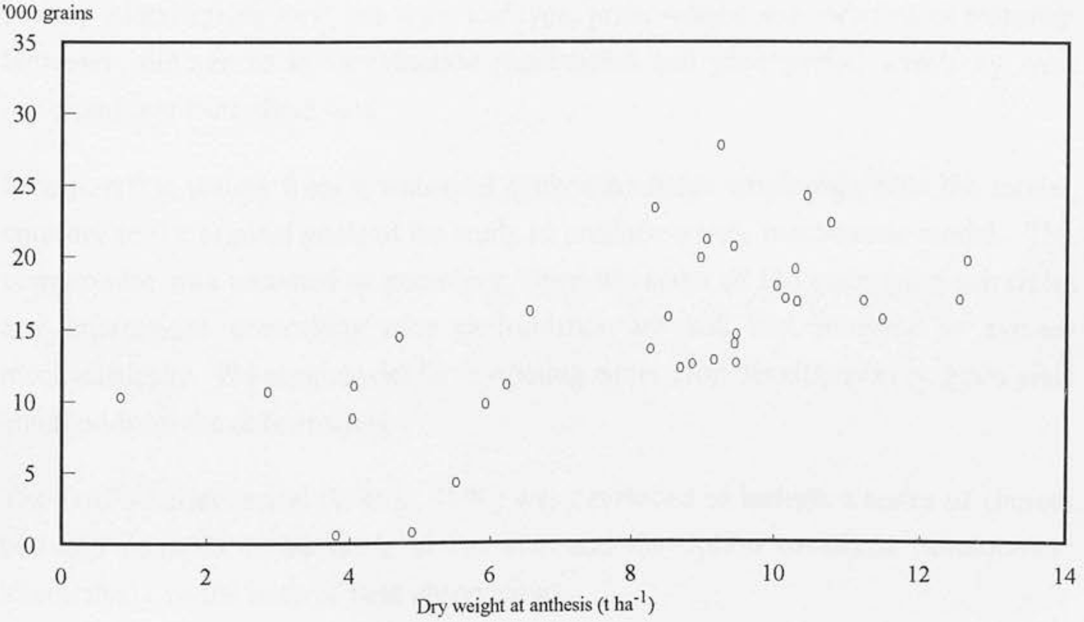
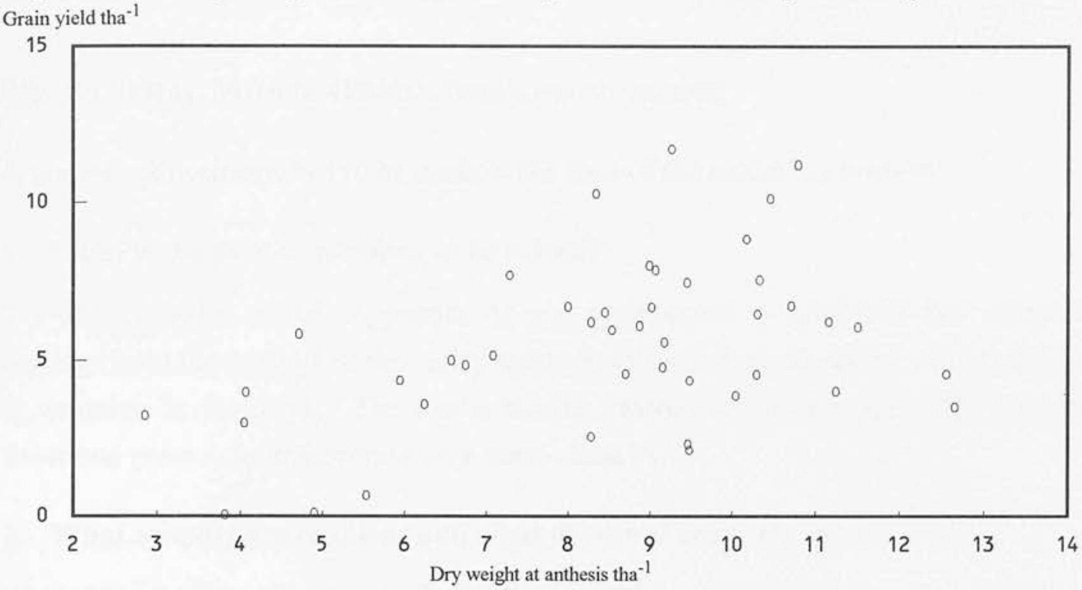


Figure 7.11. Dry weight at anthesis as a predictor of final grain weight.



7.6. CONCLUSIONS

The analysis repeatedly showed little significant difference between winter and spring cultivars from similar sowing dates, provided the vernalisation requirement of the winter cultivars was satisfied, and the establishment of the spring cultivars was not unduly affected by cold. This endorses the premise that a single model can be used for both, provided routines are included for vernalisation and cold tolerance.

The database scope did not highlight the causes of variation due to GxE interaction, but focussed on a few genotypic characters that should be incorporated into models - namely winter/spring type, ear type, leaf type, grain weight and earliness of maturity. However, differences in vernalisation requirement and photoperiod sensitivity were not quantified from these data.

Incorporating results from a statistical study introduces empiricism into the model, contrary to the original goals of the study to produce a truly mechanistic model. This compromise was accepted as necessary, since the some of the underlying principles and interactions controlling crop performance are still too complex to express mechanistically. No clear model for predicting either crop development or grain yield emerged from the data analysis.

The DAFS barley model (Wilson, 1990) was developed to include a series of choices between methods to be made at run-time and the option to adjust development interactively on the basis of field observations.

8. THE DAFS BARLEY MODEL

8.1. GENERAL MODEL OBJECTIVES AND PLANNING

A number of decisions had to be made at the start of the modelling process:

1. What is the precise problem to be solved?

The DAFS barley model (Appendix A) was constructed to synthesise the separate findings from the analysis of the barley database to see if it could reflect observed G x E variation in Scotland. The model should incorporate aspects of other models described previously and operate on a stand-alone PC.

2. What outputs are required and what degree of accuracy is required?

The initial requirements from the DAFS barley model are:

- Prediction of development, anthesis in particular.
- Prediction of dry matter yield and the components of yield:

  Grain Yield, Grains/ear, Grains m^{-2}, Ears/plant, Harvest Index, Biomass at maturity, Thousand Grain Weight

Further objectives once the initial model is verified:

- A report of potential yield, and assessment of reasons why a particular GxE combination failed to achieve its potential, including an assessment of the risks due to pests, disease, lodging, brackling etc.
- A report of nitrogen and water status of the crop throughout the growing season to assess fertilisation and irrigation efficiency
- Prediction of a range of results attached to a probability distribution.

It was deemed more important to concentrate on getting 'typical' years right, than to predict extremes accurately. An acceptable level of deviation across all genotype /environment combinations would be less than 10%, with an increase to 16% under extreme conditions.

3. How can the model be tested and what are the criteria for success?

Initial testing of the model uses data from the barley database. Further experimentation is envisaged using test data collected at a number of sites throughout Scotland. Analysis of results will be by regression of predicted against observed figures for each stage of development and component of yield. Model performance being a measure of agreement between observed/predicted data. Three main characters were assessed: final grain yield, the date of the switch to reproductive growth and the date of anthesis.

4. What inputs are needed for weather, site, genotype and treatments?

Certain constraints ensure compatibility with other models. Data is compatible with the requirements of the CERES barley model, the data in the barley database and the data recorded as in the CVT scheme. The accessibility of the end product largely depends on the availability and simplicity of model input requirements.

Genotype is specified by a range of paired choices using easily recognisable characters: vernalisation requirement (winter or spring cultivar), growth habit (tall or semi-dwarf), leaf type (erect-or lax-leaves) and ear type (2- or 6-row). Mean thousand grain weight and earliness of maturity (days before or after the mean) as recorded in Recommended Lists are also included.

5. What type of model should be used: empirical, stochastic, mechanistic, mixed?

The model uses a mechanistic approach wherever possible, supplemented by empirical relationships derived from the barley database. It is deterministic in that any set of input values will result in a unique solution which can be repeated. Forecasts on the basis of weather generator data will increase the stochastic element in the future.

The model is built using accepted assumptions from the literature and basic quantitative equations which are widely used. Parameter values are taken from the literature and tested by analysis of the barley database.

6. What level of organisation will be used?

The model is a 'crop-growth' model and in common with other models of its type, uses $1m^2$ plant stand as the basic level of organisation. Results can then be scaled up to show crop performance on a field, farm or regional scale. Additional error would be introduced by including processes at the organ or single plant level.

7. Should the population structure be included, and if so, how?

Competition between the crop and any weed or disease population can only be included once the pilot model is operational. It can be ignored by validating the model with data from experiments in which disease and weeds were controlled.

8. Should the plant weight be partitioned into stem, leaves, roots and reserves?

The assimilate in the various fractions is used directly to calculate canopy growth from Specific Leaf Area. However, reserves of soluble carbohydrates be omitted by setting upper and lower limits to SLA. Where grain number is calculated directly from above ground dry matter at anthesis, this partitioning is not necessary. A proportion, varying through the crop life cycle, is partitioned to the roots, but root morphology is not included.

9. What time step should be chosen?

Time is the chief driving variable. Crop progress is updated daily in common with other models of this type. Increments of one day link with weather data files; longer periods may be possible especially when growth is slow. This will be developed in the future to include provision for using weekly or monthly mean weather data. Calendar date will inevitably appear in the model since most data on environmental variables are collected on that basis but a second clock operating on accumulated temperature is used to predict development.

10. Will the model have a phasic structure?

Different aspects of crop growth take precedence at different phenological stages. Identification of these stages is a prime aim of this model.

11. Will the model be monolithic or will it have a modular structure?

A modular structure has several advantages: Sub-routines from CERES barley for calculation of soil water and nutrient stress can be added as an option. A modular structure eases further model development and exchange of procedures with other modellers. Individual areas of the model can be tested separately, maintenance is more straightforward and alternative routes can be chosen through the model at run-time.

12. What computer language should be used and how can maintenance be effected?

FORTRAN, reluctantly, to simplify module and data exchange with the CERES model. FORTRAN file formats are strictly specified and can extract fields from database files to form model inputs. Input data checking procedures are already well established and a library of routines available. The model is set within a framework of associated programs to generate input files, graph outputs and provide run-time debugging and interactive alteration of parameters. Documentation alongside the model programs references the source of parameters.. Each module has its own testing procedures built during development. Every effort was made to generate efficient, clear code with a minimum of redundancy.

8.2. FUNCTIONAL DESCRIPTION

The DAFS barley model contains modules for (Figure 8.1):

Data Input
Data Output - including graphical presentation and statistical analysis
Soil Water Balance
Soil Nitrogen Balance
Growth including leaf area development and partitioning
Development

Figure 8.1. General structure of the DAFS barley model

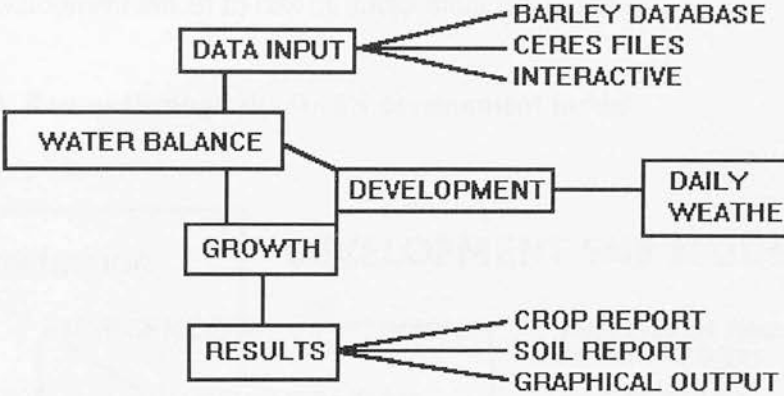
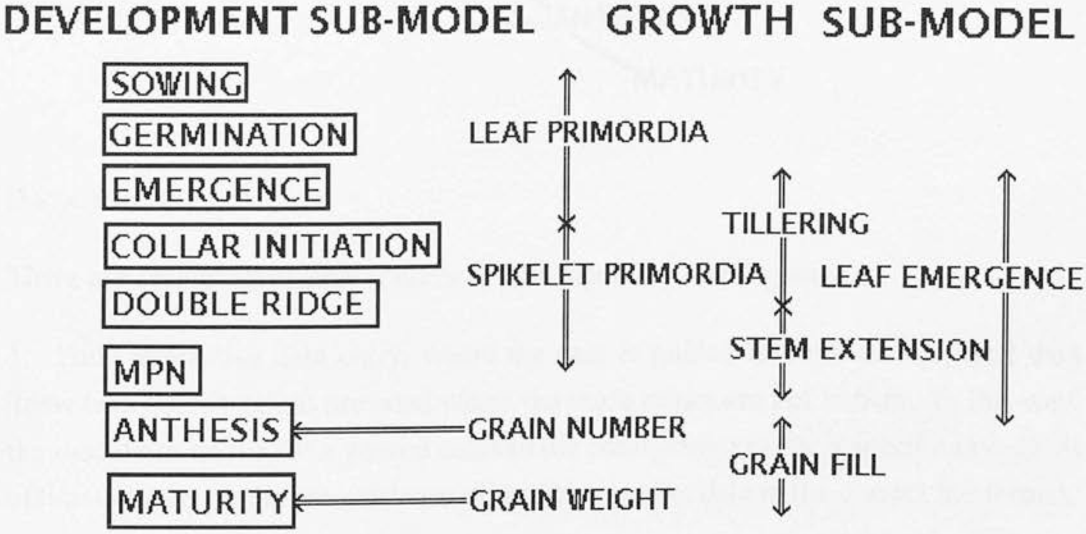


Figure 8.2. Links between the growth and development sub-models



A choice of route through the model was built in to accommodate the different methods of determining growth and development identified (Chapters 6 and 7).

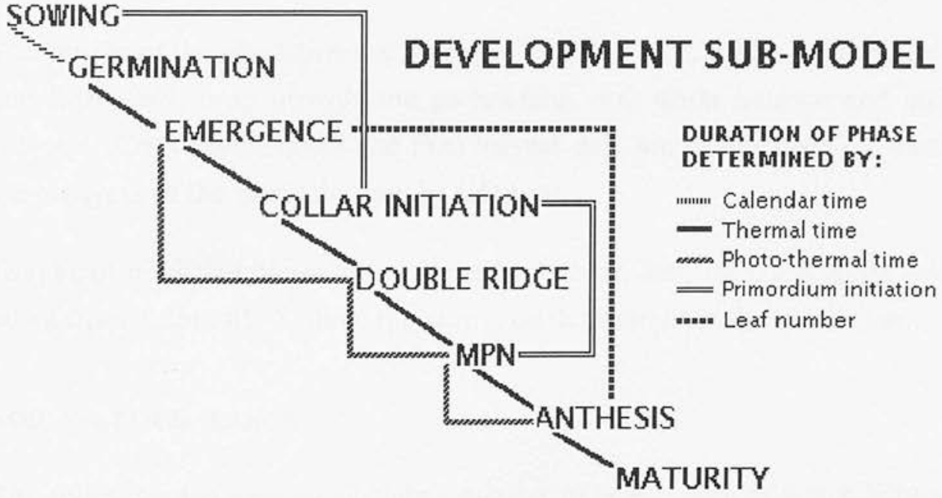
1 LAI calculated from Specific Leaf Area
LAI calculated from thermal time

2 Grain number calculated from rate of spikelet initiation
Grain number calculated from biomass at anthesis

3 Rate of grain fill increased by translocation of assimilates from the stem
Translocation not included

4 Development linked to leaf number
Development linked to rate of primordium production

Figure 8.3. Routes through the DAFS development model



DATA INPUT

There are several alternative sources of data input for the program.

1. Fully interactive data entry, where the user is guided through the required data items with default values provided where the exact values are not known. In this way, the model can be run for a general cultivar/site combination or for a specific one. This option depends on the pre-existence of suitable weather data in the correct file format.

2. A database has been compiled on the SAC Edinburgh VAX 11/750 mainframe using the relational database management system "ORACLE" (Russell, 1990). The database contains records to run the model for a variety of locations in Europe classified on their administrative NUTS region code. Data can be downloaded to PC for input to the model.

3. Records from the barley database (Appendix C) were exported into 6 ASCII files which can be read directly into the model.

4. Prepared input files (Appendix A), compatible with input files for CERES barley.

DATA OUTPUT

Output is directed both to screen and to file. The model takes less than 1 minute for a single run for an autumn-sown crop (IBM-compatible 80386-SD PC, 2Mb RAM). Information on the state of the simulated crop at daily or longer intervals throughout the growing season can be accessed after the simulation is complete for that model run. The interval is set by the user at the start of the simulation (default - 7 days).

The results of the simulation are separated into four output files for crop development and final yield, crop growth and partitioning, soil water balance and soil nitrogen balance. Crop development and final harvest data are summarised on screen so that the progress of the simulation can be followed.

Graphs of predicted biomass, partitioned into root, leaf, stem and grain using figures taken from output file 2, show the crop growth throughout the simulation.

SOIL WATER BALANCE

The soil is divided horizontally into a number of layers, each of which is considered to be homogeneous. The initial water content of each layer is calculated according to the depth of the layer and its upper limit of Stage 1 evaporation. The layers are assumed to be filled to this upper limit at the start of the simulation. This assumption will be adequate for spring sowings made in Scotland. For other locations the simulation can start from a time when this is true and the soil water balance be run for several days or weeks before a crop is sown.

Water enters the system as a result of rainfall and irrigation, and cascades down through the layers. Each layer is filled to capacity, and overflows to fill the next layer down. Evaporation from the soil surface, and transpiration from the plants simultaneously draw water in the opposite direction through the layers. Figures for potential evapotranspiration (MAFF, 1967) depend on date, rainfall, county, distance from the coast and altitude of the site. The water content in each layer is constrained to stay above the level of Stage 2 soil evaporation.

Each day, the ratio between root water uptake and available water in the rooting zone is used to calculate a Water Stress index on a scale of 0 - 1 (0 - no available water for growth and maximum stress, 1 - abundant water and no stress). The effect of soil saturation and anaerobic soil conditions on root growth are not yet included.

SOIL NITROGEN BALANCE

The CERES barley nitrogen balance module, in which a nitrogen stress index is calculated on the ratio between supply and demand, is used to simulate crop nutrition. The simulation can be run with or without the nitrogen balance calculations.

GROWTH

Crop dry weight is calculated daily, driven by the daily weather data. Dry weight does not accumulate before crop emergence; the seed reserve is divided between root and shoot growth. After emergence, starting from a minimum Leaf Area Index (L) of 0.15, daily dry matter accumulation is determined from the product of the PAR and a Dry Matter Radiation Quotient of 3.37 g MJ^{-1} d^{-1}. I is calculated by

$$\mathrm{PAR} * [1 - \exp^{(-k\mathrm{L})}]$$

PAR Photosynthetically Active Radiation (set at 0.5 of the total incoming solar radiation)

k an extinction coefficient which describes the efficiency of light interception by the canopy (0.396)

The total daily dry matter production is partitioned between root, leaf, stem and grain according to the development stage. The new LAI is obtained from a choice of methods:

A. A fixed Specific Leaf Area of 29 cm^2 g^{-1} is applied to the leaf dry weight increment as a conversion factor from weight to area.

B. Leaf Area Index is related to accumulated temperature by a regression equation obtained from detailed leaf area measurements on spring barley crops grown near Edinburgh over 3 seasons. Whilst the linear relationship obtained can be applied to crops grown under similar conditions, it is not necessarily universally applicable. This option must therefore be used with caution.

DEVELOPMENT

The duration of each development stage is controlled by a complex of genotypic and environmental factors, principally vernalisation requirement of the cultivar, daily temperature and photoperiod (length of day plus twice the duration of civil twilight).

Two alternative routes through the model are provided:

A. Development is linked to emerged leaf number on the main stem. Leaves emerge at regular intervals in thermal time and internal development is related to external plant morphology. The interval between emerged leaves, the phyllochron, is set at emergence according to the equation in the CERES barley model as

$$77.5°\text{C days} - 232.6 * \text{CHGDL}$$

where CHGDL is the rate of change of daylength at emergence. Thus the phyllochron increases for sowings during decreasing daylength, and decreases for spring sowings during increasing daylength. Crop development is divided into 7 stages. Leaf numbers required to reach each stage are taken from analysis of the barley database.

1. Sowing to germination

Germination will occur on the day following sowing provided that the water level in the sowing layer does not fall below the stage 2 limit of soil evaporation.

2. Germination to emergence

Emergence will occur within 100° days of sowing, modified by an additional 5 °Cd for every cm sowing depth. For most field crops a default sowing depth of 3 cm ensures that emergence will occur after 115 °Cd have elapsed. Water shortage will reduce the plant stand in proportion to the degree and duration of stress experienced.

3. Emergence to double ridge

Double ridge stage is reached after the production of a certain number of main stem leaves depending on sowing date and potential maximum leaf number (Table 8.1).

Table 8.1. The relationship between development stage and leaf number.

Sown in	September	October	November	Later sowings
Leaf number at				
Double Ridge	8	7	6	5
MPN	12	11	10	8
Anthesis	14	13	12	10

4. Double ridge to MPN 5. MPN to anthesis

The duration is set by the thermal time required to produce the extra leaves to reach MPN, depending on sowing date (Table 8.1). For example, a September sown crop will require the passage of four phyllochrons from double ridge to MPN, and a further two phyllochrons to anthesis.

6. Anthesis to physiological maturity. as route B

B. Development stage is calculated independently from leaf number, with duration of the early stages of development dependent on the rate of primordium production on the main stem apex and the number of primordia initiated.

1. Sowing to Collar Initiation

Leaf primordia are initiated on the main stem apex during this stage. The duration of the period is calculated from the product of the rate and number of primordia produced. The number is ascertained from predictions of final leaf number made according to cultivar and sowing date.

2. Collar Initiation to MPN

Spikelets are initiated on the main stem apex at a rate proportional to the daylength at emergence. MPN occurs when a certain thermal time interval has elapsed from collar initiation, depending on sowing date.

3. MPN to anthesis

The duration of the interval is determined from thermal time and sowing date as previously. Early maturing cultivars reach anthesis 10°Cdays earlier per day of earliness as recorded in SAC or NIAB cultivar trials.

4. Anthesis to physiological maturity

A fixed interval of 720°Cd elapses between anthesis and physiological maturity, when final yield data are presented. This interval is reduced by 15°Cd per day of earliness.

COMPONENTS OF YIELD

Grain number

Again two alternative routes are provided in the model:

A. The number of spikelets initiated is found from rate and duration of the period of spikelet initiation, with a fixed proportion of 70% fertile. 6-row ear type cultivars forming 3-times as many grains per ear.

B. Grain number is calculated from the dry weight above ground biomass at anthesis. The conversion factor of 17 grains g^{-1} is adjusted according to the average grain weight of the cultivar. Thus a large grained cultivar will produce fewer grains per gram dry matter than a small grained cultivar.

Ear number

Tiller number is closely linked to leaf production. A new tiller is added to the plant with the emergence of each main stem leaf, from the fourth leaf onwards. Tiller death occurs at the time of MPN, and varies according to sowing date, cultivar and planting density of the crop. All tillers which survive to anthesis are assumed to bear fertile ears, and grain number per ear is an average figure across all ear-bearing culms.

Grain yield kg/ha

The option is included to adjust grain and straw partitioning to take account of translocation of stored assimilate in the stem into the grain to compensate for inadequate grain filling after anthesis. Assimilate will be diverted to the grain if the desired linear rate of grain fill is not achieved.

Straw yield kg/ha

Straw yield is calculated from the sum of dry matter remaining in the leaf and stem pools at maturity. A constraint is set on the proportion of the total stem dry matter at anthesis which can be translocated to the grain, assuming that no further increase in stem dry weight occurs after this time.

Biomass is listed in the output as the sum of grain and straw dry weight at physiological maturity. Harvest index is calculated as the percentage grain yield of the total above ground biomass at maturity.

8.4. MODEL VERIFICATION

The model was verified using the original subset of the barley database (described in Chapter 4) used to test the CERES barley model. This data showed up the errors of programming and logic in the model. The model was also run with a range of fictitious data for sowing dates, site and cultivar combinations to make sure predicted output fell within sensible limits as defined in the barley database as a whole.

The four choices of route were systematically altered at run-time:

Figure 8.4. Typical output from the DAFS barley model

```
 OUTPUT SUMMARY
 RUN: 1
 SITE: PENT  EXPT_NO: 01  YEAR: 1981  TRT_NO:  1
 EXPERIMENT: Pentlandfield, T812. Russell & Ellis, 84
 TREATMENT : Golden Promise
 SOIL TYPE : Aquic Dystric Eutrochrept. Sandy Clay Loam
 VARIETY   : Golden Promise
 Water Balance ON
Nitrogen balance OFF

 Date          Development Stage   Cumdtt        Biomass
 Nov 12        Sowing                0.00           0.00
 Nov 13        Germination           5.20           0.00
 Dec  5        Emergence           130.10           0.00
 Dec 12        Collar Initiation   168.00           0.54
 Mar 31        Double Ridge        637.05          77.43
 May  8        M.P.N.              888.57         639.10
               Max. no. spikelets:  38.05
               Maximum Tiller no.:   5.00
 May 28        Anthesis           1095.02         996.99
               Stem Number           4.05
 Jul 11        Maturity           1635.52       13946.51


                           PREDICTED        OBSERVED

 Date of anthesis              151              157
 Date of maturity              193              193
 Grain Yield,kg/ha          10449.16         10120.00
 Biomass Yield,kg/ha        13946.51         17066.00
 Straw Yield,kg/ha           3497.35          6946.00
 Harvest Index                  0.75             0.59
 Grains/sq metre            24162.73         28148.00
 Grains per ear                23.15            23.00
 Thousand Grain Wt             43.24            35.50  Cv. mean : 41.90
 Maximum LAI                   10.00


 OUTPUT SUMMARY
 RUN: 2
 SITE: PENT  EXPT_NO: 01  YEAR: 1981  TRT_NO:  1
 EXPERIMENT: Pentlandfield, T813. Russell & Ellis, 84
 TREATMENT : Golden Promise
 SOIL TYPE : Aquic Dystric Eutrochrept. Sandy Clay Loam
 VARIETY   : Golden Promise
```

Figure 8.4 contd.

```
Water Balance ON

Date        Development Stage   Cumdtt      Biomass
Mar 18      Sowing                0.00         0.00
Mar 19      Germination           4.00         0.00
Apr  7      Emergence           131.68         0.00
Apr  8      Collar Initiation   140.23         0.90
May 12      Double Ridge        374.85       121.04
May 29      M.P.N.              554.05       407.05
            Max. no. spikelets:  39.01
            Maximum Tiller no.:   3.02
Jun  9      Anthesis            685.20       614.00
            Stem Number:          2.93
Jul 22      Maturity           1219.90      9752.14


                         PREDICTED      OBSERVED

Date of anthesis            167            173
Date of maturity            204            205
Grain Yield,kg/ha          7265.19        6050.00
Biomass Yield,kg/ha        9752.14       10083.00
Straw Yield,kg/ha          2486.95        4033.00
Harvest Index                 0.74           0.60
Grains/sq metre           17960.31       15640.00
Grains per ear               23.73          23.00
Thousand Grain Wt            40.45          38.70  Cv. mean : 41.90
Maximum LAI                  10.00
```

PREDICTION OF CROP DEVELOPMENT.

The predicted date of anthesis was very sensitive to the development route chosen (Figure 8.5). The CERES method relating development stage to emerged leaf number consistently shortened (see results presented in Figure 8.4) the time to anthesis (r^2=0.91 s.e. 3.07). When development stage was determined from the rate of primordium production, the date of anthesis was slightly overestimated (r^2=0.89 s.e. 3.71). The date of maturity was less well predicted (Figure 8.6). The dates of collar initiation and MPN were well predicted for spring sowings, but less reliable for early autumn sowings. The date of double ridge was particularly closely predicted for spring sowings using the leaf number model.

Figure 8.5. Predicting the date of anthesis

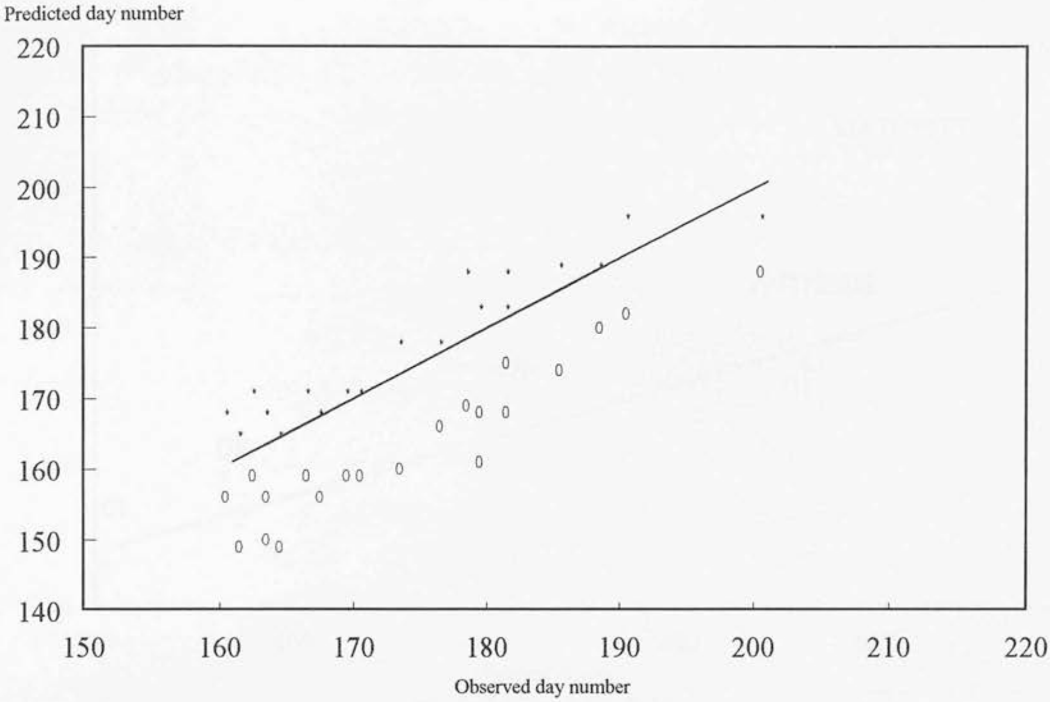


Figure 8.6. Predicted date of maturity

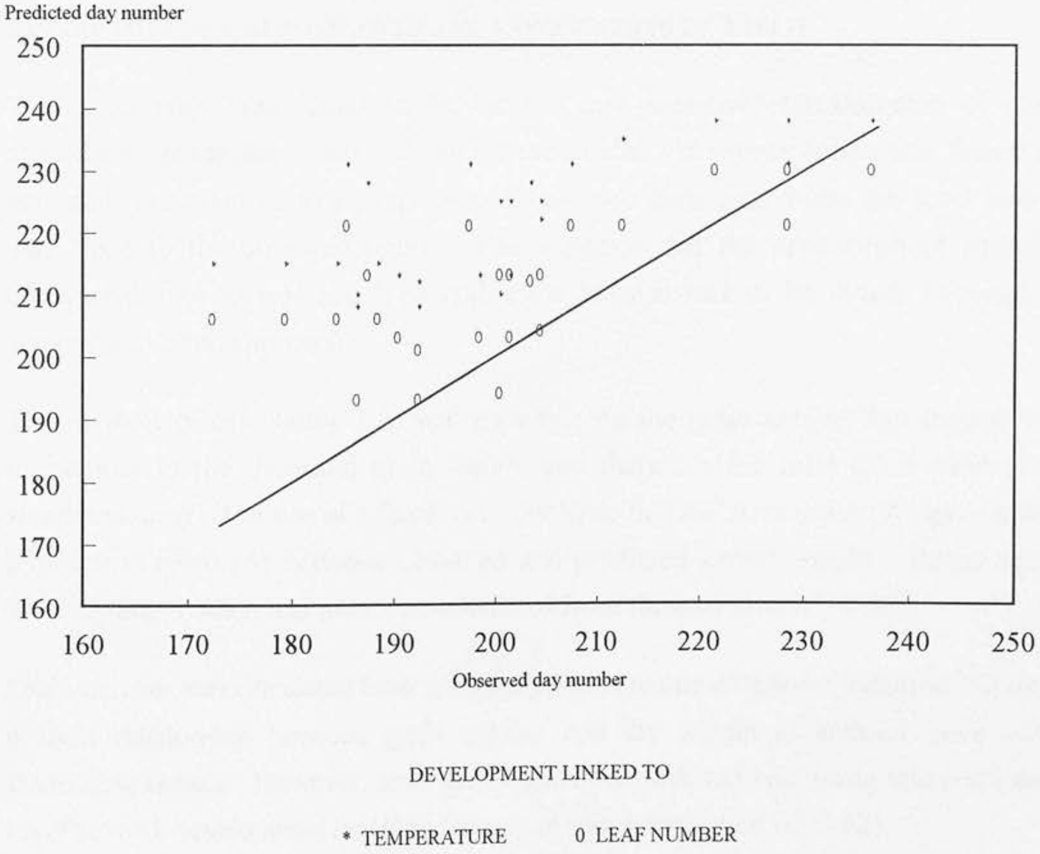
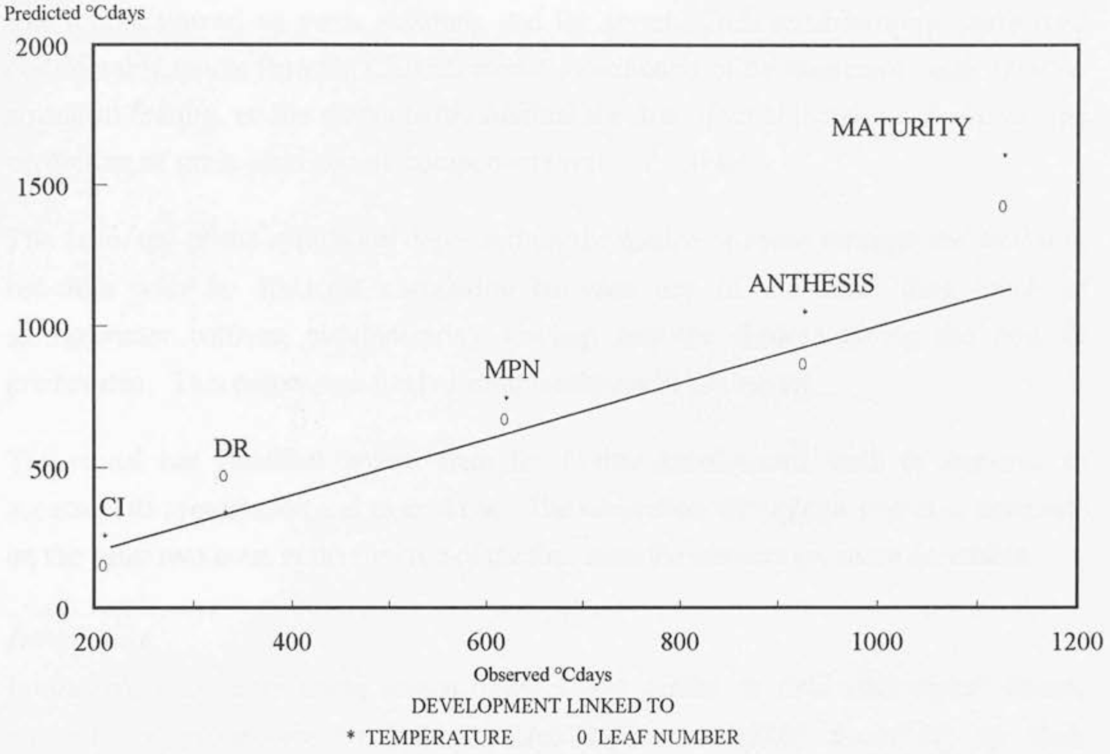


Figure 8.7. Predicted development in thermal time for the mean of all spring cultivars from two alternative routes through the model



PREDICTION OF CROP GROWTH AND COMPONENTS OF YIELD

The grain yield was found to be far too low whenever translocation of stored assimilates to the grain was left out of the model. However, when this factor was included, the grain to straw ratio was always too high even when the total biomass was close to the observed figure. This suggests that the proportion of assimilate considered mobile was too high and some balance had to be struck between the 'source' and 'sink' approach.

The method of calculating LAI had no effect on the grain number but caused wide differences in the thousand grain weight and therefore the total grain yield of the simulated crop. The use of a fixed value for Specific Leaf Area (route A) gave a weak correlation (r^2=0.16) between observed and predicted kernel weight. Better results were obtained when leaf area was calculated from thermal time (r^2=0.56).

Grain number was calculated most accurately from the rate of spikelet initiation, the use of a fixed relationship between grain number and dry weight at anthesis gave widely fluctuating results. However, total grain yield was predicted best using this relationship together with development linked to the rate of spikelet initiation (r^2=0.62).

CONCLUSIONS AND FURTHER DEVELOPMENT OF THE MODEL

The model proved no more accurate, and for several GxE combinations, performed considerably worse than the CERES model. Prediction of development stage was the strongest feature, so the model partly fulfilled the first of its objectives. However, the prediction of grain yield and its components was very weak.

The accuracy of the simulation depended on the choice of route through the model at run-time with no apparent correlation between any of the input data (such as spring/winter cultivar, autumn/spring sowing) and the choices giving the best fit predictions. This points to a fundamental weakness in the model.

The model has identified several areas for further development, both to improve its accuracy, its presentation and ease of use. The temptation throughout was to concentrate on the latter two areas at the expense of the first since the answers are more accessible.

Data input

Interactive data entry using screen based forms similar to field trial report forms, attaching a probability to any estimated inputs, weighted according to their importance, which also relates to the output from the model.

The model could be used within an expert system shell for guiding inputs, determining the route through the model and interpreting the results. The backtracking facility of the logical fourth generation programming languages used to write such a shell would be particularly useful to interrogate the model during operation.

Expert knowledge of the soil type, drainage characteristics, soil chemical composition and physical structure from other sources is accessed by the model input routines through an interface with a separate suite of data preparation programs. The expert system approach would use a stored knowledge base on a conventional database management system (dBase III+, Oracle, etc.) interrogated by the user to define the most appropriate inputs for a particular application via a series of questions (cf. the CUE model - Richards *et al.*, 1989). For example: "Here is a typical soil profile description for your chosen soil type. Do you wish to amend any part of it in the light of additional local knowledge?"

The model is restricted to sites for which soil and weather data are available. Links to a Geographic Information System (along the lines of the DSSAT) could provide suitable data to run the model for any grid square in Scotland. Links to a digitised 1:250,000 soils map may soon be feasible.

Model output

Some attempt was made to graph the partitioning of biomass between root, leaf, stem and grain within the model since graphical output makes a model more attractive and easy to interpret. However, it is costly in terms of time for program development. Links to a Lotus 1-2-3 spreadsheets were established (the graphs produced in this chapter were all produced using Lotus 1-2-3) but were rejected because the time taken to shell spreadsheet macros from within a FORTRAN program was unacceptably slow even though better graphs could be produced as a result.

Other items for graphical display include:

The relationship between leaf canopy development and thermal time
The relationship between primordium number and thermal time

Further animation of the crop life cycle as the simulation is in progress, as in PNUTGRO - the CERES groundnut model, has limited value for serious model users. However, including an element of reasoning about the simulation as it is running would be of considerable value. A debug option was included which allowed the user to interrupt the program at any stage and examine the status of crop variables. These could then be updated with the wisdom of hindsight. A series of warnings could be added to the model to aid this interactive use of the program - for example, 'frost has caused excessive tiller mortality, do you wish to proceed?'; 'Water stress is limiting the rate of grain fill'. 'Smart modification' focuses on major changes whilst leaving the smaller details alone, whilst feedback allows assessment and consistency and completeness of purpose.

The model output should show flexibility to meet the different requirements of each user, with different formats for different groups - SASS, students, farmers, research groups, field trial officers. The same model could then be used for scheduling and assessment.

Additional modules

The model has considerable limitations for it does not yet take account of the effects of pests, diseases, lodging, natural disasters and nutrient deficiencies other than nitrogen which have such major consequences for crop growth. Much of the effort of field trials is devoted to the effects of disease and its control so it is essential that a model for use in improving field trial efficiency should be broad enough to be used in all types of trials. However, these factors can only be incorporated into the model once the basic physiological processes have been modelled more reliably.

Finally, data from commercial field trials should be used to validate the model under a wide range of Genotype/Environment combinations.

9. CONCLUSIONS AND RECOMMENDATIONS

The sheer complexity of cereal plant physiology coupled with a lack of detailed field data have thwarted modellers for many years. Wareing and Phillips (1971) argued that until more information was available on changes of photosynthetic efficiency in the field, there was little to be gained in developing elaborate new models of crop growth. Since then, both the information and the number of models have snowballed although the same problems exist.

Today's models are geared for prediction, and can be used to answer questions of the 'what if...' kind. A simulation model that shows how variation in environmental conditions or crop management can affect crop growth and yields can be a powerful tool to make the results of field trials more widely applicable. Irrigation management, for example, is an important area in which simulation modelling is already in use. There is an also an increasing need for models to become prescriptive in order to answer questions of the type: 'what action will produce this behaviour?' This can only be done at present using multiple runs of deterministic models with a range of inputs, but the time needed for such analyses is being reduced by the advent of parallel processors and other developments in computers.

Farmers are not optimistic of an economic environment conducive to agricultural expansion. The assumption that the potential to increase farm output exceeds the capacity to increase commercial demand is challenged however by global food shortages affecting demand and forecasts of climatic change affecting supply. European policies to curb grain production have been introduced in the late 1980's - inducements for diversification and set aside provide incentives for the withdrawal of resources, whereas price pressures such as stabilisers and quotas are policies of compulsion. Within the UK, the grain market is in decline due to a lack of domestic buyers and grain failing to reach intervention standards fuelling the price falls. A green pound devaluation of 10.7% from July 1 1990 raised 1990/91 buying in prices by only 7.5 - 8.3%. There are calls for a Scottish malt barley promotion initiative to re-establish its reputation on the continent. The Scottish spring barley area is decreasing, as more growers opt for cultivars with malting potential to achieve premiums. The pressure is on farmers to reduce production costs without loss of efficiency. The pressure is on crop physiologists and plant breeders to bring recent technological and genetic advancements reliably within their reach and anticipate the changes in farming practice and economic pressures which will bring about these changes (Ellis, 1993).

The computer is no longer the domain of the specialist, but has increasingly brought powerful mathematical and statistical techniques for data analysis within reach of all. The farmer who once had to ask his local advisor for information on disease risks, seed and agrochemical recommendations, prices and markets can now find much of the data he requires from on-line information services. Suddenly, he is looking for more accuracy and faster response from his advisors, and modellers will have to follow suit or be left behind.

The 'best' models explain some 85-95% of the natural variation, with the more empirical models performing less well in extreme environments. Mechanistic models require considerable validation and testing before being transferred to another set of environmental conditions. A proven model could:

- extend the results of field trials to sites and seasons in which practical experimentation is either too costly or too difficult to perform.
- highlight reasons for variation in crop performance including the effects of GxE interactions
- study the effect of stresses on the crop at intermediate stages in its life cycle
- isolate the effect of a single factor which is not possible in the field
- predict the probability of a given outcome
- predict the effects of global warming and an increase in ambient carbon dioxide concentration on UK barley production
- distinguish between cultivars and examine the performance of theoretical cultivars

For use in conjunction with variety testing schemes, a model should give added information about the optimum husbandry for each cultivar. This may lead to more cultivars being recommended with 'S' status, of value for specific environments. However, until physiological information can be used to improve the current generation of models, and detailed description of cultivars is incorporated into models, they are unlikely to be of much help to the plant breeder. Any quality assessment of cultivars under test must be quick and efficient because of the thousands of small samples under test and the pressure of time, with planting plans to be prepared for the next season.

Current models attempt to describe as much of the natural system as possible and equate complexity with reality. However, the number of man-years required to create, parameterise and test these models may be out of proportion to the benefits they may bring. What value a model which can produce reliable predictions but requires an impossible number of inputs? Reducing the complexity to a simpler summary model and finally to a set of simple decision rules may make models more easily incorporated into decision making processes.

Any criticism of model output must take into account the accuracy of the input data. There is clearly a need from the modeller's point of view to record more detailed soil characteristics for field trial sites, perhaps along the lines laid down in the MDS (IBSNAT, 1988a). IBSNAT has distributed procedures for Experimental Design and Data Collection (IBSNAT, 1988b) to all Research Institutes collaborating in the project to ensure that data for model building and testing can be easily transferred. Collaborators in the project, designing field trials for model validation, complete a set of forms containing soil, climate, site, and crop management information, which are used in standard format computer files for direct input to models. Data are stored in a central database management system at the University of Hawaii.

Recent re-structuring of Recommended List trials in the UK endorses this concept of 'benchmark sites'. Trials at five core sites, within each of the five regions of the UK are fully recorded, with additional yield data being drawn from trials at a further six to eight supplementary sites.

A similar common protocol for data collection from other experiments and field trials in Scotland and the rest of the UK would allow data to be abstracted for further model development and testing. This may be more costly in the short term for an individual trial, but ultimately have the advantage of making trial results more widely available and encouraging data exchange and collaboration between researchers.

The barley database proved a powerful tool worthy of further development. Sufficient data sets were included to make this pilot study useful for hypothesis testing. If extended to include data from commercial and national variety trials, or from other countries, the data bank would be vastly increased and it could provide a body of data available to all modellers. A similar database for wheat physiology (Russell & Wilson, in prep) is being prepared from the literature in conjunction with an inventory of agronomic data prepared from questionnaire responses from agronomists from all over Europe. The inventory contains regional information on agronomy and crop development for both common and durum wheat. These data will be used as part of the crop monitoring and yield forecasting/assessment modelling initiative of the European Commission for the application of remote sensing to agricultural statistics.

Data-checking is essential since different data and methods are used in each series of experiments. Each character requires careful definition and measurement, or at least rules for conversion from one system of measurement to the other. Even when methods are standardised, discrepancies may still contribute to the residual variation (Kirby, 1993). Particular problems were encountered over definitions of development stage and leaf area index. Problems of data compatibility can only be overcome by rigorous definition of terms. However, errors in data transcription when preparing files for model testing are greatly reduced by this method.

Further field measurements are necessary from a wide range of soil types in order to understand some of the mechanisms of crop root and shoot growth which are at present only speculative. Monteith & Elston (1983) identified an urgent need for more comprehensive measurement of canopy development under field conditions to quantify the mechanisms controlling LAI and SLA: our understanding of these mechanisms has not greatly progressed. Modern technology providing reliable, non-destructive methods of estimation of leaf area and biomass may allow more frequent measurements to be made before anthesis. Further information about the duration of development stages, preferably expressed in thermal as well as in calendar time, perhaps involving a collaborative study along the lines of the 'Avalon' wheat study (Porter *et al.*, 1987), could make a significant contribution to model reliability. Field-based soil measurement and weather recording, rather than the current estimation from data collected on a grid-square or agromet-station basis, could also reduce model variation although it would increase the cost of experimentation. Results from extreme environments may provide additional information for modellers, to help establish the spectrum of responses and set upper and lower limits to parameters.

The continuous improvement of cultivars both in terms of yield and quality may mean that any such body of data needs to be strictly updated so that it remains relevant to current practice. This could be achieved by a cyclical approach whereby data is held for a prescribed number of years, or only for currently recommended cultivars. However, the frequent change in the Recommended List, and differences between lists in neighbouring countries, suggest that the choice open to farmers could be much wider than at present, despite the enormous influence that the List has on the market-place. It is inherent in the system that cultivars will remain on the list for different lengths of time, and that those with special characteristics for particular conditions may remain longer than most. Co-ordination of results from breeders' own compatible trials into the system could extend the applicability of the list without involving extra cost, although any such analysis would need independent corroboration. The implications for the recording of field trials and experiments are enormous, not least because the maintenance of such a database would be an monumental task.

The information explosion is as real in the world of agricultural research as in the world at large. The traditional numerical or textual recording of data may be supplemented by maps, diagrams, photographs, sound and video presentations, which could easily be incorporated into a database approach. The concept of an 'intelligent' database (Parsaye *et al.*, 1989) which holds knowledge instead of data, with a high-level user interface shielding the user from the mechanics of data storage, and using inference to link the user query with the appropriate knowledge, can guide the user through the system to the desired conclusion with a minimum of extraneous evidence and saturation. Integration with spreadsheet packages and text processing facilities can further enhance the presentation of the data (Power *et al.*, 1989) This could lead to inferences into the relationships between data being made increasingly by the information technologists rather than the agronomists and physiologists.

The present field trials system can identify the best cultivars and farming practice for the major barley-growing areas. Unfortunately for those who have to contend with poor land or low profitability, these trials may not be truly representative. Farmers want cultivars that are best suited for their locality, and are stable over the pressures (including those of the market-place) placed upon them. Increasing the number of trial sites and treatments is too costly, and extrapolation of results to other sites and seasons too unreliable for the farmer under such pressures to benefit. There are two alternative approaches - either the trial sites should be looked on as an unbiased sample of the whole population of possible fields, or sites should be chosen to span the range of possible environments for the crop (Russell *et al.*, 1993). The former may identify the best cultivar 'on average', the latter may indicate the spread of possible results. Perhaps the trials approach should be re-structured so that it focuses on particular problems identified by the farmer with trials designed specifically to provide the information required.

Twenty-two years ago, Wright (1971) remarked "simulation is still a relatively new technique in relation to the study of farming systems, with a number of as yet unresolved methodological problems": some would agree with Passioura (1975) that we are still little nearer to resolving them.

The goal still lies open.

APPENDIX A. THE DAFS BARLEY MODEL INTERNAL DOCUMENTATION

MODEL INPUT FILES

A master file "BAEXP.DIR" holds a directory of data files. Data for each individual experiment series are stored in 6 files, with additional files holding soil and cultivar data for any trial. Input files are of fixed format and can be prepared using any suitable text processor. Examples of inputs for two trial series are enclosed on the model disk.

BAEXP.DIR

A master directory of all data files for each experiment or trial series. These files are not all required by the model although the names appear for consistency with the CERES model requirements. Each entry consist of three lines. For example:

```
SPBS7601 The Murrays, 1976 (Kirby & Ellis, 1980) SPBS0909.W76 SPROFILE.BA2
SPBS7601.BA4 SPBS7601.BA5 SPBS7601.BA6 SPBS7601.BA7 SPBS7601.BA8 CULTIVAR.BA9
SPBS7601.BAA SPBS7601.BAB $1SPBS76.BA1 $1SPBS76.BA2 $1SPBS76.BA3 $1SPBS76.BA4
```

Variable name	FORTRAN format	Description
Format for line 1		
EXPTID	A8	Experiment identifier
DES	1X,A40	Experiment description
FILE1	1X,A12	Daily weather data file name
FILE2	1X,A12	Soil profile description file
Format for line 2		
FILE4	A12	Soil nitrogen dynamics file
FILE5	1X,A12	Soil profile initial conditions file
FILE6	1X,A12	Irrigation management file
FILE7	1X,A12	Nitrogen fertiliser management file
FILE8	1X,A12	Crop management file
FILE9	1X,A12	Cultivar file
Format for line 3		
FILEA	A12	Summary yield data
FILEB	1X,A12	Seasonal data
OUT1	1X,A12	Output for yield data
OUT2	1X,A12	Output for crop growth data
OUT3	1X,A12	Output for water balance data
OUT4	1X,A12	Output for nitrogen balance data

SOIL.DIR

Maintains a directory of all soil data held in the profile description file. For example:

```
 61 The Murrays   Scotland
 62 Cambridge     Sandy clay loam 1976
```

Variable name	FORTRAN format	Description
SOILID	I3	Soil number
SERIES	A12	Soil series
TYPE	A40	Soil classification or description

WTH.DIR

A directory of weather data files with a record of the start and end dates for each file.

Variable name	FORTRAN format	Description
Format for each line		
WTHID	A4	Weather station identifier
STAT	1X,A40	Weather station name
START	A8	First date in weather file, dd/mm/yy
END	1X,A8	Last date in weather file, dd/mm/yy
FILE1	1X,A12	Weather file name

FILE1 Weather data

Variable name	FORTRAN format	Description
Format for line 1		
WTHID	A4	Weather station identifier
LAT	1X,F6.2	Latitude of weather station
Format for daily weather data on subsequent lines		
WTHID	A4	Weather station identifier
YEAR	1X,I2	Year
DAY	1X,I3	Day number, Jan 1 = 1
RAD	1X,F5.2	Solar radiation, MJ m^{-2}
MAX	1X,F5.1	Maximum temperature, °C
MIN	1X,F5.1	Minimum temperature, °C
RAIN	1X,F5.1	Precipitation, mm
PAR	1X,F6.2	PAR , E m^{-2}

NB: PAR calculated as 50% of incoming solar radiation if data not available.

FILE2 - Soil Profile Description

Soil profiles are numbered and added to a database of soil types held in the file SPROFILE.BA2. Soil descriptions are separated by -1. For example:

```
08 Breda        Typic Calciorthid 1982-83
  0.14  6.00   0.50  72.00  16.4  11.5 1.0
   05.  0.170  0.290  0.320  0.070  0.600  1.10  0.63
   10.  0.190  0.310  0.330  0.100  0.800  1.10  0.63
   15.  0.190  0.310  0.340  0.140  0.450  1.20  0.50
   15.  0.220  0.330  0.340  0.140  0.200  1.20  0.30
   15.  0.220  0.330  0.340  0.180  0.100  1.20  0.25
   15.  0.220  0.330  0.340  0.180  0.050  1.20  0.19
   15.  0.220  0.330  0.340  0.250  0.025  1.20  0.13
   15.  0.220  0.330  0.340  0.250  0.001  1.20  0.13
   -1.
```

Variable name	FORTRAN format	Description
Format for line 1		
SOILID	I3	Number of soil from SOIL.DIR
SERIES	1X,A12	Soil series
TYPE	1X,A60	Soil classification or description

Format for line 2
leave blank
Format for line 3 and subsequent lines for each soil

DEPTH	F6.0	Thickness of soil layer L, cm
LL(L)	1X,F6.3	Lower limit plant extractable soil water, $cm^3\ cm^{-3}$
DUL(L)	1X,F6.3	Drained upper limit soil water, $cm^3\ cm^{-3}$
SAT(L)	1X,F6.3	Saturated water content for layer, $cm^3\ cm^{-3}$
WR(L)	1X,F6.3	Weighting factor for new root growth distribution
BD(L)	1X,F5.2	Moist bulk density, $g\ cm^{-3}$
OC(L)	1X,F5.2	Organic carbon concentration, %
NH4(L)	1X,F4.1	Default soil ammonium, mg elemental N kg
NO3(L)	1X,F4.1	Default soil nitrate, mg elemental N kg^{-1}
PH(L)	1X,F4.1	Default pH

Format for last line for each soil
-1

FILE4 - soil nitrogen balance parameters

These are treatment-specific parameters only required when the nitrogen dynamics component is used. For fully fertilised crops where nitrogen is not a limiting factor to growth, the file can be ignored. One set of data is required for each treatment specified in FILE8, with treatments separated by -1. For example:

```
MSMU7901  2 1000.   15.   75.  800.
MSMU7901  3 1000.   15.   75.  800.
```

Variable name	FORTRAN format	Description
Format for each line		
EXPTID	A8	Experiment identifier
TREAT	1X,A2	Treatment number
STRAW	1X,F5.0	Weight organic residue from last crop, kg ha^{-1}
SDEP	1X,F5.0	Depth of residue incorporation, cm
SCN	1X,F5.0	C:N ratio of residue, kg C:kg N (default 75.0)
ROOT	1X,F5.0	Dry wt of root residue from previous crop, kg ha^{-1}

FILE5 - soil profile initial conditions

These initial conditions specify the values of water content, ammonium, nitrate and pH for each layer of soil described in FILE2. The first line of the file gives the experiment and treatment identifier, there will then be one line of data for each soil layer, and the last line ends that treatment with -1. The body of the file for each treatment may be the same as FILE2 if treatments do not differ in nitrogen status. For example:

```
01 BUSH8678
   23.   .221   .0   .0  7.1
   20.   .233   .0   .0  7.2
   27.   .232   .0   .0  7.2
   20.   .232   .0   .0  6.8
   -1.
```

Variable name	FORTRAN format	Description
Format for line 1		
TREAT	I2	Treatment number
EXPTID	A8	Experiment identifier
Format for line2 and subsequent lines for that treatment:		
DEPTH(L)	F6.0	Depth of soil layer, cm
SW(L)	1X,F6.3	Soil water content of layer, cm^3 cm^{-3}
NH4(L)	1X,F4.1	Soil ammonium in layer, mg elemental N kg^{-1}
NO3(L)	1X,F4.1	Soil nitrate in layer, mg elemental N kg^{-1}
PH(L)	1X,F4.1	pH of layer

FILE6 - irrigation management

Irrigation data are stored for each of the treatments described in file 8 where given. The amount of irrigation is added to the rainfall in the weather file to calculate total water input into the soil system. Treatment details are separated with -1. For example:

```
 1 BUSH8305
  -1  -1.
 2 BUSH8305
  -1  -1.
```

Variable name	FORTRAN format	Description
Format for line 1		
TREAT	I2	Treatment number
EXPTID	A8	Experiment identifier
Format for all other lines		
DATE	I4	Day number of irrigation
AMOUNT	1X,F4.0	Amount of irrigation added that day, mm

FILE7 - fertiliser management

The structure is similar to FILE6. Treatment details are finished by -1. For example:

```
 1 ABER8101
  -1  -1.0  -1.0 -1
 2 ABER8101
  77  30.0   5.0  8
  -1  -1.0  -1.0 -1
 3 ABER8101
  77  60.0   5.0  8
  -1  -1.0  -1.0 -1
```

Variable name	FORTRAN format	Description
Format for line 1		
TREAT	I2	Treatment number
EXPTID	A8	Experiment identifier
Format for all other lines		
DATE	I4	Day number of fertilisation
AMOUNT	1X,F4.0	Amount of fertiliser added that day, mm
DEPTH	1X,F5.1	Depth of incorporation, cm
TYPE	1X,I2	Type

FILE8 - crop management

Details of crop management for each treatment for an experiment is recorded in this file. Each treatment takes two lines. For example:

```
SPBS7601  1 Golden Promise                              61    1
  80  85 258.00   .076  5.00  1  1 100.00  2.00     .0  75.00  0
SPBS7601  2 Maris Mink                                  61    2
  80  85 258.00   .076  5.00  1  1 100.00  2.00     .0  75.00  0
```

Variable name	FORTRAN format	Description
Format for line 1		
EXPTID	A8	Experiment identifier
TREAT	1X,I2	Treatment number
TITLE	1X,A40	Treatment description
SOIL	1X,I4	Soil number from SOIL.DIR
CV	1X,I4	Cultivar number from CULTIVAR.BA9
Format for line 2		
SIM	I4	Day number for start of simulation
SOW	1X,I3	Day number for sowing
PLANTS	1X,F6.2	Plant population, plants m^{-2}
ROW	1X,F6.3	Row spacing, m
DEPTH	1X,F5.2	Sowing depth, cm
IRR	1X,I2	Switch describing irrigation 1 - no irrigation 2 - irrigation applied from FILE6 (default) 3 - automatically applied at threshold level 4 - water balance not used - no water stress
INIT	1X,I2	Switch describing nitrogen routines 0 - nitrogen routines not used - optimum N 1 - use nitrogen routines
EFFIRR	1X,F6.2	Irrigation system efficiency, fraction
DSOIL	1X,F5.2	Irrigation management depth, m
THETAC	1X,F6.1	Available water triggering irrigation, %
PHINT	1X,F6.2	Phyllochron, °C d^{-1}

FILE9 - cultivar description

Each cultivar referred to in FILE8 has a single-line entry in this file. For example:

```
    1Golden Promise     F  T  F  T41.90  -4   0
    2Maris Mink         F  T  F  T40.00  +4   0
```

Variable name	FORTRAN format	Description
Format for each line		
CV	2X,I4	Cultivar number
NAME	A18	Cultivar name
WINTER	L	Winter = T, Spring = F
TWOROW	L	Two row = T, Six row = F
TALL	L	Tall = T, Semi-dwarf = F
ERECT	L	Erect leaves = T, Lax leaves = F
TGW	F5.2	Thousand grain weight, g
MATURE	1X,I3	Days earlier or later maturity than average
VERN	2X,I2	Vernalisation index 0 -10

FILEA - Crop summary yield data

Summary yield data can be stored on file if available and used to compare model predictions with observations. For example:

```
SCRI8010  1  11160. 37.5000 29083.  23. -9.00 20291.  9131. 155  -9
 -9.00  -9.0  -9.0  -9.0
SCRI8010  2  10250. 51.1000 19656.  16. -9.00 19450.  9200. 163  -9
 -9.00  -9.0  -9.0  -9.0
```

Variable name	FORTRAN format	Description
Format for line 1		
EXPTID	A8	Experiment identifier
TREAT	1X,A2	Treatment number
YIELD	1X,F7.0	Grain dry weight, kg ha^{-1}
KERNEL	1X,F7.4	Kernel dry weight, g kernel^{-1}
GPSM	1X,F4.0	Grain number, grains ear^{-1}
LAI	1X,F5.2	Maximum LAI, m^2 m^{-2}
BIOM	1X,F6.0	Biomass at anthesis, kg ha^{-1}
STRAW	1X,F6.0	Straw dry weight, kg ha^{-1}
ANTH	1X,I3	Day number of ear emergence
MAT	1X,I3	Day number of physiological maturity
Format for line 2		
NPC	F6.2	Grain N% at maturity
TOTALN	1X,F5.1	Total N uptake, kg ha^{-1}
STRAWN	1X,F5.1	Straw N content, kg ha^{-1}
GRAINN	1X,F5.1	Grain N content, kg ha^{-1}

PERFORMANCE AND RESOURCES

Hardware :

The program is designed to run on an IBM compatible micro computer with colour monitor and a minimum of 512K RAM.

Software :

The program requires the following supporting software:

Ryan McFarlane FORTRAN Compiler and Linker

Library routines for data entry and screen handling, held in the file 'LIBRARY.LIB'

Data files for input of soil, weather, site and cultivar data as described above.

Store :

The compiled source code is a 254 Kb block sequential file.

The program code is divided between 12 text files requiring a total of 238 Kb store.

NOTES ON THE SOURCE LISTING

Library subroutines are not included in this section.

FILE	SUBROUTINES	CALLS
MODEL	MAIN	start, head, intro, dataload, route, modify, initial, report, menu, outpts, mainproc
Introductory routines		
HEADERS	HEAD	none
	INTRO	notes
	START	none
	NOTES	none
HELP	HELP	menu
Data reading		
INPUT	DATALOAD	menu, reflist, initial, dbase, enter
	MENU	none
REFLIS	REFLIST	none
DBASE	DBASE	reflist, setsoil, readsoil, nine
	SETSOIL	two
MODIFY	MODIFY	help
INITIAL	INITIAL	reflist, readf4, readf5, readf6, readsoil, readf7, readvar, readfa, outpts, mainproc
READFILE	SETF1	none
	READSOIL	none
	READF4	none
	READF5	none
	READF6	none
	READF7	none
	READFA	none
	READVAR	none
Data file creation		
INSOIL	TWO	display,
	FOUR	display
	FIVE	display
	SIX	display
	DISPLAY	help
SEVEN	SEVEN	help
FINDLAT	FINDLAT	display
	EIGHT	display, two, nine, help
WEATHER	WEATHER	potential, metinfo
	POTENTIAL	none
	METINFO	ptcalc, calcrad
	PTCALC	none
	CALCRAD	none

INPUT2	ENTER	eight, findlat, weather, four, five, seven, six, a
	NINE	menu, reflist, dafsvar, ceresv
	DAFSVAR	help
	CERESV	none
	A	none

Growth and development routines

ROUTE	ROUTE	help
MAIN	MAINPROC	setf1,setpar,route, setup, date, temper, waterb, growth, develop, update, yieldout
	SETPAR	none
	WATERB	none
	YIELDOUT	cropreport
LEAP	JULI	none
	JULIAN	leap
	LEAP	none
	DATE	leap
LEAVES	TEMPER	none
	LEAVES	none
	PARTIT	none
GROWTH	GROWTH	nitrogen, partit
NITROGEN	NITROGEN	none
DEVELOP	DEVELOP	leaves

Output routines

OUTPUT	OUTPTS	none
	REPORT	none
DEBUG	SETUP	none
	UPDATE	none
GRAPH	GRAPH	none
	SWAP	none
CROP	CROPRE	none

EVIDENCE OF TESTING

The evidence of program testing appears in the main body of the accompanying thesis in chapter 8. The variable DEBUG is included to allow monitoring of the contents of a number of memory variables as an additional check on performance. Values are also written to output files during the course of the simulation. A graphical output option is also provided. Testing of the different routes available within the program is simplest using the option to run through all of the simulations on file in succession, and extracting the results via subsidiary programs (Appendix B).

VARIABLE LIST

RS	Switch controlling development route		LOGICAL
NS	Switch controlling grain number route		LOGICAL
TRANS	Switch controlling translocation of stored assimilate		LOGICAL
COMP	Switch controlling LAI route		LOGICAL
JDAYS	number of DAYS from sowing		I3
NDAYS	Number of DAYS from start of simulation		I3
DTT	Daily Thermal Time	°Cdays	F8.3
LAI	Leaf Area Index		F5.2
AWC(I)	Available Water Capacity in layer I	mm	F6.2
AW(I)	Available Water in layer I	mm	F6.2
ROOTED(I)	Rooted in layer I of soil		LOGICAL
SUMDTT	Accumulated temperature from start of development stage	°Cdays	F8.3
DAYLEN	DAYLENgth at emergence	h	F6.2
LIVENO	Number of leaves active photosynthetically		I2
LEAFNO	Total leaf number		I2
RIPE	TRUE if crop has reached physiological maturity		LOGICAL
YR	YeaR		I4
JUL	JULian date		I3
RAD	Incident solar RADiation	MJm^{-2}	F5.2
MAX	Daily MAXimum Temperature	°C	F5.1
MIN	Daily MINimum Temperature	°C	F5.1
RAIN	Daily rainfall	mm	F5.1
PAR	Photosynthetically Active Radiation	MJm^{-2}	F6.2
PT	Potential Evapotranspiration	mm	F6.2
DEBUG	Switch for DEBUGging program		LOGICAL
ISOW	SOWing date		I3
DLAYR(I)	Depth of soil LAYeR,I	cm	F6.2
PHINT	PHyllochron	°C	F6.2
RWUL(I)	Root Water Uptake from Layer I	mm	F6.2
RWU	Total Root Water Uptake	mm	F6.2
WSTRES	Water STRESs index 0 (max) - 1 (no stress)		F3.2
LAT	Latitude of site	°N	F5.2
LONG	Longitude of site	°N	F5.2
ALT	Altitude of site	m	I4
COUNTY	County name		C25
COAST	Within 10km coast		LOGICAL
STAT	Weather STATion name		C4
DAY	Day number		I3
DATE	Date (DD/MM/YY)		DATE
BDATE	First date of weather file (DD/MM/YY)		DATE
EDATE	End date of weather file (DD/MM/YY)		DATE

APPENDIX B. SUBSIDIARY PROGRAMS

PROGRAM **DATALOAD** - is a subset of the routines in the DAFS barley model, to generate model input files without running the simulation.

PROGRAM **SOILPROG** - is a FORTRAN program which reads an input file containing conventional soil profile description in terms of layer by layer particle size analysis, and converts this to estimates of the water holding and drainage properties of the soil in a format ready to be used in the file SPROFILE.BA2 for input into the model. The method was supplied by Bradshaw (pers comm).

PROGRAM **READOUT** is a FORTRAN program which extracts the yield and development data from output file 1 and lists it in columns of observed and predicted values, suitable for input into MINITAB, spreadsheet or database.

PROGRAM **MINIREAD** is a sequence of MINITAB commands to read from the results of program READOUT and prepare graphs of observed against predicted data. Model performance is then analysed by linear regression.

APPENDIX C. THE BARLEY DATABASE

A relational database for organisation and storage of field trial data is described. Output from the database can be used for hypothesis testing, to generate reports or to provide inputs for models. Verification and standardisation of the data are considered of key importance. Examples relate to the barley crop but the methods and database structure could apply to other crops as well.

Hypothesis formulation is the starting point of scientific research on which experimental design has logically been founded, However, time and money frequently prevent the collection of as wide a range of data for an individual project as would be desirable. Moreover there may be hidden sources of bias in an individual trial series that are only apparent when the results are compared with parallel trials conducted according to slightly different protocols...As the costs of data acquisition increase there is pressure to develop a more systematic way of utilising existing data and knowledge. Sometimes another researcher will have already have gathered data which can be used to test the hypothesis of interest. If the original hypothesis succeeded, the supporting data may have been published in the scientific press: if not, they may not have been submitted for publication. Many data remain unpublished for this and other reasons - for example, lack of funding to continue the project.

Assumptions in the literature based on a restricted series of experiments may be challenged when evidence from further experiments comes to light. The re-examination of 'old' data may allow new hypotheses to be tested without recourse to costly and time-consuming experimentation. Experimental design may then begin with a search for suitable existing data. Organisation and accessibility of this data become of paramount importance.

This study has arisen from the need to assemble an independent body of data for validation of mechanistic models to predict barley yield and development.. The scope of the database and definition of the data items is described in Chapter 5. Table C.1 shows the specification of the database. Indexed entries within each entity are shown in bold type. These attributes formed the keys linking the entities of the database together. Many of the attribute names are self-explanatory, but some of them need further definition beyond the discussion in Chapter 5. Data from controlled environment experiments were flagged by the attribute FIELD, so that separate analysis was possible.

Table C.1. Database specification.

ENTITY	ATTRIBUTES	DATA TYPE	LENGTH
REF	**Ref**	Character	6
	Author	Character	25
	Title	Character	50
	Journal	Character	25
EXPERIMENT	**Exp**	Character	6
	Ref	Character	6
	Site_ref	Character	6
	Met_file	Character	12
	Field	Character	1
	Drilled	Logical	1
	Harvest_year	Integer	4
	Previous_crop	Character	1
	Plot_size (m^2)	Decimal	5.2
	Plot_width (m)	Decimal	5.2
	Record_interval	Integer	1
	Other_data	Memo	Variable
SITE	**Site_ref**	Character	6
	Soil_ref	Integer	3
	Met_ref	Character	4
	Latitude	Decimal	6.2
	Altitude (m)	Integer	4
	Grid_ref	Character	8
SOIL	**Soil_ref**	Integer	3
	Type	Character	25
	Series	Character	25
	Description	Character	25
	Parent_material	Character	25
	Depth (mm)	Integer	4
	Texture	Integer	1
	Drainage	Character	1
	pH	Decimal	5.2
	Organic_matter	Decimal	5.2
	P2O5	Decimal	5.2
	K2O	Decimal	5.2
	Liming_ratio	Decimal	5.2
WEATHER	**Met_file**	Character	12
	Met_ref	Character	4
	Start	Date	8
	End	Date	8
METSTATION	**Met_ref**	Character	4
	Name	Character	20
	County	Character	15
	Latitude	Decimal	5.2
	Altitude (m)	Integer	4
	Coastal	Logical	1
	Solar_radiation	Logical	1

ENTITY	ATTRIBUTES	DATA-TYPE	LENGTH
TREATMENT	**Exp_ref**	Character	6
	Cv_ref	Integer	3
	Input_ref	Integer	3
	Description	Character	25
	Sowing_date	Date	8
	Seed_rate	Integer	4
	Dry_wt_anth	Decimal	8.3
	PAR_em_anth	Decimal	8.3
	DMRQ	Decimal	8.3
	Max_stem_no	Decimal	5.2
	Final_stem_no	Decimal	5.2
	Stem_survival (%)	Decimal	5.2
	Harvest_Index	Decimal	5.2
	Grain_yield (kg/ha)	Decimal	8.3
	Biomass (kg/ha)	Decimal	8.3
	Straw (kg/ha)	Decimal	8.3
	Grains_ear	Decimal	6.2
	Ears_m2	Decimal	6.2
	Kernel (g)	Decimal	5.2
	N_grain (%)	Decimal	5.2
	N_straw (%)	Decimal	5.2
	N_uptake (kg/ha)	Decimal	5.2
	Daylength_em (h)	Decimal	8.3
	CHGDL	Decimal	8.4
Primordium initiation	Rlpi (leaves °Cd^{-1})	Decimal	5.3
	Rlpi_d (leaves d^{-1})	Decimal	5.3
	Rs (spikelets °Cd^{-1})	Decimal	5.3
	Rs_d (spikelets d^{-1})	Decimal	5.3
	Max_spikelet_no	Decimal	6.1
	Fertile_spikelet_no	Decimal	6.1
	Spikelet_survival (%)	Decimal	5.2
Canopy data	Rl (leaves °Cd^{-1})	Decimal	5.3
	Rl_d (leaves d^{-1})	Decimal	5.3
	Phyllochron (°Cd leaf^{-1})	Decimal	6.2
Development data	Emergence	Date	8
	Collar Initiation	Date	8
	Double Ridge	Date	8
	MPN	Date	8
	Ear_emergence	Date	8
	Anthesis	Date	8
	Maturity	Date	8
	Harvest	Date	8
For each development stage	Day_no	Integer	3
	Days_from_sowing (d)	Integer	3
	Thermal_time (°Cd)	Decimal	8.3
	Acc_Photoperiod (h)	Decimal	8.3
	Leaf_number	Decimal	5.2
	LAI (m^2 m^{-2})	Decimal	5.2
INPUTS	**Input_ref**	Integer	3
	Date	Date	8
	Amount (kg/ha)	Decimal	6.2
	Type	Character	1

ENTITY	ATTRIBUTES	DATA TYPE	LENGTH
CULTIVAR	**Cv_ref**	Integer	3
	Name	Character	16
	Winter	Logical	1
	Ear_type	Logical	1
	Leaf_type	Logical	1
	Height	Logical	1
	TGW	Decimal	5.2
	Earliness (d)	Integer	2
	Vernalisation	Integer	1
	Frost	Integer	1
	Drought	Integer	1
	Lodging	Integer	1
	Photoperiod	Integer	1
	P1V	Decimal	5.2
	P1D	Decimal	5.2
	G1	Decimal	5.2
	G2	Decimal	5.2
	G3	Decimal	5.2
	P5	Decimal	5.2

REF

Details of the reference from which the data are extracted link into a reference management system in which the display of selected records can be programmed for particular styles.

EXPERIMENT

Each data set is identified by a unique identifier (EXP), a source (REF) and site and weather station identifiers. These fields relate to the other entity tables.

Continuous observation of the crop system is seldom possible, a compromise has to be made and recording is done at weekly, fortnightly or less regular intervals. A loss of precision is inevitable when considering the recording of development stage. The recording interval is included in the experiment file (RECORD_INTERVAL). The chief interest in the previous cropping pattern for treatments in which weeds and disease were controlled relates to the likely nitrogen status of the soil. The codes for previous crop (PREVIOUS_CROP) correspond to the Low, Medium or High soil nitrogen status based on the number of years of grass in the rotation and the last crop grown (SAC, 1990; Table C.2).

Seeds for a number of small plot experiments are spaced rather than drilled in rows, which may affect plant establishment and early canopy closure. Plot size was also recorded, as yield variability increases with decreasing plot size (Talbot & England, 1984). Details of any additional data were noted in a variable length memo field.

Table C.2. Codes for experiment description

FIELD	
F	Field
C	Controlled environment
G	Unheated greenhouse

PREVIOUS CROP	
L	Cereals, silage, potatoes (seed)
M	Potatoes (ware), oilseed rape, beans, peas, field vegetables
H	Ley, grazed forage

RECORD_INTERVAL	
1	1-3 days
2	4-7 days
3	8-14 days
4	>14 days

DRILLED	
1	Drilled plot
0	Spaced plot

SITE

2-letter, 6-digit grid references were included to cross check latitude and longitude from Ordnance Survey maps of the area.

SOIL

The SOIL_REF field is cross-referenced to a numbered entry in a file of soil types (SPROFILE.BA2 - see Appendix A) as required for CERES barley. This soil file holds descriptions of 85 different soils, including representatives of the main agricultural soils of the UK (Ragg & Claydon, 1973) and can be searched to provide estimates for soils where actual characteristics are not known. Trials for which no soil data were gathered, were located on the appropriate soil survey map sheet and soil depth, texture and chemical composition estimated.

The TYPE field gives the classification according to the USDA Comprehensive System (Ragg & Claydon, 1973). The DESCRIPTION lists the major soil group to which the soil belongs (gley soil, brown earth, forest soil etc.).

UK soils are categorised in CVT records according to texture, drainage and chemical composition (Talbot for SAC, pers comm; Ryall for NIAB, pers comm). The simpler SAC classification was used in the database (Table C.3) as direct conversion from the NIAB to the SAC classification is possible, whereas the reverse may not be true. The chemical composition records soil potash (K2O) and phosphate (P205) levels on a 0-9 scale. The liming ratio brings the soil to pH 6.25.

Table C.3. Soil data categories

CATEGORY	TEXTURE
1	Sandy
2	Fine/very fine loamy sand, Coarse loamy sand
3	Loam, Sandy clay, Clay and Silty clay loam, Clay
4	Fine/very fine sandy loam
5	Chalk
6	Organic, Peaty soils, Peats
CATEGORY	**SOIL DRAINAGE**
F	Free
I	Imperfect
P	Poor

METSTATION

Latitude and altitude for the agrometeorological stations were recorded. Availability of on-site solar radiation measurements was flagged (SOLAR_RADIATION). Stations within 10km of the coast were also flagged (COASTAL). COUNTY was required to cross-reference estimates for potential evapo-transpiration in MAFF (1967) which were listed by county.

WEATHER

A master directory of weather data files was kept on the database to cross-reference with the model input file WEATHER.DIR (Appendix A). The start and end dates for each data file were recorded. The model was run only with historical weather data. Part of the reason for this was the large fluctuation in the mean annual figures for Eastern Scotland (Table C.4), making the concept of 'average' weather meaningless.

Table C.4. **Range of mean annual temperature, rainfall and sunshine hours for three agrometeorological stations in Scotland (1970 to 1987).**

	Bush House	**Mylnefield**	**Craibstone**
Temperature	7.0 - 8.2	7.6 - 8.9	7.2 - 8.2
Rainfall	1.6 - 2.9	1.2 - 2.5	1.5 - 2.9
Sunshine hours	2.8 - 3.9	3.4 - 4.3	3.2 - 4.2

TREATMENT

Details of the crop growth and development data are discussed in Chapter 5.

Where maximum stem numbers (MAX_STEM) per plant were not recorded, they were approximated by stem number at MPN where available (Kirby & Riggs, 1978; Kirby & Ellis, 1980). Each stem at maturity was assumed to bear an ear, therefore FINAL_STEMS could be equated with ears per plant and calculated from the other components of yield if not recorded separately.

Above ground dry weight at anthesis (DRY_WT_ANTH) and photosynthetically active radiation absorbed between emergence and anthesis (PAR_EM_ANTH) may give a guide to expected yield. The conversion efficiency was also stored (DMRQ).

GRAIN_YIELD, STRAW and BIOMASS all refer to dry weights at maturity, excluding any root component of biomass. Any one of these could thus be calculated from the other two. Similarly, GRAINS_EAR, EAR_M2 and KERNEL could often be obtained by calculation. Crop nitrogen uptake (N_UPTAKE) was partitioned between grain and straw as a percentage of dry weight (N_GRAIN, N_STRAW) at maturity.

INPUTS

Nitrogen fertilisation was recorded as date, amount and type (Table C.5). The type was recorded for compatibility with CERES barley owing to the differential rate between fertilisers, of breakdown in the soil and availability to the plant. Irrigation was excluded since irrigated barley crops are uncommon in the UK.

Table C.5. Codes for Nitrogen fertiliser type (selected from IBSNAT, 1986)

CODE	TYPE
01	Ammonium nitrate
02	Ammonium sulphate
05	Urea
08	Calcium nitrate
22	Green manure
23	FYM
25	Straw ploughed in

CULTIVAR

Cultivars were described by a unique reference number (CV_REF), name and several logical attributes under genotypic control (Table C.6). Indices for vernalisation requirement, cold (FROST) and drought tolerance and lodging susceptibility were based on values in the Recommended List on an arbitrary scale of 0 to 9. Thousand grain weight (TGW) and earliness of maturity (EARLINESS), recorded as the number of days before or after the mean of control varieties were also taken from the Recommended List. Values for the genetic specific coefficients for CERES barley were included for some cultivars (page 40).

Table C.6. Attributes for cultivar description.

ATTRIB	VALUE	NOTES
Winter	1 0	Winter Spring
Ear_type	1 0	Two-row Six-row

ATTRIB	VALUE	NOTES
Leaf-type	1 0	Erect Lax
Height	1 0	Tall Semi-dwarf

APPENDIX D. FIELD EXPERIMENTS

ESTIMATION OF GENETIC SPECIFIC COEFFICIENTS - A STUDY OF THE DEVELOPMENT AND PERFORMANCE OF 10 SPRING BARLEY CULTIVARS

INTRODUCTION

Selection by plant breeders for high yield and quality grain has narrowed the range of barley genotypes grown. The important considerations for the grower include the suitability of the grain for malting, and the resistance of the cultivar to adverse environmental conditions and disease. The grower selects a cultivar for use according to the quality required, and its suitability for the local environment.

A field experiment was conducted in 1988 to test the hypothesis that cultivars do not differ significantly in their development rates, when grown under similar conditions.

A second objective of the study was to derive values for growth and development characteristics which can be applied in simulation modelling. Distinction between cultivars is attempted in the CERES family of models, but quantification of varietal differences is a complex exercise (Hunt, 1988a). Transport of models to other sites and seasons may necessitate adjustment of the genetic specific 'constants'. Parameters derived from field measurements can be compared with constants required to run the CERES barley model.

MATERIALS AND METHODS

General Agronomy

The trial was sown at the East of Scotland College of Agriculture Crop Production Glasshouse Unit, Bush Estate, Penicuik, near Edinburgh.

Soil characteristics: Sandy clay loam of the Winton series (Anon, 1971).
Altitude: 160m
Latitude: 55°51'N
Longitude: 2°45'W
Grid reference: NT244636
Weather recording: Edinburgh Bush House Agrometeorological Station, recording rainfall, maximum and minimum temperatures, is within 1km of the trial site. Solar radiation (300 - 3000nm) was recorded on site. Maximum and minimum air temperatures were also recorded on site.

Seed rate: 100 seeds/m^2, seed spaced at 10cm.
Sowing Date: 4th April 1988
Harvest Date: 24th August 1988
Plot Size: 1m x 1m. Plots spaced 25cm apart.
Fertilisation: Fertilisers applied to seedbed and raked in prior to sowing
i) 60 kg ha^{-1} 24:24 P_2O_5:K_2O
ii) 130 kg ha^{-1} Nitrogen applied as Nitram (34% N)
30 kg ha^{-1} Nitram on 3.6.88
iii) 3 kg ha^{-1} Manganese sulphate in 400 l water on 6.6.88
Pest Control: Crop netted against mice, rabbits, birds etc.
Weed control: 30 g ha^{-1} 'Ally' in 200 l water on 26.5.88
Disease Control: 'Tilt Turbo' applied at standard rate on 7.6.88
second application on 1.7.88
Field Procedure: The plots were hand sown and harvested.
Experiment Design: Randomised block layout, 2 replicates for each of 10 varieties. Plots were planted at a wide spacing to reduce competition between plants. Pests and disease were treated at an early stage, before any check on the growth of plots was apparent.
Cultivars: Yields of spring barley cultivars in fungicide treated Co-ordinated Variety Trials by SAC in 1987 ranged from 5.77 - 6.52 t ha^{-1} (mean of control cultivars = 6.21 t ha^{-1} s.e. 0.31). The date of maturity varied over 4 days only. Ten 2-row cultivars were selected for study which spanned this diversity (Table D.1)

Sampling Methods and recording

Each plot was divided into 2 parts

a) three row border for destructive sampling for individual plant sampling, in which each plant taken must be surrounded by an intact group of 8 plants (Kirby & Ellis, 1980).

b) 25 plants in the centre of the plot for yield measurements from the final harvest.

Samples were taken at approximately weekly intervals between seedling emergence and anthesis to monitor leaf growth and development, tiller survival and fertility, and development rate. At each sampling date, the Zadoks (Tottman & Makepeace, 1979) development stage of the plot was assessed by non-destructive methods, the average height of plants was measured, the number of stems per five plants counted, and a single plant removed for detailed measurement.

Table D.1. Cultivars used in the trial

NAME	PEDIGREE	HABIT	YIELD t ha^{-1}	MATURE days
Blenheim	Triumph x Egmont	Semi-prostrate	6.40	154
Camargue	Complex cross which includes Triumph	Semi-prostrate	6.33	154
Golden Promise	Gamma ray mutant	Erectoid	5.78	151
Lotus		Tall	6.27	153
Klaxon		Tall	6.21	154
Oboe		Tall	6.46	152
Prisma	(Trumpf x Cambrinus) x Piccolo	Semi-prostrate	6.52	152
Sherpa	Complex cross	Semi-prostrate	6.27	154
Triumph	Diamant x ST11402964	Semi-prostrate	6.15	154
Tyne	(Goldmarker x Athos) x (Goldmarker x Magnum	Erectoid	6.21	151

The following measurements were taken after dissection of a single plant:

decimal stage of development
tillers/plant
leaves/plant and leaves/tiller
leaf blade length and area
height to leaf nodes, collar, ear tip and awn tip
number of spikelets in the developing spike

In addition, dry weights were measured at the three leaf stage, approximately one week before anthesis, and at anthesis. The date of anthesis was assessed by daily examination of anthers from the first appearance of awn tips, and recorded as having occurred when approximately 50% of main stem and primary tiller ears had shed their pollen. Dry weights were determined on oven dried samples (90°C for 24 hours). Leaf Area was determined using an Delta-T Area Measurement System

At harvest the following components of yield were determined:

grain and straw dry weight
mean grain weight
ears / m^2
grains / ear
grains / m^2 was then calculated.

RESULTS

Plant establishment of 100% was recorded in all plots. Lodging occurred on all plots to some extent. Strong winds occurred in two prolonged periods in late June and July. The more susceptible cultivars appeared to be Prisma and Golden Promise. Plots were assessed at anthesis and harvest for lodging on a subjective scale from 0 - no lodging to 5 - severe lodging. Late tillering occurred in all the worst affected plots. A more objective assessment of the degree of lodging was obtained at the final harvest, from the number of immature ears forming on late, green tillers in each 25 plant sample.

There was little disease apparent in any plot although powdery mildew (*Erysiphe graminis*) affected the Golden Promise plots slightly. Damage from insects was minimal, however bird damage occurred on all plots after severe weather dislodged part of the protective netting and aphids were recorded on Golden Promise I, Triumph I and Blenheim I. Ear loss was recorded by detailed counting of stems and ears at the final harvest.

The time taken to reach each stage of development varied little between cultivars (Table D.2). The CERES model recognises a stage 'end of vegetative growth' between MPN and anthesis, contrary to popular opinion, at which point the partitioning of assimilate altered. This point could not be confirmed by experiment. The full results were recorded in the barley database (Chapter 5; Appendix C)

Table D.2. Development stages - mean date of all ten cultivars.

STAGE	JULIAN DATE	DAYS FROM SOWING
Sowing	95	
Emergence	108	13
MPN	147	52
End ear growth	175	80
Anthesis	179	84
Beginning grain fill	184	89

Estimation of genetic characteristics

Six Genetic Specific Constants are used in CERES barley (page 40). A further four parameters quantify the general development of barley, not distinguishing between cultivars in these values (page 51). Calculation of appropriate values was carried out following the guidelines of Dr. Hunt (pers. comm.), who was responsible for writing the genetic inputs to CERES barley. G1, G2, G3 and P5 were determined separately for each of the ten varieties (Table 4.7): P2, P3, P4 and P9 from averages across all the varieties (Table 4.4). There was no significant difference between cultivars in these parameters.

Table D.3. Yield and its components

CULTIVAR	YIELD ($g\ m^{-2}$)	STRAW ($g\ m^{-2}$)	HI	GRAIN WT (mg)
Blenheim	621	921	0.40	4.66
Camargue	515	961	0.35	4.52
Golden Promise	484	572	0.46	3.77
Klaxon	651	860	0.43	4.4
Lotus	669	1040	0.39	4.9
Oboe	676	959	0.41	4.8
Prisma	671	778	0.46	5.1
Sherpa	767	920	0.46	4.78
Triumph	620	935	0.40	4.52
Tyne	667	702	0.49	4.03

Discussion and Conclusion

The growth, development and yield of the plots reflect the complex interactions of genotype, season, environment and crop management.

Using the equation in CERES barley for the phyllochron and a value of 0.085 for the rate of change of daylength at emergence (CHGDL - latitude 55.85°N, day of emergence - 108), the experiment gave a phyllochron of 57.84 °Cdays leaf^{-1} (Tb=0°C). The measured value in the field was 74.3 °Cdays leaf^{-1} (Table 4.4).

The assumption that the values obtained for genetic specific coefficients are constants from one season to the next remains unproven.

ESTABLISHMENT OF INITIAL PARAMETERS FOR GROWTH - A STUDY OF THE EARLY GROWTH AND DEVELOPMENT OF WINTER WHEAT AND BARLEY.

INTRODUCTION

The CERES barley model was adapted from CERES wheat by alteration of various parameters pertaining to specific leaf area, leaf area production, and rate of grain fill. Both models specify the same initial conditions, and use the same relationship relating dry matter production to LAI. Barley and wheat are closely related cereal crops requiring similar husbandry. However, field observations suggest that barley increases its leaf area faster than wheat in the early stages and also begins tillering earlier. Also, 6-row spring barleys generally have fewer tillers than 2-rows (Kirby & Riggs, 1978) and broader leaf blades (Rasmusson, 1985). The ear of a 6-row barley more closely resembles the morphology of the wheat ear than does a 2-row barley due to the maturation of the lateral spikelets.

This raises several questions:

a. Are the differences between winter wheat and winter barley during the early stages of growth, greater than the differences between a 2-row and a 6-row barley ?

b. To what extent are these differences related to seedling vigour and the contribution of stored carbohydrate reserves in the germinating seed ?

c. Are the early differences between individual plants of contrasting barley cultivars greater than the varietal differences ?

d. What is the temperature requirement for seedling emergence ?

e. How is tiller production related to leaf number ?

f. Are the specified initial conditions in the CERES model suitable for Scotland ?

The weather plays an integral role in determining the successful establishment of a crop, and is the source of considerable variation between crops. Variation in the experiment was minimised by using controlled environment conditions.

MATERIALS AND METHODS.

The experiment was conducted in a controlled environment growth room, maintained at a constant 10^{O}C, with a 12 hour photoperiod. Winter wheat cv. 'Riband', 2-row winter barley cv. 'Igri', and 6-row winter barley cv. 'Plaisant' were sown 4 seeds per pot. 2 pots of each variety were removed every 4 days until emergence and every 3 days thereafter, 12 samples in all. 6 plants were selected for detailed measurement from each variety: 3 for dry weight measurements and 3 for leaf area measurement (Table D.4).

Table D.4. Sampling programme

SAMPLE	DAYS FROM SOWING	THERMAL TIME*
1	4	41
2	8	80
3	11	112
4	14	141
5	17	170
6	20	201
7	23	230
8	27	270
9	29	290
10	32	320
11	35	350
12	38	380

* Accumulated temperatures adjusted for time of day when sample was removed from the growth room (T_b=0°C)

The following measurements were recorded for sample plants: total height above ground, root length, coleoptile length, leaf blade length and width, sheath and tiller lengths. Leaf areas were measured directly using a belt driven meter. For each leaf of the sample plant, leaf blade and leaf sheath areas were recorded separately. Leaf area index could not be determined since the plants were pot-grown.

Samples for dry weight measurement were weighed, and stored in polythene bags in the freezer until the end of the experiment, then dried overnight at 90°C before weighing again. Weights were accurate to 4 decimal places.

The following measurements were recorded for each sample of 3 plants: main stem leaf blade weight, root weight, seed weight, above ground weight excluding leaf blades.

RESULTS.

Germination and Emergence

Germination had occurred in all varieties within 4 days. None of the seeds sown failed to germinate. The radicles elongated at a similar rate in all varieties, but the plumule extended from beneath the seed coat most rapidly in Riband. Emergence of the coleoptile above soil level occurred simultaneously on the 11th day after sowing in all pots.

Root Growth

Root extension (L) shows a linear relationship with accumulated temperature (T) in all three varieties:

Igri $L = -44.9 + 0.801\,T$ $(r^2 = 98.4)$
Plaisant $L = -32.3 + 0.689\,T$ $(r^2 = 98.6)$
Riband $L = -63.8 + 0.866\,T$ $(r^2 = 94.1)$

Differences in rooting depth between the three varieties were not significant. When root length is expressed as a proportion of the total plant length, again the three varieties were similar. However, observation suggested that the barley cultivars produced thicker roots, and explored a greater volume of soil. This was borne out by root dry weight measurements. Difficulties in accurate measurement of dry weight for the smallest samples meant that there were many missing values when calculating partitioning coefficients. Dry matter increase of the roots accounted for 35.5% of the total dry matter produced (s.e. 3.59). Shoot dry matter increase accounted for 56.5% of the total (s.e. 10.6).

Seed Weight

Loss in seed weight more than compensated for the gain in root weight until a point some 25 days after sowing. Seed size affected the vigour of individual plants. Larger seeds produced larger plants, with longer root systems.

Leaf Number

All the barley plants reached the 3-leaf stage within the 38 days of the experiment, but the third leaf on Riband had still to fully unfold. The barley cultivars produced each new leaf earlier than Riband and maintained the advantage (Table D.5).

Leaf Area Development

Successive leaves were larger in all varieties. The increase was in both leaf blade and leaf sheath with significant differences between varieties. After full leaf emergence, growth continues in the leaf sheath, having virtually ceased in the leaf blade, so that the proportion of the total length, area and weight as leaf blade declines. These data show no significant difference between the proportion of leaf blade in successive leaves, despite the overall size increase. Leaf blade area reaches a maximum within three days of full leaf emergence. Growth prior to this follows an exponential curve with each successive leaf gaining leaf area more rapidly.

Table D.5. Leaf Development. I = Igri, P = Plaisant, R = Riband

SAMPLE	LEAF 1			LEAF 2			LEAF 3			LEAF 4		
	I	P	R	I	P	R	I	P	R	I	P	R
1												
2												
3	d	d	d									
4	c	c	c	d								
5	c	c	c	c	d							
6	b	b	b	c	c	d						
7	a	a	b	b	b	c	d	d				
8	a	a	a	a	b	b	c	d	d			
9	a	a	a	a	b	b	b	c	c	d	d	
10	a	a	a	a	a	a	b	b	b	c	d	d
11	a	a	a	a	a	a	a	b	b	c	d	d
12	a	a	a	a	a	a	a	a	b	b	b	d

a ... auricles visible
b ... leaf visible
c ... leaf tip visible
d ... leaf tip enclosed
Fully emerged leaves are highlighted

I ... Igri
P ... Plaisant
R ... Riband

Table D.6. Leaf development and temperature

Accumulated temperature to leaf appearance from seedling emergence (°Cdays)			
Leaf no.	**I**	**P**	**R**
1	120	120	160
2	160	210	210
3	240	270	>270

*

Igri $A = -24.8 + 0.131\ T$ $(r^2 = 86.9)$
Plaisant $A = -37.7 + 0.167\ T$ $(r^2 = 78.7)$
Riband $A = -18.6 + 0.0768\ T$ $(r^2 = 94.7)$

Leaf Blade weight (B) also increased with time showing a significant difference between varieties. Leaf Area increased in a log linear fashion with thermal time with a significant difference between varieties.

Igri $B = -0.0919 + 0.000446\,T$ $(r^2 = 95.2)$

Plaisant $B = -0.115 + 0.000503\,T$ $(r^2 = 77.7)$

Riband $B = -0.0842 + 0.000358\,T$ $(r^2 = 94.9)$

Each leaf of Riband was smaller than the corresponding leaf of barley, as a result of narrower leaf blade and sheath, although overall plant height and total leaf length was not significantly different. Plaisant was the leafiest of the three varieties, having a larger leaf area. The increased leaf area over Igri was accounted for by broader leaf blades. There was no significant change in Specific Leaf Area of the leaf blade of any of the varieties as the leaf aged.

Tillering

Each variety had a distinctive pattern of tiller production. Igri formed T1: Plasisant, Tc, using the notation of Kirby & Appleyard (1984). The first tiller to form in each variety was clearly visible as the 3rd leaf above it was unfolding. Tillering was most advanced in the barley varieties.

DISCUSSION AND CONCLUSIONS

The above results were derived from mean data. When each crop is represented by only a single cultivar it is also necessary to look at the individual plant variation to see if it is greater than the between cultivar variation. However, several of the CERES models initial conditions can now be examined in the light of these results.

a. Seed Weight 34mg

This value is equivalent to a thousand grain weight of 34g, which is low for many modern barley cultivars (Table D.7).

Table D.7. Mean thousand grain weight for Scottish Co-ordinated Disease controlled Variety Trials. 1983-1986

WINTER BARLEY		SPRING BARLEY	
Igri	51.4	Golden Promise	41.9
Plaisant	43.9	Triumph	46.2
Masto (lowest)	39.7	Tyne (lowest)	41.4
Mimosa (highest)	56.4	Prisma (highest)	52.2
Mean (s.e.)	47.2 (1.1)	Mean (s.e.)	47.2 (0.7)

The model allocates half the remaining seed dry weight each day for shoot growth, until the seed weight is zero. This would occur within 5 or 6 days of emergence. These results show a slow but steady fall in seed weight until about 14 days after emergence and then a constant weight which represents the seed husk alone. The processes of respiration and predation by soil organisms are at work simultaneously with the mobilisation of stored reserve from the seed to the developing plant.

b. Thermal time to emergence = 50 + 10.4 * SDEPTH ($T_b = 2$)

SDEPTH is the sowing depth in cm. The observed thermal time from sowing to emergence for this experiment was 88 °Cdays ($T_b = 2$) (adjusted from 110 °Cdays, $T_b = 0$). The calculated thermal time according to the model was 81.2 °Cdays for a sowing depth of 3 cm. Values of 100 - 120 °Cdays ($T_b = 0$) have been recorded in the field (Chapters 4 and 5).

c. Root partitioning coefficient >= 0.35

The root fraction of dry matter decreases during development according to the model. Initially, over 35% of the total dry matter is allocated for root growth. This is confirmed by these results with a mean value of 35.5% total dry matter partitioned to the roots over the period of the experiment.

d. Area to Weight Ratio = 150 g m^{-2}

Area to Weight Ratio (Specific Leaf Area) of the leaf blade is related in the model to photo-vernal-thermal time using arbitrary thermal development units (TDU) during the vegetative stage. After double ridge stage the AWR drops to 127.

$\mathrm{AWR} = 150 - 0.075 * \mathrm{TDU} * 1.1$

These data give a calculated AWR = 150 according to the model formulation. This compares with mean measured values of Igri 290, Plaisant 280 and Riband 480.

e. Leaf production related to thermal time

New leaves are produced at fixed intervals of photo-thermal time. A phyllochron of 77.5 °Cdays is used in the model, modified according to the rate of change of daylength at emergence whereas this experiment used a fixed daylength of 12 hours. The mean thermal time for a new leaf to unfold was

Igri	80 °Cdays
Plaisant	90 °Cdays
Riband	96 °Cdays

These results appear to be higher than the model values, but the relationship between leaf number and thermal time may not be linear over such a short time scale.

f. Thermal time from seedling emergence to the start of tillering 193.75 °C days
Tiller production begins after the passage of 2.5 phyllochrons according to the model, or 2.5 leaves have emerged on the main stem, and 193.75 °Cdays have elapsed. The first tillers in this experiment were visible on sample 8, just 160 °Cdays after emergence, as 2 leaves were fully unfolded in both barleys, but sample 9 (180 °Cdays) in Riband winter wheat, again as 2 leaves were fully unfolded.

NB: Firm conclusions about differences between wheat and barley, or between 2- and 6-row barley cannot be drawn from this data as there are only 1 or 2 degrees of freedom in the statistical tests. Further experiments involving a range of wheat and barley cultivars would be necessary to extrapolate results to other varieties or conditions of growth. Pot-grown plants are not suitable for measurement of leaf area index.

Figure D.1. Leaf Area Development Data Recording Sheet

Date: Cultivar: Sample No:

(all measurements in mm; weights in grams)

		Plant 1	Plant 2	Plant 3	Mean
Height above soil surface					
Height to spike tip					
Developmental stage code					
Number of expanded leaves					
Fresh weight					
above ground					
roots					
main stem & leaves					
tillers					
Dry weight					
above ground					
roots					
main stem & leaves					
tillers					
Tillers present**					
Height	Tc				
	T1				
	T1p				
	T2				
	T2p				
	T3				
	Other				
Leaf 1					
Development*					
Blade length					
Blade width					
Blade area (calc)					
Blade area (meas)					
Total area					
Blade fresh wt					
SLA					
Height to auricles					
Total length					
Leaf 2					
Development*					
Blade length					
Blade width					
Blade area (calc)					
Blade area (meas)					
Total area					
Blade fresh wt					
SLA					
Height to auricles					
Total length					

Leaf 3

Development*
Blade length
Blade width
Blade area (calc)
Blade area (meas)
Total area
Blade fresh wt
SLA
Height to auricles
Total length

Leaf 4

Development*
Blade length
Blade width
Blade area (calc)
Blade area (meas)
Total area
Blade fresh wt
SLA
Height to auricles
Total length

Key to Development:

A	auricles visible
B	leaf visible
C	leaf tip visible
D	leaf enclosed
E	enclosed (<1 cm)

Key to Tillers:

Tc	Coleoptile tiller
T1	Subtended by leaf 1
T2	" " " 2
p	subtended by tiller

Key to Developmental Stage:

G	germination
C	coleoptile emerged
E	first leaf emerging through coleoptile
F	first leaf auricles visible
V1	vegetative
V2	late vegetative
DR	double ridge
TM	triple mound
GP	glume primordium
LP	lemma primordium
SP	stamen primordium
AP	awn primordium - maximum number of primordia

Ear at 1 cm ..Zadoks stage 30

APPENDIX E. BARLEY PRODUCTION

Table E.1. Cereal production in the United Kingdom, 1977-1987[*] Area ('000 ha)

Year	Total	Barley	%	Wheat	%	Oats	%
1977	3711	2404	64.8	1078	29.0	219	5.9
1978	3816	2352	61.6	1258	33.0	197	5.2
1979	3878	2347	60.5	1372	35.4	152	3.9
1980	3938	2330	59.2	1441	36.6	161	4.1
1981	3979	2327	58.5	1491	37.5	155	3.9
1982	4030	2222	55.1	1663	41.3	139	3.5
1983	3960	2143	54.1	1695	42.8	116	2.9
1984	4037	1978	49.0	1939	48.0	114	2.8
1985	4015	1965	48.9	1902	47.4	140	3.5
1986	4024	1916	47.4	1997	49.6	104	2.6
1987	3936	1830	46.5	1994	50.7	105	2.7

[*] Data from CSO Annual Abstract of Statistics no. 125, 1989

Oats figures include Mixed Corn. Percentage totals less than 100% due to area of Rye and other cereals.

Table E.2. Cereal production in Scotland, Area grown: 1951 - 1986[*] ('000) ha

YEAR	TOTAL	BARLEY	%	WHEAT	%	OATS	%
1951	462	70	15.2	28	6.0	364	78.8
1961	423	130	30.7	37	8.8	256	60.5
1966	458	271	59.2	26	5.7	161	35.2
1970	452	287	63.5	40	8.9	125	27.6
1975	463	369	79.7	28.	6.0	66	14.3
1976	468	387	82.5	26	5.6	56	12
1977	481	407	87	22	4.7	52	11.3
1978	494	426	86.2	21	4.3	47	9.5
1979	497	436	87.7	24	4.8	37	7.5
1980	509	444	87.2	26	5.1	39	7.7
1981	510	439	86.1	30	5.9	41	8.
1982	526	455	86.5	40	7.6	31	5.9
1983	522	450	86.2	47	9	25	4.8
1984	535	438	81.9	71	13.3	24	4.9
1985	527	416	78.9	82	15.6	29	5.5
1986	535	418	79.3	89	16.9	28	5.3

Data from the Scottish Abstract of Statistics, no 16, 1987.

Table E.3. Summary of Land Capability Classification Classes

CLASS	CLIMATE			SLOPE	SOIL		
(div)	temp min °Cday	PMSD min mm	wind max ms^{-1}	max °	stones max %	drought*	depth min cm
1	1150	130	5	4	5	0	60
2	1050	95	5	7	15	0-2	45
3(1)	975	80	5	7	35	<=2	45
3(2)	925	70	5.5	11	35	<=3	20
4(1)	875	60		11	70	0-3	20
4(2)	850	30		15	70		plough
5(1)	750	30		11	>70	>2	
5(2)	750	30		15	>70	>5	
5(3)	750			25	>70	>=5	
6(1)	625						
6(2)	625						
6(3)	625						
7							

Part B

CLASS	WETNESS	LIMITATION DUE TO		
(div)	class	drainage	flood	workability
1	I,II	good	0	0
2	I-III	moderate	0	>=2
3(1)	I-III	good-poor	1	2-3
3(2)	I-IV	good-poor	1	>=3
4(1)	I-III	free-imperfect	2	>=3
4(2)	I,IV			4
5(1)	I-III		2	>80% usable
5(2)	III-V		2	60-80%
5(3)	I-VI			>40% usable
6(1)	I-IV	good-moderate		
6(2)	I-V			
6(3)	IV-VI			
7				

* 0 negligible, 1 very slight, 2 slight, 3 moderate, 4 moderately severe, 5 severe

spaces indicate no limitation for that soil characteristic

Data from The Soil Survey of Scotland Monograph "Land Capability Classification for Agriculture" (1982)

See reference for full explanation of terms

Table E.4. Importance of barley to land use in Scotland, 1986.*

Region	% Scotland barley area	% Region as barley	% Arable as barley
SCOTLAND	100.0	5.4	62.6
Highlands & Islands	6.6	1.0	57.4
Strathclyde	6.8	2.1	73.7
Grampian	31.5	15.1	67.7
Tayside	19.1	10.6	58.4
Dumfries & Galloway	5.4	3.5	77.3
Borders	11.6	10.4	57.0
Central	2.7	4.3	64.7
Lothian	7.2	17.1	55.6
Fife	8.4	26.9	60.3

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