



**PROJECT REPORT No. 90**

**IDENTIFICATION AND  
PREDICTION OF STAGES OF  
WHEAT DEVELOPMENT FOR  
MANAGEMENT DECISIONS**

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# IDENTIFICATION AND PREDICTION OF STAGES OF WHEAT DEVELOPMENT FOR MANAGEMENT DECISIONS

by

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## Summary

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The identification and prediction of developmental stage in wheat is an important aid to crop management. Efficacy of various management operations is determined by stage of plant development, i.e. the physiology or morphology of the plant, but recommendations for the timing of application of agrochemicals are generally in terms of 'growth stages'. Relations between developmental and growth stages are clarified in this report.

Development of the wheat plant is a highly co-ordinated phenomenon and leaf emergence, shoot apex development and stem elongation are all integrated. In this report the relationships between the various elements of development are examined and are summarised as equations where stage of development is expressed in terms of number of emerged leaves and final number of leaves. This enables developmental stages to be described in terms of 'Zadoks' growth stages.

To use these relationships for prediction purposes it is important to know what regulates the rate at which leaves emerge. Four models to explain and predict leaf emergence are investigated and their relative performance and sources of errors are evaluated. Two models to predict final number of leaves are also assessed.

The co-ordination between various aspects of development is summarised in the form of a template of wheat plant development, that is a framework which shows how the elements relate to each other.

The template will form the basis of a personal computer program to predict wheat development for specific varieties, using average or current weather records. Because output is in terms of Zadoks growth stages it can be directly applied to timing of management operations. Parts of the template can be adapted as a pencil and paper nomogram which will predict from stage 30 onwards, for example, 31, 32, 37 or 39 which are relevant for fungal disease control.



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# 1. Introduction

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The ability to recognise or predict cereal plant development is useful in crop management. Some operations such as the application of growth regulator or fungicide are most effective if they are done at defined developmental stages.

Attempts have been made to present plant development information so that it can be used by farmers and crop consultants for timing critical operations. There have been two approaches to this objective. Developmental scales, which are more botanically based, recognise that the response to chemicals or other management operations may depend on fundamental changes in plant physiology and development, such as the transition from vegetative to flowering (ear formation) stage, the onset of culm elongation and anthesis. Descriptions of cereal plant development based on this approach concentrate on changes at the 'growing point' or meristematic shoot apex (Kirby & Appleyard 1987; Landes & Porter 1989). To understand and use developmental scales entails some knowledge of basic botany and the use of specialist techniques and equipment. Although many crop managers understand the underlying principles and articles in the popular agricultural press sometimes give details of shoot apex development (e.g. double ridge and terminal spikelet stage), the use of development scales is probably too complicated for general use.

The alternative method is to describe development in terms of stages which can be observed on the whole plant without, or with only minimal, dissection. This approach is generally referred to as 'growth stage' scales. In Britain the most commonly used scales are the 'Feekes-Large' (Large 1954) and the 'Zadoks' (Zadoks *et al.* 1974).

Most information about stages for the application of agricultural chemicals is couched in terms of these scales.

Development and growth stage scales are not always apparently related. For example, a particular shoot apex stage may occur at different points on a growth stage scale because of varietal difference or sowing date and other effects.

To use the principles of optimal developmental stages for crop management some reconciliation of these apparent differences is necessary and a comprehensive scheme offering information on fundamental changes in plant development in terms of generally understood growth stages is desirable.

In this report the highly co-ordinated nature of wheat plant development is explained and it is shown that leaf emergence, shoot apex development and stem elongation are all closely integrated. These relationships are summarised in the form of a template, that is a framework or pattern which shows how the various elements of development relate to each other.

The template shows that a developmental stage can be assessed by the number of emerged leaves and represented by a Zadoks growth stage. Possible further developments of the template as a basis for a computer simulation models or nomograms for wheat crop management are discussed.

The remainder of the report considers each of the elements of the template in detail. Data and experiments used to establish metrical functions are described and the accuracy of alternative functions for particular processes is assessed.



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## 2. A template for wheat development

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Many different processes are involved in the development of the plant from seed to seed. On sowing, the shoot apex and three primordial leaves which are present in the dormant seed resume growth. More leaves are formed at the shoot apex and the leaves emerge in an organised sequence. During this phase tiller buds are initiated and may grow to form leafy tillers. After the leaf formation phase (vegetative phase), the shoot apex changes in form to initiate spikelets (ear formation phase). As the spikelet 'initials' or 'primordia' grow the structures which will become glumes, lemma and palea (chaff) and the ovaries (grain sites) are differentiated. These changes mark the progress of development of the ear and a number of stages have been defined, e.g. double ridge and terminal spikelet stages. During the ear formation phase, the culm (flowering stem) starts to grow. Shortly afterwards, the formation of spikelets ceases with the formation of a terminal spikelet. The ear formation phase is followed by a phase of vigorous ear and stem growth, culminating in the emergence of the ear and anthesis (flowering). The final phase is that of grain filling and ripening.

Each of these developmental processes has been studied in detail. The various stages have been described and defined and the responses to environmental factors such as daylength and temperature have been measured. The functions relating development to environmental factors have been used to make computer simulation models which can predict development ('phenology models'). Such models have been used as crop management tools (ADAS Growth Stage Forecasting Service 1988 - 1992) and also are important parts of bigger models used to simulate crop growth and yield.

Most commonly, phenology models are formulated to simulate a particular process such as apex development. For example the AFRC wheat model (Weir *et al.* 1984) predicts the double ridge stage. Other processes are modelled, for example leaf emergence, but these are treated as separate, discrete processes (Weir *et al.* 1984). Few models have used growth stages explicitly to define phases of the life cycle.

That each element of plant development does not occur in isolation is self evident and the co-ordination of development and growth phenomena have been described (Aitken 1974; Malvoisin 1984; Kirby 1990). Below, some of the relationships in the wheat plant are described and a template or framework linking the various processes is suggested. Details of the relationships and the data

from which they were derived are given in Sections 3 - 7.

### Co-ordination of development in the wheat plant

#### *Seedling and leaf emergence*

After sowing and imbibition of the seed, radicle and shoot growth commences. Growth of the first leaf and the coleoptile are co-ordinated and as the coleoptile penetrates the soil surface, its further growth is inhibited by light, and the first leaf emerges. The time at which the seedling emerges depends principally on thermal time (see Section 3) from sowing (Kirby 1993).

#### *Leaf emergence and shoot apex development*

Leaves emerge in a regular sequence (Section 4) and this is co-ordinated with ear formation. The emergence of a particular leaf is associated with the attainment of a development stage, for example, under certain conditions, terminal spikelet stage will occur when 8.5 leaves have emerged. However, the relationship between number of emerged leaves and shoot apex development is not absolute, but depends on the final number of leaves on the shoot (Section 5).

Using the relationship between number of emerged leaves, final number of leaves on the shoot and shoot apex development, morphological stages can be defined in terms of number of emerged leaves (Section 6). For purposes of crop management, the double ridge and terminal spikelet stages have been shown to be of particular significance and these are shown in the template, but any other stage could be included.

#### *Leaf emergence and stem and ear development*

The first formed, basal internodes do not grow much in length and remain crowded together at the base of the shoot. When the shoot apex is at the glume to lemma stage in wheat, growth of the culm (the flowering stem) begins. Generally, the culm comprises six elongated internodes. The most basal one elongates first, at a particular number of emerged leaves, which depends on the final number of leaves (Section 5). The elongation of each internode is co-ordinated with the growth of its associated leaf and the length of each internode can be defined in terms of number of emerged leaves (Section 7).

### *Ear emergence and anthesis*

The elongation of the distal internode of the culm (peduncle) first pushes the ear out of the sheath and then, as the peduncle attains its full length, anthesis occurs. The duration of peduncle elongation (in thermal time) is determined by the rate of leaf emergence.

### *Leaf emergence, tillering and root initiation*

Although not incorporated in the template, both tillering and initiation of the nodal roots are co-ordinated with leaf emergence (Friend 1965; Klepper *et al.* 1984; Masle-Meynard & Sebillotte 1981) and could be included in the proposed framework.

### **Template**

The phenomenon of co-ordinated development described above means that there is a strict relationship between the development of various organs throughout the life cycle of the plant. This concept, with functions to quantify the relationships, is the basis of the template. An example of the application of the template is shown in Fig 2.1. As the physiological and metrical relationships are studied further, improved functions may be substituted in the template.

For each element of the template, stage of development can be expressed in terms of an independent variable, number of emerged leaves. This can be readily observed without dissection or use of a microscope and several functions which

relate leaf emergence to environmental factors have been proposed.

### *Relationship between emerged leaves and growth stages*

Number of emerged leaves translates directly to the Zadoks scale (Zadoks *et al.* 1974). For example, a plant with 4.5 emerged leaves has 4 unfolded leaves (Tottman 1987) and a growth stage score of 14 (principal growth stage 1, seedling growth). Knowing the final number of leaves on the shoot, the equivalence between number of emerged leaves and internode elongation, Zadoks principal growth stage 3 can be derived. For example, in Fig. 2.1, where an 11 leaf plant is shown, the second elongated internode is >20 mm (growth stage 32) when 8.7 leaves have emerged (growth stage 18).

### *Leaf emergence*

Central to the use of the template is the ability to measure and predict the number of emerged leaves on the shoot. Leaf emergence has been extensively studied and a number of alternative hypotheses have been proposed to explain the relationship between leaf emergence and environmental factors. Amongst these the function relating leaf emergence to temperature and rate of change of daylength was the most accurate (Section 4).

### *Final number of leaves*

It is essential to know the final number of leaves on the shoot to determine the relationship between

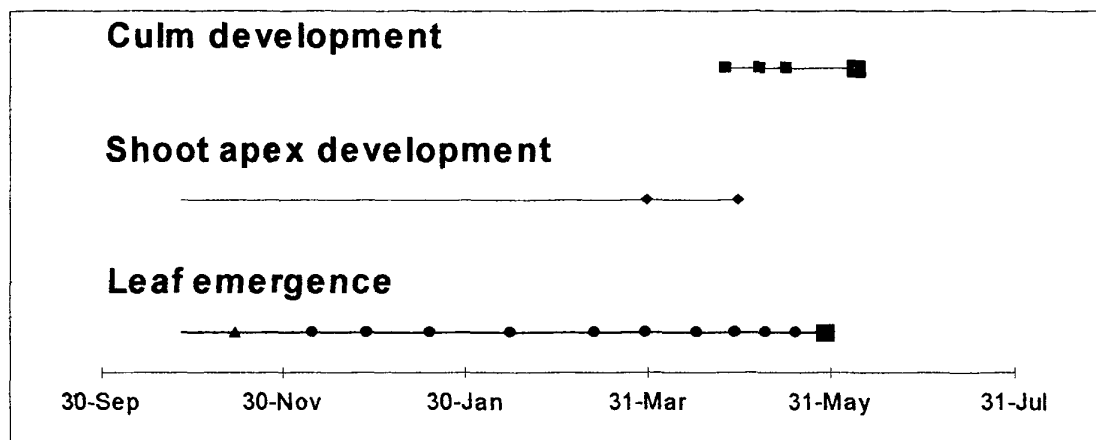


Fig. 2.1. An example of the template to show the relationship of the number of emerged leaves to shoot apex and culm development of a main shoot with eleven leaves. The line for leaf emergence extends from sowing to flag leaf emergence: flag leaf, ■; seedling emergence, Δ; leaves 1-10, ●. The shoot apex development line shows the time of double ridge (◆, LH) and terminal spikelet (◆, RH) stages. The culm development line shows, from left to right, Zadoks growth stages (■) 30, 31, 32 and 55 (ear emergence).

number of emerged leaves and stage of development. The final number of leaves is principally dependent on daylength and temperature and a regression function incorporating measures of daylength and vernalisation gave satisfactory accuracy (Section 5).

### Application of the template

Computer simulations of plant development, using weather data, have been used to predict critical stages for application of chemicals and other operations on the crop. An outline of a model to predict growth stages based on the template is shown in the Appendix. The principal inputs are sowing date, variety, latitude of the site and maximum and minimum temperatures. Details of

a hand calculator to estimate thermal time. The necessary tables could be supplied from a local weather station allowing predictions to be made for sowing date and variety. An example is shown in the Appendix.

### Analysis of varietal differences

The template gives some insight into the significance of varietal difference in number of leaves and rate of leaf emergence.

Many of the varieties on the NIAB, SAC and DANI recommended lists have similar maturity ratings (most varieties score 7 for 'Earliness of ripening'). Amongst these varieties some tend to have fast leaf emergence and more leaves, while others have slow leaf emergence and few leaves.

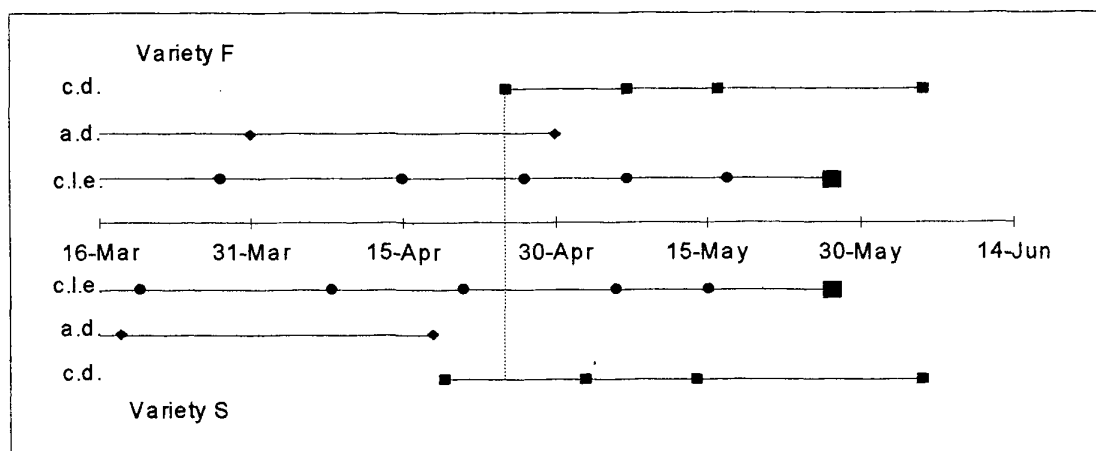


Fig. 2.2. Development of two varieties with similar maturity (ear emergence occurs on the same day). Variety F has fast leaf emergence ( $120^{\circ}\text{Cd}$  per leaf) and 11 leaves, and variety S has slow leaf emergence ( $130^{\circ}\text{Cd}$  per leaf) and 10 leaves.

c.d. - culm development: Zadoks growth stages (■), from left to right, 30, 31, 32 and 55 (ear emergence).

a.d. - shoot apex development: double ridge (◆, LH) and terminal spikelet (◆, RH) stages.

c.l.e. - culm leaf emergence : ●, culm leaves 1 to 5; ■, flag leaf (Zadoks growth stage 39).

the functions and coefficients are shown in the Appendix. This model, programmed to run on a personal computer, using average or current weather data could be used to monitor crop development from a farm office. As output is couched in terms of Zadoks growth stages, it relates directly to much management practice and facilitates checking the model predictions by people skilled in the use of growth stages.

Parts of the template might be developed to give simple nomograms to combine monitoring and prediction of stages of the life cycle, e.g. culm elongation and the emergence of stem leaves (stages 30, 31, 32...37, 39 and intermediate culm leaves). This is less complicated than a computer program but could give the same information using

The consequences of these differences is shown for the two types of development (Fig. 2.2). The two variety types were 'sown' in October and development is shown from the middle of March until ear emergence. Differences of this sort have been observed amongst the varieties measured in the experiments described in this report.

Such differences have implications for crop management. Decisions based on the maturity ratings would not indicate a necessity for any differences in a management regime. In fact the diagram shows there was a difference of 6 days between the times of occurrence of Zadoks growth stage 30 which might affect efficient management and the allocation of priorities.

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### 3. Sources of data

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In Sections 4 - 7 hypotheses about plant development are tested or new functions are proposed (e.g. stem elongation, Section 6). The data for these analyses came from four sources:

#### 1. Data from old experiments

A data base of wheat development has been built up from experiments done at the Plant Breeding Institute (some in collaboration with other institutions), Western Australian Department of Agriculture, University of Western Australia, United States Department of Agriculture (Temple, Texas) and Consiglio Nazionale Ricerche (Florence, Italy) from 1962 till 1992. The results of these experiments have been published (see reference list). In this report the data have been reworked to test hypotheses (e.g. about rate of leaf emergence, Section 4) or to establish metrical relationships which depend on co-ordination of processes in the plant (e.g. between leaf emergence and apex development, Section 6).

#### 2. ADAS data

This data was collected to support predictions made by the ADAS Growth Stage Forecasting Service from 1989-90 to 1991-92. It provided a valuable data base of number of emerged leaves, shoot apex development and stem elongation. Plots were sited at ADAS Crop Centres and on farms in most of the main wheat growing regions of the country and were sown at a range of dates during the normal sowing season. Several recommended list varieties were included in the trials. All the plant measurements and shoot apex dissections were done by Margaret Appleyard.

An analysis of some of this data will also be published in the Journal of Agricultural Science (Kirby *et al.* 1993).

#### 3. Data from Hyde Hall

Margaret Appleyard also provided data from farm crops and other experiments at Hyde Hall, Great Fransham, Norfolk and gave assistance with interpretation of the data and definitions of stages.

#### 4. Experiments at Anstey Hall

Experiments were done at the ADAS trial grounds at Anstey Hall, Cambridge. ADAS provided and sowed the seed and helped with disease and pest control. In two experiments the effect of variety

and sowing date on plant development was investigated. In the first, three sowings of winter and spring wheat varieties were made from 4 February to 17 March 1991 and in the second, five sowings were made from 17 September 1991 to 17 March 1992.

#### Materials and methods

Details about materials and methods are given in papers listed in Section 8, but were similar in all experiments. Plots were hand sown on a precise grid layout or were sown using a precision drill designed for cereal experiments. Experiments were managed using good agronomic practices except that wherever possible no herbicides or growth regulators were used as these affect apex development (Kirby *et al.* 1989).

Experimental design varied but attention was paid to appropriate replication, guard plots and rows, and sampling procedures.

Observations were made both on marked plants and on plants sampled at intervals throughout the season. Measurements were generally confined to the main shoot and included time of seedling emergence, counts of emerged leaves, counts of final number of leaves, stage of apex development, length of internodes and growth stages.

#### Thermal time

Some analyses (e.g. rate of leaf emergence) were done in relation to thermal time (accumulated temperature, heat units) rather than calendar time. Temperature data were obtained from a weather station as near as possible to the experiments. In most cases this was an agro-met station sited within a kilometre of the plots.

Unless otherwise stated thermal times were calculated using 0°C base temperature.

Methods to calculate thermal time differed slightly between experiments. The method described by Weir *et al.* (1984) was used to calculate thermal time ( $Tt$ ) in the functions relating final number of leaves to temperature and photoperiod (Kirby 1992). This assumes a cosinusoidal variation in temperature, as follows:

$$Tt = \frac{1}{8} \sum_{r=1}^{r=8} [T_H - T_{base}] \quad ^\circ\text{Cdays}$$

where

$$T_H = T_{\min} + f_r (T_{\max} - T_{\min}) \quad ^\circ\text{C}$$

and

$$f_r = \frac{1}{2} [1 + \cos \frac{90}{8} (2r - 1)]$$

$T_{\min}$ , max and base are minimum, maximum and base temperatures in °C, respectively.

A method given by the Meteorological Office (Form 3300) was also used:  
if both maximum and minimum temperature > base temperature

$$Tt = 0.5(T_{\max} + T_{\min}) - T_{\text{base}}$$

but if maximum temperature > base temperature and minimum temperature < base temperature then  
i) if mean temperature > base temperature

$$Tt = 0.5(T_{\max} - T_{\text{base}}) - 0.25(T_{\text{base}} - T_{\min})$$

ii) if mean temperature < base temperature

$$Tt = 0.25(T_{\max} - T_{\text{base}})$$

In some cases a sum of daily mean temperatures was used.

The Weir *et al.* (1984) and the Met Office method gave very similar results and the latter method was easier to use in spreadsheet calculations. All methods give the same result if temperatures do not fall below base temperature.

#### Photoperiod

Throughout the report photoperiod and daylength are synonymous and refer to the period from sunrise to sunset plus the period of civil twilight, which starts and finishes when the sun is 6° below the horizon. Photoperiod (P) was calculated using the method given by Keisling (1982). No correction was made with reference to leap years:

$$P = \frac{2}{15} \arccos[\cos \alpha \sec \phi \sec \delta - \tan \phi \tan \delta]$$

where

$\alpha$  = zenithal distance in degrees of the sun (96° for civil twilight),

$\phi$  = latitude in degrees (positive in the northern hemisphere)

and

$\delta$  = declination of the sun in degrees.

The equation relating declination of the sun to time of year is:

$$\delta = \arcsin\{0.39779 \sin \lambda\}$$

where

$$\lambda = M + 1.916 \sin M + 0.02 \sin 2M + 282.565$$

and

$$M = 0.9856t - 3.251$$

where  $t$  is the day of the year (days after 31 December).

#### Statistical analysis

Appropriate statistical analyses were done using Genstat or Microsoft Excel spreadsheet functions.

Comparisons were made among the various functions to predict number of emerged leaves or final number of leaves with the root mean square error (RMSE) (Wallach & Goffinet 1991):

$$RMSE = \left[ \frac{\sum_{i=1}^{i=n} (\text{observed}_i - \text{predicted}_i)}{n} \right]^{\frac{1}{2}}$$

## 4. Leaf emergence

Leaves emerge on the shoot of a cereal plant in a regular sequence. They start as 'primordia' or 'initials' and accumulate on the shoot apex (Kirby & Appleyard 1987; Williams 1975). Each leaf grows up within the next oldest, enclosing leaf. The leaves are arranged in a concentric manner and emerge rather like sections in a telescopic aerial. The leaf tip emerges first and then, as the leaf grows in length, the ligule emerges and finally the sheath. Shortly after the sheath appears the leaf is fully elongated. Only one, or sometimes two, leaves are emerging on a shoot at a time (Fig. 4.1).

Thus on a shoot at any time there will be a number of fully emerged leaves plus an emerging leaf. This is recorded as a decimal number where the integer part is the number of fully emerged leaves and the fraction refers to the length of the emerging leaf as a proportion of the fully emerged, enclosing leaf (Haun 1973) (Fig. 4.1).

The rate at which leaves emerge depends on temperature so that early in autumn and in the spring leaves emerge quickly, and slowly in winter (Fig. 4.2a). If, instead of plotting number of leaves

versus date, it is plotted versus thermal time, leaf emergence rate is more or less constant (Fig. 4.2b) and the slope of the regression line is the rate. The

reciprocal of the rate of leaf emergence, i.e. the number of degree-days for a leaf to emerge, is called the 'phyllochron'.

Experiments have shown that the rate is slowest for September-sown plants and increases steadily throughout the season, so that leaf emergence is fastest in March sowings. Based on these observations attempts have been made to find a metrical function (model) relating leaf emergence to the environmental factor or factors which determines the

response. In this section the accuracy of four models and sources of error are examined:

- Model 1: Rate of change of daylength model (Baker *et al.* 1980)
- Model 2: Thermo/photo ratio model (Cao & Moss 1991)
- Model 3: Photothermal time model (Masle *et al.* 1989)
- Model 4: Ontogenetic model (Miglietta 1991a).

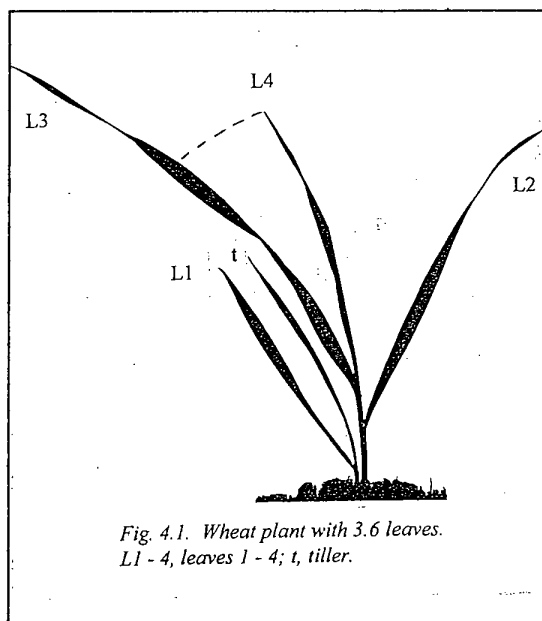


Fig. 4.1. Wheat plant with 3.6 leaves. L1 - 4, leaves 1 - 4; t, tiller.

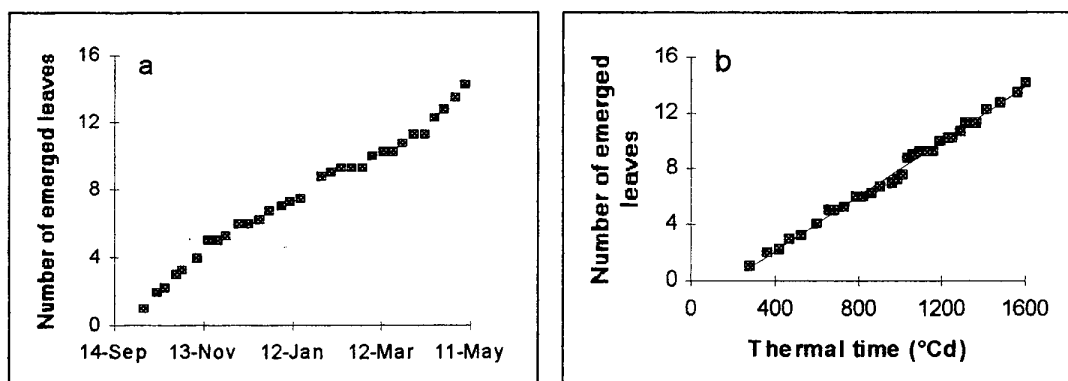


Fig. 4.2. Typical patterns of leaf emergence. Number of leaves versus a, date and b, thermal time; the line is fitted by linear regression.

## Leaf emergence models

### Model estimates of the number of emerged leaves

The accuracy of the models was assessed by comparing observed with calculated values, using first the published form of the functions relating number of emerged leaves to environmental variables (see below). The calculations are generally based on intercept ('a') and slope ('b') coefficients in a linear equation. For none of models 1 - 3 are values of 'a' given in the published descriptions. At seedling emergence the number of emerged leaves is 0 (the first leaf is about to emerge through the tip of the coleoptile) and thermal time at this stage is estimated by  $-a/b$  (where seedling emergence is estimated by  $-a/b$ , it is written 'seedling emergence'). Seedling emergence is observed at about 125 °Cd (base temperature 0 °C). For the prediction of number of leaves by models 1 and 2, the origin of the regression line was set at 'seedling emergence' (initially 125 °Cd) i.e. thermal time was (thermal time from sowing - thermal time from sowing to seedling emergence);  $a = 0$  and  $L = bt$ .

Seedling emergence occurs at about 85 °Cd in photothermal units. In model 3 the technique described above was also used but an initial value of 85 °Cd was used for 'seedling emergence'.

#### Assumptions and coefficients

##### 1) Rate of change of daylength model

Assumptions:

- i) rate of leaf emergence is constant in thermal time ( $t$ )

$$L = a_d + b_d t$$

where  $L$  is the number of emerged leaves and  $a$  and  $b$  are constants

- ii)  $b_d$  is a function of rate of change of daylength ( $D$ ) at seedling emergence.

$$b_d = \alpha_\delta + \beta_\delta D$$

Coefficients:

$$\alpha_\delta = 0.0104$$

$$\beta_\delta = 0.026$$

base temperature for thermal time = 0°C

seedling emergence = 125 °Cd

##### 2) Thermo/photo ratio model

Assumptions:

- i) rate of leaf emergence is constant in thermal time ( $t$ ) as for rate of change of daylength model.

$$L = a_r + b_r t$$

where  $L$  is the number of emerged leaves and  $a_r$  and  $b_r$  are constants

- ii)  $b_r$  is a function of the thermo/photo ratio ( $R$ ). This is defined as temperature/photoperiod. Temperature (°C) is the mean temperature at seedling emergence (from 3 days before till 7 days after seedling emergence). Photoperiod (hours, civil twilight) is measured at seedling emergence.

$$b_r = \alpha_p + \beta_p R$$

where  $\alpha_p$  and  $\beta_p$  are constants which depend on variety.

Coefficients:

$$\alpha_p = 0.0135$$

$$\beta_p = -0.0025 \text{ (coefficients for variety 'Stephens', Cao \& Moss (1991))}$$

base temperature for thermal time = 0°C

Seedling emergence = 125 °Cd

##### 3) Photothermal model

Assumption:

- i) rate of leaf emergence is constant in photothermal time ( $P$ )

$$L = a_\pi + b_\pi P$$

Where  $a_\pi$  and  $b_\pi$  are constants.

Photothermal time is calculated as follows:

$$P = \sum l(T_l - T_b)$$

where  $l$  is the light period as a proportion of a day (24h),  $T_l$  is the average temperature in the light and  $T_b$  is the base temperature.  $T_l$  is calculated from

$$T_l = T_{min} + k(T_{max} - T_{min})$$

where  $T_{max}$  and  $T_{min}$  are daily maximum and minimum temperatures, respectively and  $k$  is the relation between  $T_{max}$  and  $T_{min}$  and the average temperature during the light period.

Coefficients:

$$b_\pi = 0.16 \text{ (varies with variety and season)}$$

Base temperature ( $T_b$ ) = 0°C

$$k = 0.65$$

Seedling emergence = 85 °Cd

##### 4) Ontogenetic model

Assumptions:

- i) the rate of initiation of vegetative primordium is a linear function of temperature

$$dI/dt = -0.038 + 0.0149T$$

where  $I$  is the number of primordia,  $t$  is time in days and  $T$  is air temperature (°C).

- ii) Number of emerged leaves ( $L$ ) is a function of number of primordia as follows:

$$L = 1 - \exp[-a(I - I_0)]$$

where 'a' is a constant and  $I_0$  is the number of primordia at seedling emergence. (Note: the predicted number of primordia at seedling emergence was different from the observed number of primordia and was very variable.  $I_0$  was set to zero and number of leaves was calculated from observed seedling emergence.)

Coefficients:

$a = 0.03$

Table 4.1. Mean RMSE for each model, using published coefficients and settings for 'seedling emergence' shown in text, above

	Model			
	1	2	3	4
RMSE	0.89	2.43	1.07	0.81

### Model accuracy

The accuracy of each model was tested by calculating observed minus predicted values for each observation of number of emerged leaves for each variety x site case. The root mean square error (RMSE) (Wallach & Goffinet 1991) was calculated for each case using the coefficients described above (Table 4.1); the smaller the values of RMSE, the more accurate the model.

### Minimisation of RMSE by varying coefficients

The RMSE values in Table 4.1 were the result of setting ' $a/b$ ' at a typical value for seedling emergence. Also, the values of ' $b$ ' in models 2 and

3 were estimated from counts of number of leaves in America (Oregon) or France using local varieties. The effect was investigated of varying 'seedling emergence' and, in the case of models 2 and 3, ' $b$ ', either directly (model 3) or by changing the function from which it was derived (model 2). The settings which minimised RMSE and the associated values of RMSE are shown in Table 4.2.

At the values which minimised the overall RMSE, there was considerable variation between sowing dates. Sowing dates were grouped by the month of sowing and, by varying 'seedling emergence', the mean RMSE for each month was minimised (Table 4.3).

### Sources of error

Errors in the prediction of number of leaves may arise from uncontrolled factors such as variation in sowing depth (Kirby 1993), nutrient levels (Longnecker *et al.* 1993), stress from frost, drought or disease, or mistakes in recording. Another source of error may be because the assumptions of the models are not justified.

Table 4.2. Values of 'seedling emergence' and other coefficients which minimised RMSE for each model

	Model			
	1	2	3	4
RMSE	0.72	0.90	0.76	0.81
'Seedling emergence'	180 °Cd	130 °Cd	-20 °Cd	See text
Rate	Unchanged	$=f(\alpha_p, \beta_p)$	0.013	Unchanged
' $\alpha$ '		0.0103		
' $\beta$ '		-0.0025		

Table 4.3. Thermal time to 'seedling emergence' (S. em.; °Cd for models 1 and 2, °Cdl for model 3) and mean RMSE for each month. For models 1 - 3 the thermal time to 'seedling emergence' was selected to minimise RMSE. In model 4 the prediction was calculated using observed seedling emergence (see text)

	Model 1		Model 2		Model 3		Model 4
	S.em.	RMSE	S.em.	RMSE	S.em.	RMSE	RMSE
Sep	180	0.85	70	0.76	-30	0.70	0.72
Oct	210	0.61	170	0.61	0	0.75	0.66
Nov	230	0.51	130	0.42	-10	0.45	0.73
Feb	100	0.34	-60	0.83	-40	0.66	1.19
Mar	50	0.63	-130	1.16	-70	0.94	2.02



### *Non-linear response*

In models 1 and 2, a linear response to thermal time is assumed. In order to detect curvilinearity frequent observations over the whole growing season from seedling emergence to flag leaf are necessary and a wide range of sowing dates is desirable. In the data used to test for model performance, only the Anstey Hall experiments met these requirements. Plots of observed values compared with the fitted regression line, or inspection of observed minus fitted values showed a strong curvilinear trend in the September sowing (Fig. 4.3). The deviations were also largest for the September sowing and declined and became more randomly distributed in later sowings.

Similar trends were seen in the data from two experiments at the Plant Breeding Institute, Cambridge (Kirby *et al.* 1985a).

The changes in the size of the deviations accords with the values of the errors (RMSE) which, after minimisation for each month, were greatest in September and March and least in February (model 1) or November (model 2) (Table 4.3). Curvilinearity also affects the estimation of 'a' in the linear regression and therefore the estimation of 'seedling emergence' ( $-a/b$ ).

In model 3 strong curvilinearity was found in the relationship between number of emerged leaves and photothermal time. It was most evident in September and October sowings and was not readily discernible in November and spring sowings (Fig. 4.4).

The curvilinearity of response inflated the RMSE for early sowings and late sowings (Table 4.3). The RMSE was lowest in November (0.45). It also affected the estimation of 'a' and 'seedling emergence' occurred at 0°Cd or at negative values of photothermal time.

Model 4 does not allow for date of sowing. It simulates the change in rate because of a slowing down in rate of leaf emergence which, together with changes in total number of leaves, produces differences in the mean rate of emergence (Migletta 1991a).

The RMSE is comparable to the other models for September and October sowings (Table 4.3), but shows a systematically increasing error as sowing becomes later (Fig. 4.5). The error also increases with higher leaf position.

In its original form where 'seedling emergence' was estimated by  $I_0$ , the errors were greater because the estimates of number of leaf primordia were not consistent with the observations.

### *Low temperature and ontogenetic effects*

Some plots of number of leaves versus thermal time show systematic deviations from a fitted line. The

trend of the deviations is different from those discussed in the previous section on curvilinearity. There is a transient slowing down of the rate of leaf emergence, which later resumes the original rate (Fig. 4.6). The effect was seen in several varieties in different experiments and in some cases the trends appeared to coincide in consecutive sowings of the same experiment.

Changes in rate of leaf emergence have been noted by other people and these have sometimes been attributed to ontogenetic changes i.e. the changes have coincided with a developmental stage such as the terminal spikelet stage. No relationship between terminal spikelet stage and change in rate were found in the data examined in this report. For example in the Hyde Hall experiment there was a clear trend with a well defined maximum negative deviation, indicating a change in rate, in twelve of the fifteen varieties measured in the October sowing. The change in rate occurred between 20 February and 5 March and the terminal spikelet stage was noted between 8 and 16 April.

When change in rate or deviations from the predicted rate were compared with temperature, the lower rate coincided with a period of low temperature, more particularly with a period when the minimum air temperature was below 0°C for most days and the lowest temperatures were around -5°C. At these temperatures there were no frost damage effects.

Changes in rate which may be due to low temperature are difficult to separate from other non-linear trends, particularly in September sowings where a more systematic curvilinear trend occurs. Similar trends have been observed by other workers who have speculated about low temperature effects (Masle *et al.* 1989).

In seasons where periods of sub-zero temperatures occur low temperature effects may have considerable distorting effects on the prediction of number of emerged leaves.

### *Depth of sowing*

The depth at which the seeds are sown affects both thermal time to seedling emergence and the rate of leaf emergence (Kirby 1993).

### *Variety*

There were significant differences in rate of leaf emergence amongst varieties. Variety coefficients are not given for models 1 and 4 and the original coefficients for models 2 and 3 are for USA or French varieties. Values for the coefficients in the rate of change function (Model 1) are given later.

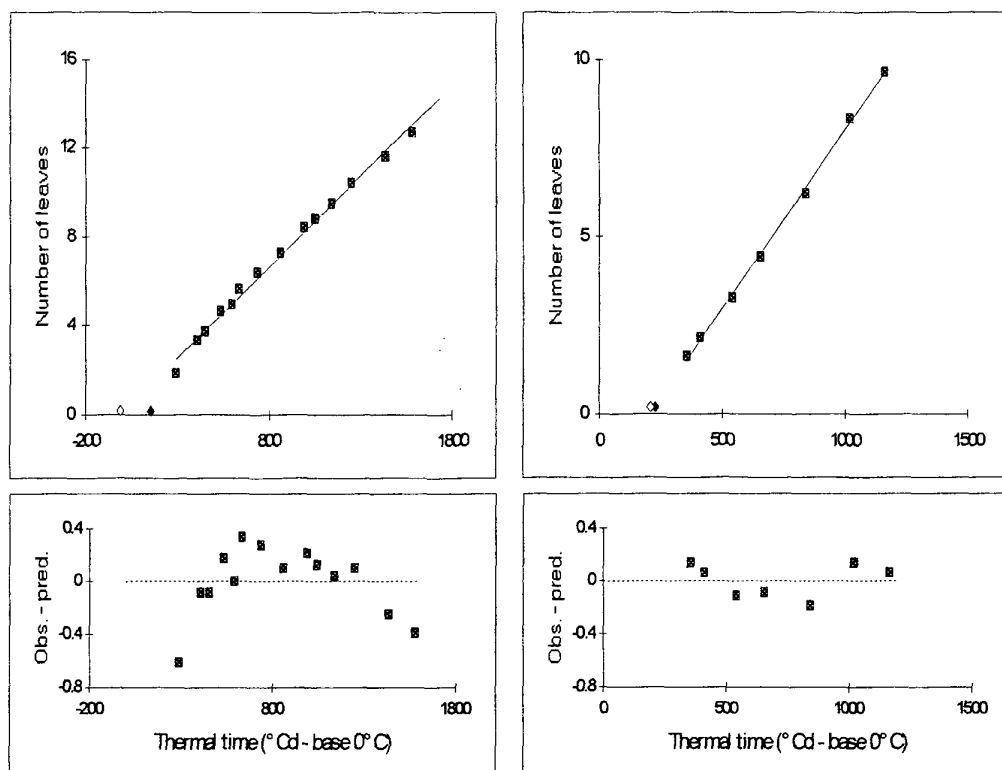


Fig. 4.3. Avalon, Anstey Hall 1991-92. Left, September sowing; right, November sowing. Upper panels, number of emerged leaves versus thermal time. The line was fitted by linear regression.  $\diamond$  'seedling emergence' ( $-a/b$ ),  $\blacklozenge$  observed seedling emergence; lower panels, observed minus predicted (by regression) number of leaves.

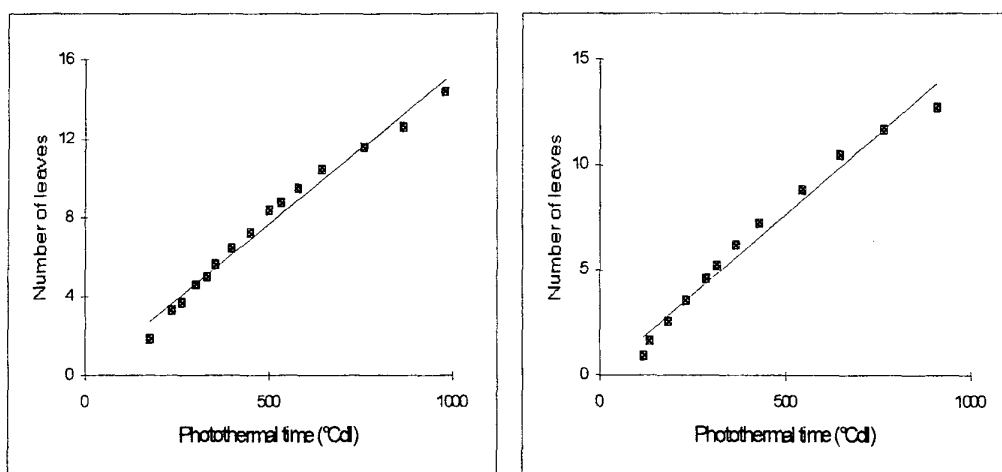


Fig. 4.4. Avalon, Anstey Hall 1991-92. Number of emerged leaves versus photothermal time (model 3). Left, September sowing; right, November sowing.

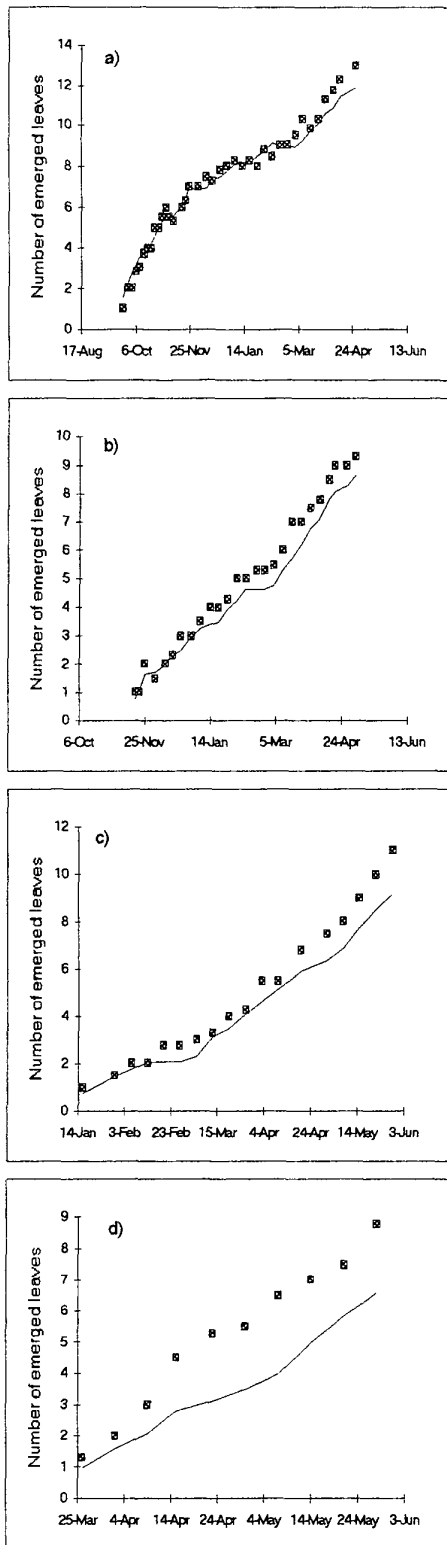


Fig. 4.5. Avalon, PBI 1981-82. Number of emerged leaves versus date; ■ observations, ----- predicted by model 4. a) September, b) October, c) November and d) March sowings.

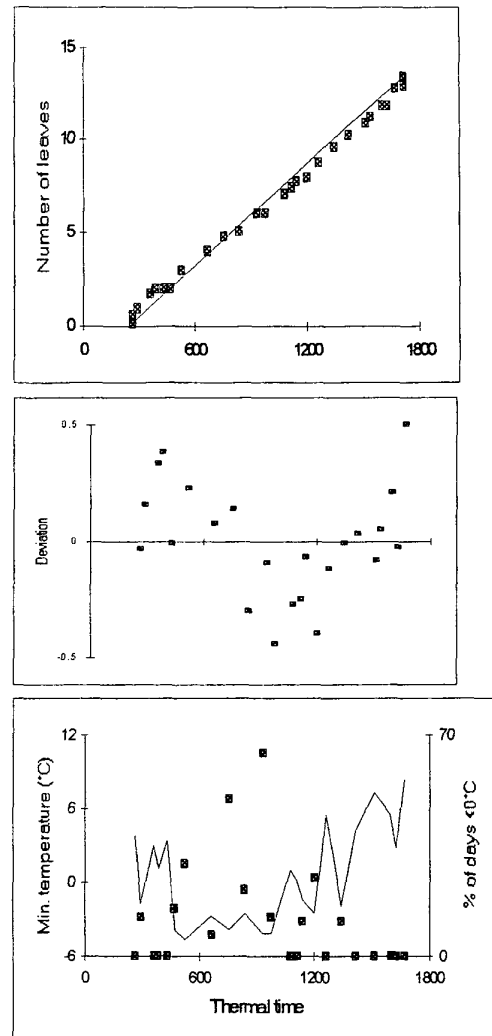


Fig. 4.6. Mercia, Hyde Hall 1987-88. Upper panel: number of emerged leaves versus thermal time. The line is eye fitted to show the trend for early and late observations; middle panel: deviations from the fitted regression line and lower panel: -----, minimum temperature and ■, percentage of days when minimum temperature was < 0° C for each period between samples.

## Factors which may affect rate of leaf emergence

Each of models 1 to 3 invokes a different environmental variable to explain changes in leaf rate with sowing date.

In formulating model 1, Baker *et al.* (1980) considered photoperiod, but rejected it partly on the grounds of a single observation of leaf rate in a small trial sown on 8 June. This rate was comparable to those of plants sown in mid-winter, although the photoperiod was almost maximal. They considered that the rate of change of daylength, which has zero values at mid-summer and mid-winter, was a more satisfactory factor, and the only one which gave an unambiguous key to the time of year. The correlation between leaf rate and rate of change of daylength was stronger than that with photoperiod, but Baker *et al.* (1980) did not rule out a secondary effect of photoperiod. They could find no supporting evidence for a physiological mechanism.

Cao & Moss (1991) found that a thermo/photo ratio was equally effective in accounting for seasonal variation in leaf emergence rate. They considered that the thermo/photo ratio was theoretically sound, although they did not adduce any evidence of a physiological mechanism.

Model 3 used photothermal time which accounted for a greater proportion of the variance than thermal time although there was still an appreciable effect of sowing date (Masle *et al.* 1989). A decline in leaf emergence rate in sowings made in April and May was considered to be due to a high temperature effect.

A plot of rate of change of daylength, thermo/photo ratio and photoperiod is shown in Fig. 4.7, top. The value of each variable is normalised from 0 to 1. In the case of rate of change of daylength the sign is reversed so that it changes in the same sense as the other variables. All show the same general response to date but rate of change of daylength (in the form plotted) and thermo/photo ratio decline to a minimum later in the season than photoperiod.

Temperature, as a factor which may affect seasonal changes in rate of leaf emergence, has not been investigated. At first sight temperature might seem to be an unlikely candidate because of rapid short term fluctuations, i.e. daily temperatures during transient warm spells in winter may be little different from those in cold spells in summer. However, if temperatures are considered over periods of 20 - 30 days (Fig. 4.7, bottom) there is a relatively smooth trend. Seasonal trends of thermo/photo ratio and temperature are similar (Fig. 4.7, bottom).

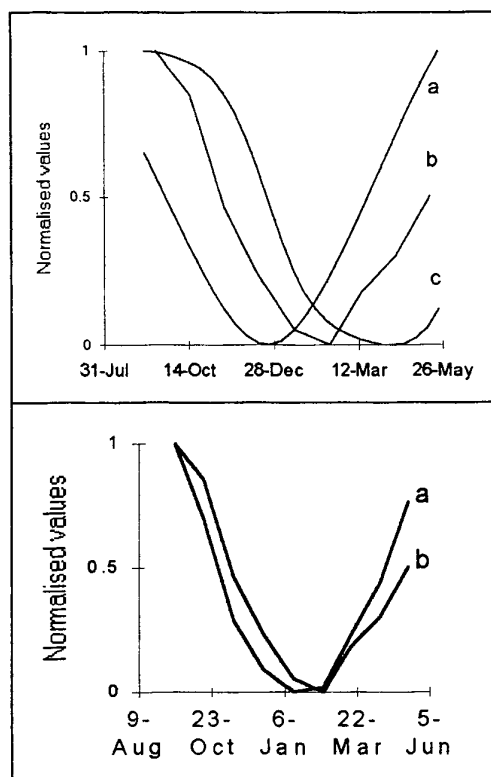


Fig. 4.7. Upper panel: a, photoperiod (civil twilight); b, thermo/photo ratio and c, rate of change of daylength; lower panel: a, mean temperature and b, thermo/photo ratio. Values have been normalised and in the case of rate of change of daylength, the sign has been changed. The data are for latitude 52°N and the temperature data are the 35 year average for NIAB, Cambridge.

### Rate of change of daylength, temperature and thermo/photo ratio as predictors of leaf emergence

The similarity of changes in the rate of change of daylength, thermo/photo ratio and temperature through the season suggested a comparison of the relationship of these variables with the rate of leaf emergence.

An analysis was made with the variety Avalon. Because of curvilinearity of the response of leaf emergence to thermal time (base temperature 0°C) in early-sown plants, the data were restricted to sets where counts had been made throughout the leaf production period. The ADAS data sets for which leaf counts did not start till February were excluded. In addition to the results from Anstey Hall 1991-92 experiments, data sets from Hyde Hall, PBI experiments (Kirby *et al.* 1985a) and the 'Avalon survey' (Porter *et al.* 1987) were used, a total of 41 cases.

Average temperatures and average minimum temperatures were calculated for a 30 day period from sowing. The thermo/photo ratio was calculated for a similar period as average daily temperature / average photoperiod.

For all variables there was a very highly significant correlation both with the rate of leaf emergence and the phyllochron. Thermo/photo ratio was more strongly correlated to rate of leaf emergence than temperature (Table 4.4).

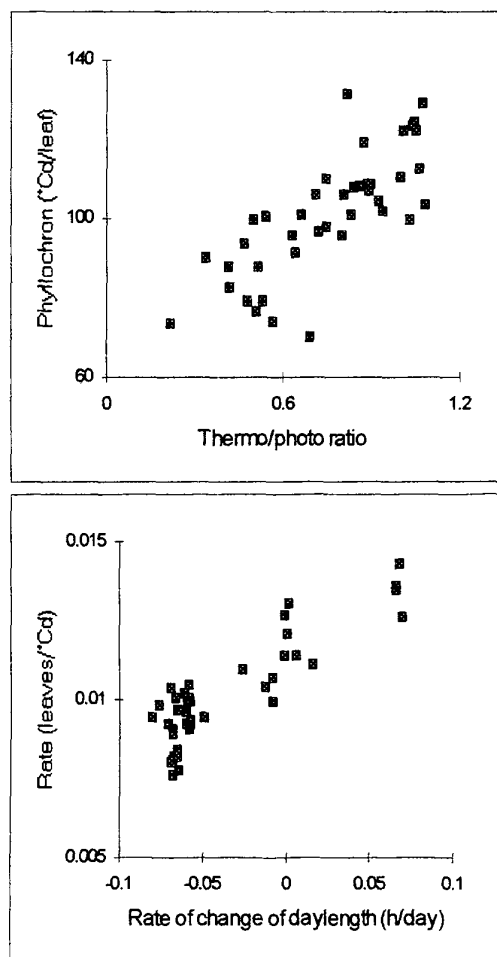


Fig. 4.8. Avalon, data from PBI, Anstey Hall, Hyde Hall and Avalon survey.

Upper panel, phyllochron versus 30 day mean thermo/photo ratio;

lower panel, rate of leaf emergence versus rate of change of daylength.

For the same data the correlation between leaf emergence and the rate of change of daylength was considerably stronger than for thermo/photo ratio (Table 4.4). Regression coefficients for the rate of change of daylength ( $D$ ) relationship were

$$b_d = 0.0114 (\pm 0.00016) + 0.0334 (\pm 0.0029) D$$

where  $b_d$  is the rate of leaf emergence.

Table 4.4. Correlation coefficients of rate of leaf emergence and phyllochron versus various environmental parameters for Avalon (for details, see text)

		Correlation coefficient
Rate versus	mean temperature	-0.701
	min. temperature	-0.688
	thermo/photo ratio	-0.755
Phyllochron versus	mean temperature	0.732
	min. temperature	0.717
	thermo/photo ratio	0.771
Rate versus	rate of change of daylength	0.879

#### Rate of change of daylength model (model 1)

This model had the lowest RMSE and the highest correlation coefficient in the analysis of Avalon data and further analysis was done on 'seedling emergence' and varietal differences.

#### 'Seedling emergence'

The precision of the model (measured by the RMSE) was improved by changing the value of 'seedling emergence'. Regressions of number of leaves on thermal time (base temperature 0°C) were fitted to the ADAS and Anstey Hall 1991-92 data and from the coefficients the values of 'seedling emergence' ( $-a_d/b_d$ ) were calculated. A plot of 'seedling emergence' versus sowing date showed that in general there was a decline as the season advanced, from about 200°Cd in October to <100°Cd in March (Fig. 4.9). A trend was not obvious in the ADAS data as all sowings were made in the autumn, but the values are distributed similarly to Anstey Hall and Hyde Hall values. Exception to the generalisation were the values for the earliest sowing at Anstey Hall and three early sown ADAS cases. These values were negative, i.e. the plants appeared to 'emerge' before they were sown. This was because ' $a_d$ ' was positive, probably a consequence of the curvilinearity of the response of number of leaves to thermal time.

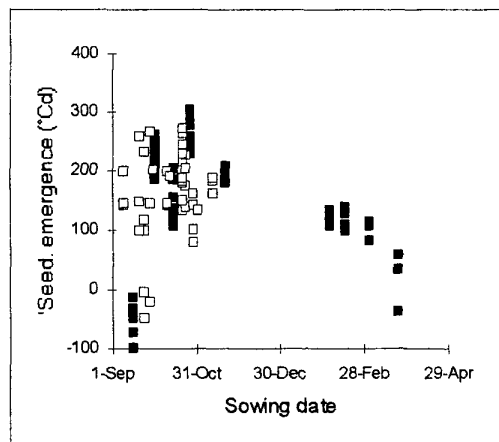


Fig. 4.9. Estimated thermal time (base temperature  $0^{\circ}\text{C}$ ) to 'seedling emergence' ( $-a/b$ ) for Anstey Hall 1991-92 (■) and ADAS (□).

Inspection of observed thermal time to seedling emergence data for Anstey Hall and Hyde Hall revealed a small but significant trend from about  $168^{\circ}\text{Cd}$  for autumn sowing to  $125^{\circ}\text{Cd}$  for spring sowings ( $r = -0.47$ ,  $P < 0.001$ ). There was no correlation between observed and calculated values ( $r = 0.211$ ,  $P > 0.5$ ). There was little difference in the mean and calculated values for seedling emergence, nor between means for ADAS and other trials, but the variation was much greater for calculated 'seedling emergence' ( $-a_d/b_d$ ).

### Rate of leaf emergence

The response of leaf emergence ( $b_d$ ) to rate of change of daylength ( $D$ ) at seedling emergence was similar to that found by Baker *et al.* (1980). Analysis of a data set restricted to varieties with several sets of data revealed very highly significant differences between varieties ( $P < 0.001$ ), but no significant variety  $\times$  rate of change of daylength interaction. That is, in the function:

$$b_d = \alpha_{\delta} + \beta_{\delta} D$$

$\alpha_{\delta}$  varied amongst varieties (Table 4.5), but  $\beta_{\delta}$  did not ( $\beta_{\delta} = 0.0359$ ).

Table 4.5. Variety values of  $\alpha_{\delta}$  in the above equation

Variety	$\alpha_{\delta}$
Avalon	0.0112
Beaver	0.0100
Hereward	0.0093
Mercia	0.0109
Riband	0.0099
Soissons	0.0104
Tonic	0.0099

### Discussion

Models 1, 2 and 3 all gave roughly comparable accuracy of prediction of number of emerged leaves, which was to be expected as they all use environmental variables which are closely correlated. Overall, model 1 had the least error and an analysis of Avalon data (above) gave stronger correlation with leaf rate than model 3 (Fig. 4.8, Table 4.4).

Model 1 predicts that leaf rate will continue to increase until the maximum rate of change of daylength ( $0.66 \text{ hd}^{-1}$  for latitude  $52^{\circ}$ ) which occurs early in April. This is consistent with results from several experiments in Cambridge (Kirby *et al.* 1985a and this report). However Masle *et al.* (1989, Fig. 3) found that the highest rate occurred in plants sown early in February and rates for plants sown in March and April were considerably lower.

The assumption of a linear response to thermal and photothermal time (base temperature  $0^{\circ}\text{C}$ ), explicit in models 1, 2 and 3 was not supportable. The curvilinearity of response biased the estimates of ' $a$ ', and therefore assumptions about thermal time of 'seedling emergence' ( $-a/b$ ), and increased the RMSE.

Such curvilinearity can result from the choice of base temperature and Kirby *et al.* (1985a) and Jones & Allen (1986), for barley, have suggested different base temperatures. A changing base temperature in response to environmental differences is consistent with changes in response of photosynthesis and other growth phenomena to changes in temperature ('acclimation'). Such changes may be due to differences in leaf structure in different temperature regimes (Ludlow 1983) and may involve differences in several metabolic processes including enzyme reactions (Lawlor & Ward 1991).

### Conclusions

The rate of change of daylength model (model 1) is the most satisfactory for the prediction of numbers of emerged leaves. The appropriate value for thermal time to 'seedling emergence' is  $180^{\circ}\text{Cd}$  and the rate determining coefficients for varieties ( $\alpha_{\delta}$ ,  $\beta_{\delta}$ ) are given in Table 4.5.

### Further research

To use the model most effectively in its present form the rate determining coefficient ( $\alpha_{\delta}$ ) should be measured for new varieties.

Further research on the physiological basis of changes in leaf rate is desirable. Sowings made over a wider range of dates, particularly from April

to July will further test the relationship with environmental factors. The relationship between sowing date and curvilinear response merits further investigation, particularly with regard to temperature and base temperature. It is doubtful if

much more insight can be gained by correlation methods applied to field sowings. Modified environment experiments (e.g. using a glasshouse or soil warming), particularly involving transfers between temperatures, may give useful information.

## 5. Final number of leaves

In Britain the final number of leaves on the main shoot varies from eight in spring wheat sown late in the spring to about 14 in winter wheat sown early in the autumn. Wheat is a determinate plant, that is, the shoot apex becomes an inflorescence (ear) and the change from vegetative to floral condition determines the number of leaves on the main shoot and tillers. The number of leaves is primarily a function of variety, daylength and exposure to low temperature (vernalisation), but it is modified by agronomic factors such as plant population, depth at which the seed is sown and mineral nutrition.

Variation in final number of leaves affects shoot apex and culm development and also tillering and root initiation (the two latter characters are not considered in this report).

The number of culm leaves varies proportionately much less than the final number of leaves and therefore the duration of ear development, measured by number of leaves emerging, is shorter in plants with few leaves than those with many. The relationships between number of leaves and stage of ear and culm development have been quantified (Kirby 1988; Section 6). In this section variation in final number of leaves is examined and two hypotheses to predict number of leaves are briefly described and their accuracy and suitability for the template are assessed.

### Variation in final number of leaves

The effect of sowing date and variety is shown in Fig. 5.1 for ADAS 1990-91, ADAS 1991-92 and for Anstey Hall 1991-92 sowing date experiments. For both ADAS groups of sites a decline in number of leaves is apparent as sowing is delayed. At Anstey Hall, the same set of varieties was sown at dates ranging from 17 September to 17 March. In this experiment the number of leaves for winter varieties declined from September to November, but increased in the February sowing; no counts of final number of leaves was possible in the March sowing before recording ceased at the end of May. The number of leaves for a spring variety, Tonic, was lower at the first than the second sowing. It then declined as sowing was progressively delayed, and in contrast to the winter varieties, fewest leaves were recorded for the March sowing. At Hyde Hall sowings were made at the beginning and end of October; the mean number of leaves declined from 12.6 to 11.0, respectively. In the spring sown experiment at Anstey Hall 1991, the number of leaves of the winter varieties increased from 10.8 to

12.9 in the 4 February and 4 March sowings

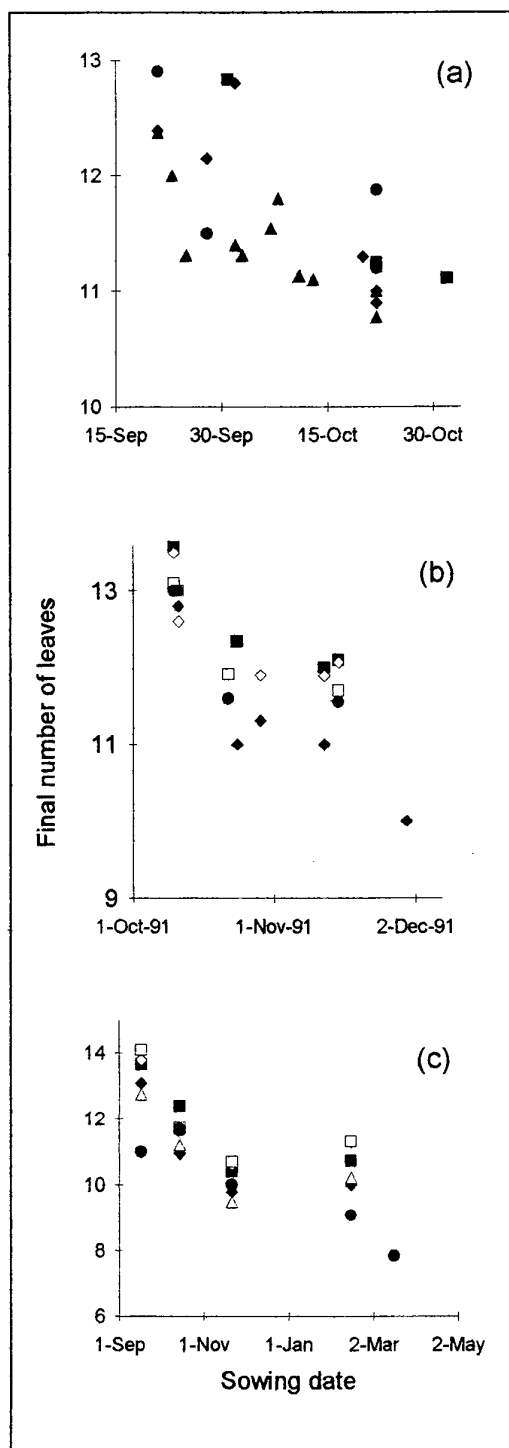


Fig. 5.1. Final number of leaves v. date of sowing. a) ADAS 1990-91; b) ADAS 1991-92; c) Anstey Hall 1991-92. Avalon, ■; Riband, ◆; Tonic, ●; Mercia, ▲; Beaver, ◇; Hereward, □; Soissons, △.



Table 5.1. Coefficients a, b, and c in the equation,  $L = a + bt + cp$ , relating number of leaves on the main shoot (L) to thermal time for full vernalisation (t) and photoperiod at full vernalisation (p). Variance is the percentage variance accounted for by regression and n is the number of entries. Number of vernalisation days for full vernalisation was 50 for winter varieties (Fv50) and 20 for spring varieties (Fv20)

Variety	n	a	b	c	variance
All winter	74	9.9	0.00593	-0.109	61
Avalon	13	9.9	0.00591	-0.075	68
Beaver	6	10.5	0.00514	-0.104	80
Mercia	8	9.3	0.00604	-0.088	69
Riband	15	9.4	0.00551	-0.075	72
Tonic	13	16.8	0.00137	-0.589	75
Kirby (1992)					
All winter	134	11.0	0.00690	-0.294	82
Avalon	34	11.2	0.00743	-0.316	80
All spring	47	13.0	0.00392	-0.333	74

respectively; no counts were possible in the 25 March sowing. For these sowings the number of leaves for Tonic was 9.1, 9.0 and 8.4 respectively.

There were highly significant differences in number of leaves amongst varieties ( $\chi^2$  test,  $P < 0.001$ ). At Anstey Hall, 1991-92, Avalon, Beaver and Hereward always had more leaves than Riband and Soissons (Fig. 5.1c) and in the spring sown experiment, 1991, Avalon had more leaves than Mercia and Riband. Differences are less clearly seen in the ADAS groups of trials, as the varieties monitored varied from site to site. However, in 1990-91 when Mercia was the most commonly grown variety, it tended to have fewest leaves (Fig. 5.1a). In ADAS 1991-92, Riband had fewest leaves amongst the set of most commonly included varieties (Fig. 5.1b).

#### Prediction of final number of leaves

Two models relating number of leaves to the environment are considered.

Kirby (1992) uses a multiple linear regression of final number of leaves on vernalisation and photoperiod. Vernalisation is estimated as thermal time to full vernalisation, calculated by a function which estimates the vernalisation effectiveness of each day. For winter varieties it is assumed that 50 vernalisation days are required (Fv<sub>50</sub>) and for spring varieties, 20 days (Fv<sub>20</sub>). (In this report thermal time is calculated using the procedure of Met. Office form 3300 and vernalisation was calculated using mean daily temperature, cf. Kirby (1992).) Photoperiod was the daylength (civil twilight) at full vernalisation.

Miglietta (1991b) uses a negative exponential function which, for spring varieties, relates final

number of leaves to photoperiod (civil twilight) at seedling emergence. The function contains a term which depends on the photoperiodic sensitivity of the variety under investigation and which can be estimated from the 'latitude at which the variety is selected'. For winter varieties the procedure is amended to allow for vernalisation effects by estimating the final number of leaves for a plant sown 'at the beginning of the coldest period of the year'. For plants sown earlier than this a term is added which depends on the number of leaves already formed at the coldest period, i.e. at full vernalisation.

The predicted number of leaves was calculated for those sites for which weather data was available using the coefficients given in Kirby (1992, Table 2, and also shown in Table 5.1) and equation 1, Miglietta (1991b). In the latter function the coefficient  $\sigma$  was set at 64, the estimate for latitude 52°.

The observed minus predicted value was calculated for each case using the Kirby (1992) function and was used to compute the root mean square error (RMSE). This was done for each group of observations and over all groups. As Avalon was the only variety for which coefficients were given, the 'All winter' coefficients were used for winter varieties and 'All spring' for Tonic (the only spring variety). When the RMSE for winter varieties was computed over all sowings (i.e. both autumn and spring), it was higher than for winter sowings alone (Table 5.2). The highest RMSE (1.81) occurred in the Anstey Hall 1991 experiment, in which sowings were made from early in February to 25 March.

Table 5.2. Root mean square error (RMSE) for each group of sites and the overall RMSE for winter varieties and for a spring variety (Tonic). Predicted values were calculated using the 'All winter' and 'All spring' equations for winter and spring groups (Kirby 1992; see Table 5.1)

	All sowings winter vars		Winter sowings winter vars		All sowings spring vars (Tonic)	
	RMSE	count	RMSE	count	RMSE	count
Anstey Hall 91-92	0.77	20	0.57	15	0.83	5
Anstey Hall 91	1.81	6			0.36	3
Hyde Hall 87-88	0.65	30	0.64	28		
ADAS 90-91	0.46	11	0.46	11	1.28	4
ADAS 91-92	0.66	11	0.66	11	1.10	1
Overall RMSE	0.85		0.65		0.95	

Observed minus predicted values were also calculated using the Miglietta (1991b) function for the spring variety, Tonic, and for several winter varieties in a late (Hyde Hall, 21 October) sowings only. The latter case was that which most nearly fitted the criterion of having been sown at 'the coldest period of the year'. Generally the RMSE was higher than for the Kirby function (Table 5.3) and the errors (observation minus prediction) were substantially greater for sowings made at the beginning or end of the normal sowing season when there was a long period was required for full vernalisation.

#### Estimation of regression coefficients

The coefficients  $a$ ,  $b$ , and  $c$  in the regression of final number of leaves ( $L$ ) on thermal time to full vernalisation ( $t$ ) and photoperiod at full vernalisation ( $p$ ) in the equation:

$$L = a + bt + cp$$

were estimated from the data of ADAS 1990-91 and 1991-92, Hyde Hall and Anstey Hall 1991 and 1991-92 (Table 5.1)

#### Discussion

The 'all winter' and 'all spring' regression equations (Kirby 1992; Table 5.1), used to predict final number of leaves, were based on data from Aquila,

Avalon, Huntsman and Norman (winter varieties) and Fenman, Highbury and Wembley (an alternative and spring varieties, respectively). Amongst these, Avalon was the only variety common with those considered in this report. For winter varieties the average error was 0.6 and for spring variety, Tonic, it was 0.95.

This was generally better than the predictions made by the Miglietta (1991b) function, which was also more complicated to use. However, some aspects of the Miglietta (1991b) function may be more relevant than those of the Kirby (1992) function. The negative exponential used to estimate the response to photoperiod follows the trend of number of leaves on photoperiod better than a linear function. However, the estimation of the effect of vernalisation from number of leaves 'at the beginning of the coldest period of the year' needs defining more precisely. In addition the estimation of a coefficient on the basis of the latitude of the breeder may not be appropriate. Sources of variation are often sought from material from other latitudes and there is often considerable variation in response to photoperiod within a group of varieties from the one breeder. Further investigation of the function and calibration, rather than estimation via latitude, of the coefficients might considerably improve the accuracy of prediction.

Unlike the experiments used by Kirby to estimate the coefficients in the regression function, the trials considered in this report were relatively unstructured. There was no consistent set of

Table 5.3. Root mean square errors computed by different functions for selected groups

Function	Hyde Hall (winter vars.)	Anstey Hall 91 (Tonic)	Anstey Hall 91-92 (Tonic)
Kirby (1992)	0.50	0.36	0.83
Miglietta (1991b)	0.62	0.21	1.73

varieties over all sites nor were the sowing dates planned to encompass the whole range of sowing environments (i.e. from early in September until late in January or early in February; cf. NIAB latest safe sowing date). In all trials, except those at Anstey Hall, the great preponderance of sowings were made in October. The way in which the data was collected from the ADAS sites may also have resulted in greater errors in estimation of final number of leaves. No observations were made until February, so that there was no experience of leaf death or non-development of tillers to help with counts of number of leaves. (The counts at Hyde Hall and Anstey Hall were comparable to those described in Kirby (1992), where there was continuous monitoring and leaves were ringed on some plants.)

The difference in technique may be seen in the comparison of the two sets of equations (Table 5.1). The estimates of 'variance accounted for' from the trials considered in this report were lower than those in Kirby (1992). The 'a' term was also lower, perhaps reflecting the effect of plant population, as the experiments in Kirby (1992) were all hand sown on a precise grid, whereas the trials reported here were drilled at a higher seed rate and sometimes at greater than normal depth. The varietal differences in the 'a' term were consistent with the differences seen in the plots of number of leaves versus sowing date (Fig. 5.1). Both the 'b' and 'c' terms for winter varieties were lower than those of Kirby (1992). This may indicate that the more recently released varieties have a lower response to vernalisation and photoperiod than varieties such as Norman and Huntsman, or it may be an effect of the distribution of the sowing dates of the trials.

The coefficients for Tonic appear to show that this variety has a weaker response to vernalisation and a stronger response to photoperiod than Highbury or Wembley; however the data do indicate that there is a significant response to vernalisation.

## Conclusions

Final number of leaves responds strongly to date of sowing and there are differences among varieties. Both factors must be allowed for in prediction functions. The multiple linear regression function proposed by Kirby (1992) gave an acceptable estimate. The regression coefficients listed in Table 5.1 are suggested for use in the template (Appendix table). These are based on drilled plots, sown at the same time as most farm crops.

## Further research

Further research on response of final number of leaves to both vernalisation and photoperiod would help to improve predictions. As new varieties appear some calibration of their response may be necessary.

The whole phenomenon of vernalisation in cereals, an important character affecting crop management, has been much neglected in recent years. In particular the function relating temperature to vernalisation effectiveness is based on a few, old experiments (Chujo 1966; Hänsel 1953; Trione & Metzger 1970). This data has been reworked to give a number of minor variants of a function (Weir *et al.* 1984; Reinink *et al.* 1986; Kirby 1992). A new look at the response of vernalisation to temperature is overdue.

## 6. Apex development

Throughout the life cycle of the plant the shoot apex changes in form. Some of the stages reflect a physiological status which may be significant for crop management.

At first the shoot apex initiates leaf primordia (a description of shoot apex development, illustrated with photographs and diagrams may be found in Kirby & Appleyard 1987). After a number of leaf primordia have been formed (Section 4) about 20 spikelet primordia are initiated. The end of the spikelet initiation phase (ear formation phase) is marked by the formation of a characteristic 'terminal spikelet'. The initiation of leaves and spikelets is closely correlated with leaf emergence (Fig. 6.1) and functions describing the relationship between number of primordia, emerged leaves and final number of leaves are given in Kirby (1990).

The apex (ear) continues to grow and develop after the terminal spikelet has formed and various stages can be recognised as the florets mature. Ear development culminates in anthesis, after which grain development and growth ensues.

Some apex stages have particular significance in relation to such agronomic factors as herbicide application or nitrogen nutrition. In this context, the stages which have been most closely investigated are the double ridge and terminal spikelet stages (Kirby & Appleyard 1987, Figs. 5.18 & 5.26).

Apex stage may be monitored with reference to primordium initiation. As the number of primordia increases, the apex changes in form e.g. the double ridge stage occurs when about half the spikelet primordia have been formed and the terminal spikelet stage is observed when spikelet primordium initiation is complete (Fig. 6.1). Therefore, stage of apex development can be predicted using the functions described in Kirby (1990).

An alternative method depends on the direct relationship between number of emerged leaves, final number of leaves and apex stage (Kirby *et al.* 1985b and below).

The trials data examined in this report did not have counts of number of primordia, but number of emerged and final number of leaves and apex stage were recorded for several sites. Therefore the latter method, rather than the one based on primordium initiation rates was used to investigate prediction functions for double ridge and terminal spikelet stages.

### Double ridge stage

The relationship between number of emerged leaves at the double ridge stage and final number of leaves is shown in Fig. 6.2 using data from Anstey Hall 1991-92. In this trial, sowings were made from 17 September to 17 March and consequently there was a wide range of final number of leaves.

The mean number of emerged leaves was calculated over all plants at the double ridge stage. It has a relatively long duration of about one or more phyllochrons, depending on sowing date, so that the mean estimates the number of emerged leaves at mid stage, rather than at the onset of the double ridge stage. The graph shows a very highly significant,

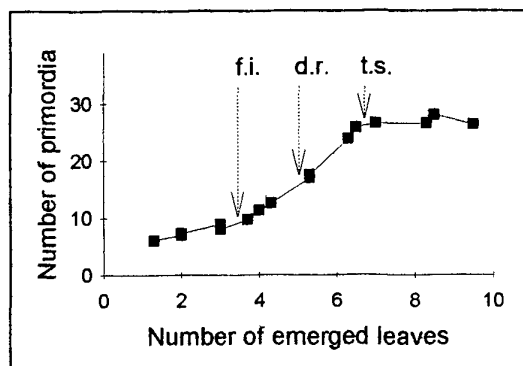


Fig. 6.1. Diagram to show the co-ordination between leaf emergence, primordium initiation, and stage of shoot apex development. f.i., floral initiation; d.r., double ridge stage; t.s. terminal spikelet stage.

linear response (Fig. 6.2 and Table 6.1).

The response was very similar to that found by Kirby *et al.* (1985b) for W1+W2 and W3, but the line for W1+W2 lies about half a leaf above the fitted lines for Anstey Hall and W3 (Fig. 6.2a and Table 6.1).

The regressions for ADAS 1990-91 and 1991-92 were also very highly significant, with coefficients similar to Anstey Hall 1991-92 (Table 6.1). In the case of the Avalon survey data (Fig. 6.2b and Table 6.1) the response was similar, but the position of the fitted line was about one leaf below the Anstey Hall fitted line. The consistency of response may be also judged from Western Australian data (Fig. 6.2c). This was collected over several varieties, environments (some severely stressed) and by a number of researchers (E.J.M. Kirby, unpublished data).

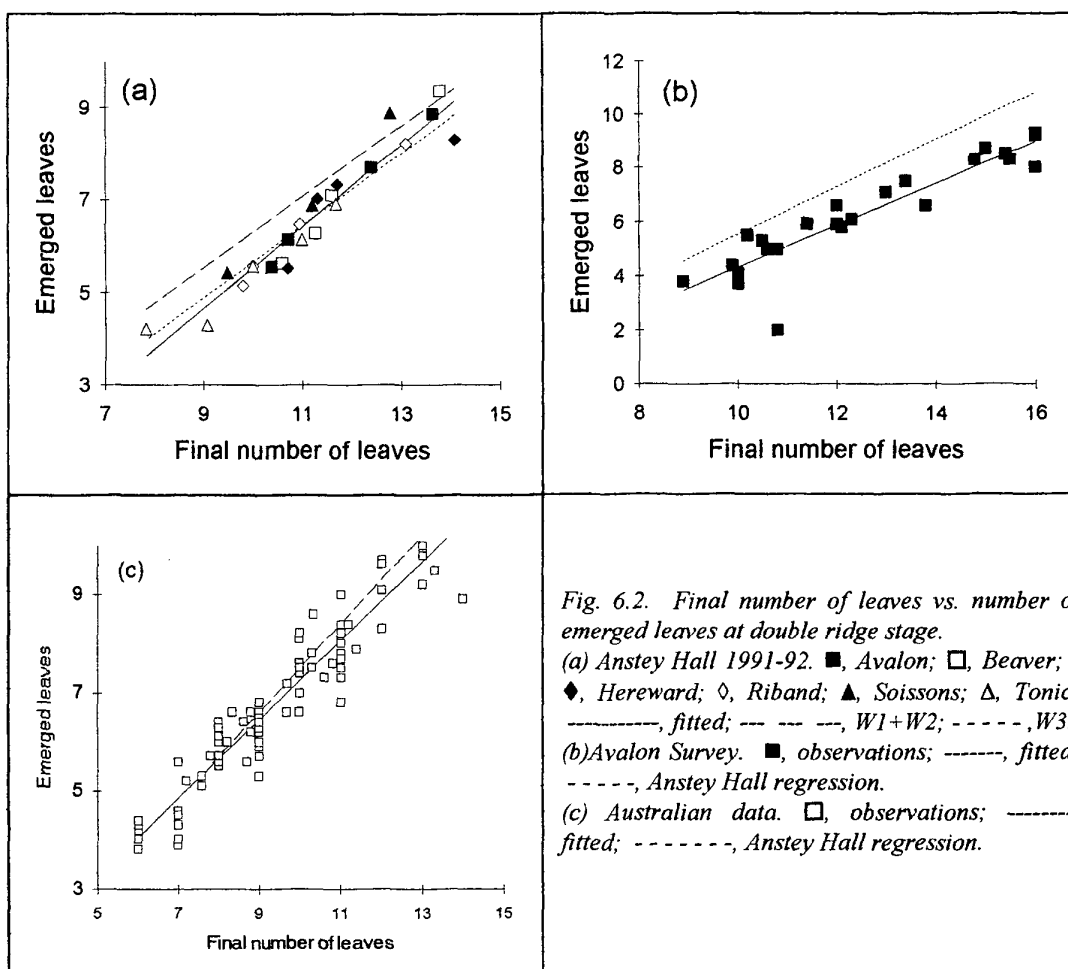


Fig. 6.2. Final number of leaves vs. number of emerged leaves at double ridge stage.

(a) Anstey Hall 1991-92. ■, Avalon; □, Beaver; ◆, Hereward; ◇, Riband; ▲, Soissons; △, Tonic; —, fitted; ---,  $W1+W2$ ; ···,  $W3$ .  
 (b) Avalon Survey. ■, observations; —, fitted; ---, Anstey Hall regression.  
 (c) Australian data. □, observations; —, fitted; ---, Anstey Hall regression.

There were rather few data for each variety statistically to examine variety differences, but Fig. 6.2a indicates that any such effect is likely to be small. The ADAS trials were not structured in such a way that possible variety differences could be investigated.

#### Prediction errors

The magnitude of errors of prediction were examined using root mean square error (RMSE).

Table 6.1. Regression statistics of number of emerged leaves at double ridge stage ( $L$ ) on final number of leaves ( $f$ ) in the equation  $L = a + bf$  for various experiments.  $a$  and  $b$  are regression coefficients; Var. is percentage variance accounted for;  $F$  is the variance ratio and  $df$  is degrees of freedom

	$a$	$b$	Var.	$F$	$df$
Anstey Hall	-3.27	0.881	92	247	22
ADAS 1990-91	-2.20	0.744	73	58	22
ADAS 1991-92	-3.71	0.879	89	217	26
* $W1+W2$	-1.35	0.765			
* $W3$	-2.12	0.778			
#Avalon Survey	-3.42	0.775	84	115	22
~Australia	-2.84	0.845	90	1089	116

\* Kirby *et al.* (1985b); # Porter *et al.* (1987); ~ E.J.M. Kirby (unpublished data).

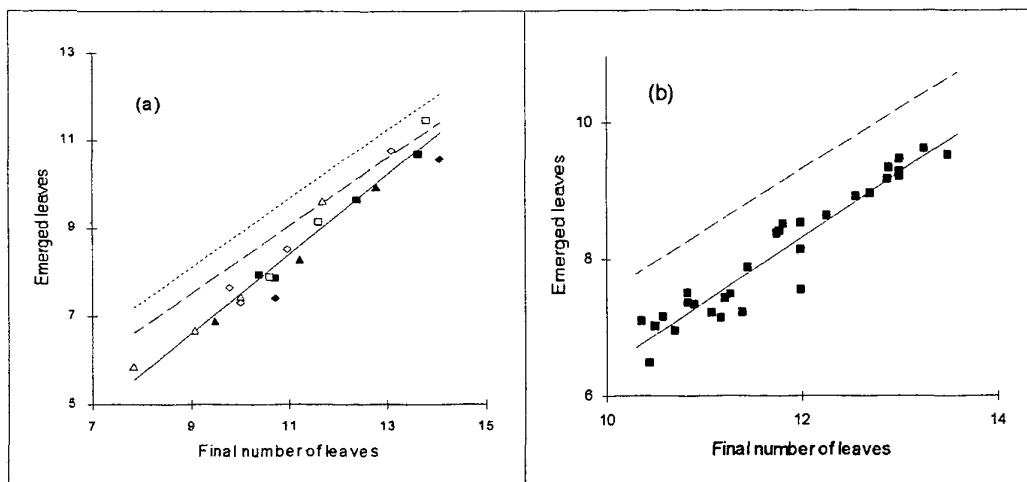


Fig. 6.3. Final number of leaves versus number of emerged leaves at terminal spikelet stage.

(a) Anstey Hall 1991-92. Symbols are the same as Fig. 6.2.

(b) Hyde Hall. ■, observations; -----, fitted; ----, Anstey Hall regression.

very highly significant regression (Table 6.2 and Fig. 6.3) and the variance accounted for was generally greater than for the double ridge stage. As in the case of the double ridge stage, the response (slope) was similar, but the fitted line was displaced relative to the fitted line for Anstey Hall 1991-92 in the case of Avalon Survey, Hyde Hall (Fig. 6.3b), and W1+W2 and W3 (Kirby *et al.* 1985b).

#### Prediction errors

The function calculated for Anstey Hall (Table 6.2) predicted the number of emerged leaves for ADAS 1990-91 with an RMSE of 0.33 and for ADAS 1991-92 with an RMSE of 0.46

#### Discussion

For both the double ridge and the terminal spikelet stage a very highly significant linear relationship

was found between emerged leaves at the chosen stage and final number of leaves (Tables 6.1 and 6.2). The differences amongst the coefficients were due in part to changes in the definition of stages and changes in the way that emerged leaves were counted.

For both stages, definitions have become more rigorous with experience of shoot apex development. For example, as the double ridge stage progresses the axillary, spikelet ridge grows more quickly than the lower, leaf ridge and towards the end of the stage the leaf ridge cannot be seen but glumes are not yet formed. A category of 'late double ridge' is now used more precisely to define this stage.

The technique of recording emerged leaves has also changed and the method described by Haun (1973) is now in general use. In the earlier groups of trials (W1+W2, W3, Avalon Survey and Hyde Hall) number of emerged leaves was counted as either leaves where the ligule was visible or total

Table 6.2. Regression statistics of number of emerged leaves at terminal spikelet stage (L) on final number of leaves (f) in the equation  $L = a + bf$  for various experiments. *a* and *b* are regression coefficients; Var. is percentage variance accounted for; *F* is the variance ratio and *df* is degrees of freedom

	<i>a</i>	<i>b</i>	Var.	<i>F</i>	<i>df</i>
Anstey Hall	-1.49	0.900	95	338	18
ADAS 1990-91	-1.14	0.858	74	61	22
ADAS 1991-92	-1.64	0.880	89	196	25
*W1+W2	0.634	0.765			
*W3	1.11	0.778			
#Avalon Survey	-2.08	0.860	92	268	21
Hyde Hall	-3.12	0.952	92	320	28
~Australia	-0.77	0.803	90	877	96

\* Kirby *et al.* (1985b); # Porter *et al.* (1987); ~ E.J.M. Kirby (unpublished data).

visible leaves, that is leaves which were not fully emerged were counted as whole leaves rather than fractions of a leaf. The data for Anstey Hall 1991-92, ADAS 1990-91 and 1991-92 were all gathered using the Haun (1973) method and are therefore consistent. The regression equations were not significantly different and the equations used in the template are based on regression over all these groups of sites.

### Conclusions

There is a very highly significant linear relationship between number of emerged leaves at a stage and the final number of leaves on the shoot, which appears to hold over a wide range of environments and varieties. The calculated functions predicted number of emerged leaves at a

stage (in different trials) with an RMSE of 0.5 leaves or less.

The equations used in the template are based on the data for Anstey Hall 1991-92, ADAS 1990-91 and 1991-92 and are, for the double ridge stage:

$$L = -2.82 + 0.814f$$

(percentage variance accounted for, 85; variance ratio, 412; 74 degrees of freedom)  
and for the terminal spikelet stage:

$$L = -1.04 + 0.845f$$

(percentage variance accounted for, 90; variance ratio, 568; 69 degrees of freedom)

where  $L$  is the number of emerged leaves, counted by the Haun method and  $f$  is the final number of leaves.

## 7. Stem elongation

Growth of the flowering stem is accomplished by the elongation, in sequence, of a number of internodes. The start of stem elongation and the number of elongated internodes is codified in the Zadoks growth stage scale, Section 3 (Zadoks *et al.* (1974), as refined by Tottman (1987)). Many important crop management decisions are made by reference to Zadoks stages 3 (30, 31, 32; 37 and 39).

The wheat main shoot forms a variable number of leaves (Section 5). Each leaf is associated with an axillary (tiller) bud, a node and internode (Kirby & Appleyard 1987). In the case of the lower leaves the buds may grow to form tillers, and the internodes remain very short. When ear initiation is in progress, the buds in the axil of the stem leaves are suppressed (tillering stops) and the internodes elongate. After the first basal internode starts growth the remaining, distal internodes grow in sequence.

Because Zadoks stage 3 (excepting 37 and 39 which refer to the flag leaf) are based on the number of elongated internodes, a study of the rules which govern the relationship between internode elongation and leaf emergence is important to the formulation of a prediction function. In this section the process of stem elongation is examined and a function to predict Zadoks stages 3 from the number of emerged leaves is derived.

### Methods

#### *Sampling and measurements*

Internode lengths were measured on Anstey Hall 1991-92 and ADAS 1990, 1991 and 1992 groups of trials. At each sampling 10 plants were dug up, avoiding edge rows, and measurements were made on five modal plants selected on the basis of tiller number and size. On each plant the number of emerged leaves (see below) was counted, shoot apex stage was scored (Kirby & Appleyard 1987) and the length of all internodes longer than 3 mm was measured. Zadoks principal growth stage 3 was recorded as follows: stage 30 was scored when the length of the stem from the plane of insertion of the roots to the tip of the ear was at least 10 mm (épi à 1 cm, Couvreur *et al.* 1980). Subsequent stages were scored as  $3n$  where  $n$  is the number of elongated internodes; an elongated internode was defined as 10 mm or more for the first internode and 20 mm or more for the more distal ones. This is exactly equivalent to the definition of Tottman

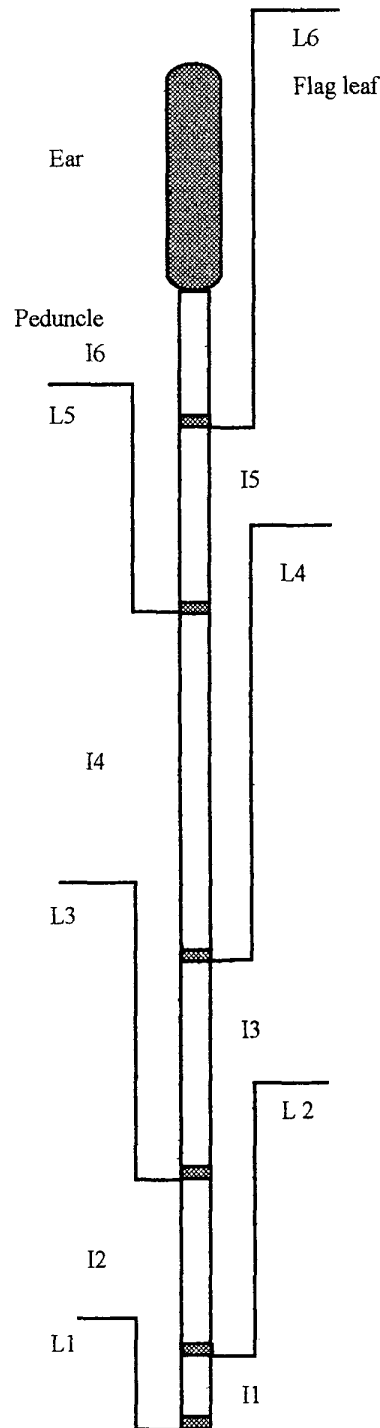


Fig. 7.1. Diagram to show the nomenclature used to count culm leaves (culm decimal system - CDS). L1 to 6 are culm leaves and I1 to 6 are elongated internodes.



(1987), which is couched in terms of 'detectable nodes', following Zadoks *et al.* (1974).

#### Leaf counts

In the analyses in this paper, internode elongation or Zadoks stage is related to emerged leaves. The method of counting from the first, most basal leaf used in Section 3 was not appropriate because the variable number of leaves with unelongated internodes would give different relationships depending on the final number of leaves. An alternative method, to number leaves from the flag leaf down (F (flag), F-1, etc. or 1, 2, 3 etc.) is not suited to metrical analysis, using fractional parts of an emerging leaf. Therefore, leaves were numbered from the lowermost elongated internode distally (Fig. 7.1). This accorded with the method of measurement where leaves were stripped from the shoot until an elongated internode (> 3 mm) was exposed and then the number of emerged and unemerged leaves was noted. The number of emerged leaves was recorded using a decimal scoring system, following Haun (1973). These leaves on the 'flowering stem' or 'culm' are referred to as culm leaves and the system as a culm decimal score (CDS). In some experiments only 'leaves to emerge' were counted; this was transformed to CDS making the assumption that there were six culm leaves (see later).

## Results

#### Internode elongation and leaf emergence

Length of internodes when plotted against number of emerged culm leaves gave typical sigmoid curves (Fig. 7.2). An internode started to elongate (> 3 mm) c. 1.5 phyllochrons before its associated leaf (the leaf inserted at the distal end of the internode) was fully emerged. The grand (main) period of growth started as the leaf emerged fully and was maximal when the next, distal leaf was about half emerged. Elongation was more or less complete when this leaf was fully emerged. The interval between the growth curves of successive internodes measured, for example, between inflexion points

was one phyllochron. There was no difference in the relationship between emerged culm leaves and internode length among sowings at Anstey Hall 1991-92 (Fig. 7.2a) nor between Anstey Hall 1991-92 and a glasshouse experiment (Fig. 7.2b), except that the internodes in the latter were shorter at maturity.

Comparison of Anstey Hall 1991-92 and ADAS growth curves revealed a difference in the course of internode growth. Before the associated leaf was fully emerged some internodes in ADAS groups were longer (e.g. ADAS 1992, internode 3 (Fig. 7.3c), the internode mean lengths for CDS >2 and <4 were significantly different ( $P < 0.0001$ )). At the beginning of rapid elongation they were of similar length and subsequently grew more slowly than the internodes from Anstey Hall 1991-92. The difference was greatest for internode 2 and was not apparent for internode 4.

#### Zadoks score and leaf emergence

There was a close relationship between Zadoks score and number of emerged culm leaves (Fig. 7.4). (Note that Zadoks score took only integer values and that the fractional mean scores were derived from different proportions of each Zadoks class.) Linear regression of Zadoks score on number of emerged culm leaves was in all cases very highly significant (Table 7.1). There was no significant difference between sowing dates or cultivars for Anstey Hall 1991-92; factor effects were not tested within ADAS groups. The data from the first year of sampling, ADAS 1989-90, was more variable and sampling finished at an earlier growth stage than in subsequent years. Excluding ADAS 1989-90, there were no differences between groups (ADAS 1990-91, 1991-92, Anstey Hall 1991-92: variance ratio for groups = 0.72 and for emerged culm leaves x groups = 0.16). The overall regression was:

$$Z = 28.2 (\pm 0.046) + 0.981 (\pm 0.0113) \text{ CDS}$$

(variance accounted for = 75%) where Z is the Zadoks growth stage and CDS is the number of emerged culm leaves.

Table 7.1. Coefficients *a* and *b* and percentage variance accounted for (Var %) for linear regression of Zadoks score on number of emerged leaves (CDS) for each group. Note that the 'a' values are only applicable to the regression equation and do not represent a Zadoks stage 2 score. Standard errors for 'a' and 'b' were similar among groups. The value for 'a' was about 0.03 and for 'b', 0.05

Group	<i>a</i>	<i>b</i>	Var %
ADAS 1989-90	28.7	0.782	0.446
ADAS 1990-91	28.2	0.978	0.706
ADAS 1991-92	28.4	0.912	0.757
Anstey Hall 1991-92	28.2	0.989	0.790

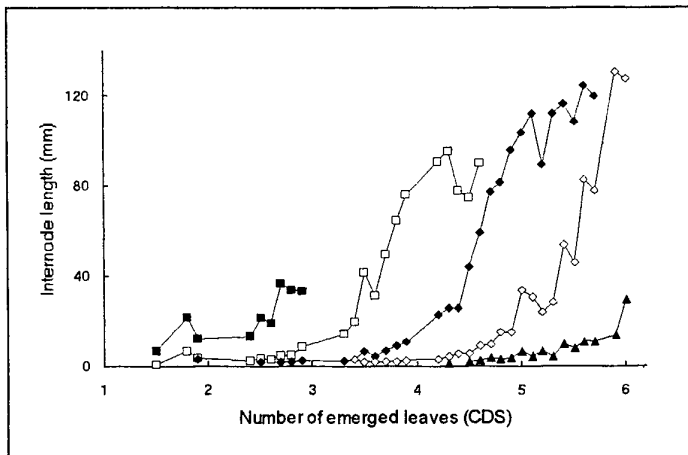


Fig. 7.2. Internode length vs. number of emerged culm leaves at Anstey Hall 1991-92. Internode 1, ■; 2, □; 3, ◆; 4, ◇; 5, ▲.

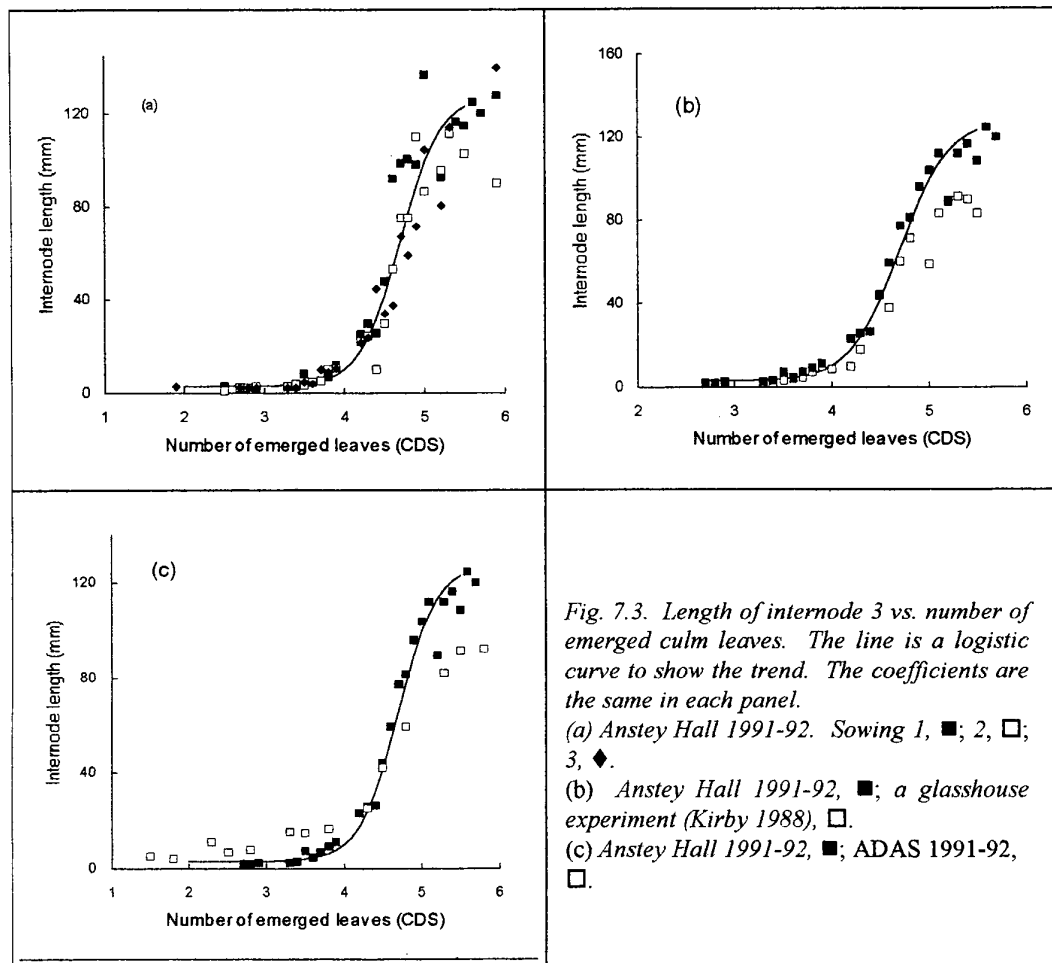


Fig. 7.3. Length of internode 3 vs. number of emerged culm leaves. The line is a logistic curve to show the trend. The coefficients are the same in each panel.

(a) Anstey Hall 1991-92. Sowing 1, ■; 2, □; 3, ◆.

(b) Anstey Hall 1991-92, ■; a glasshouse experiment (Kirby 1988), □.

(c) Anstey Hall 1991-92, ■; ADAS 1991-92, □.

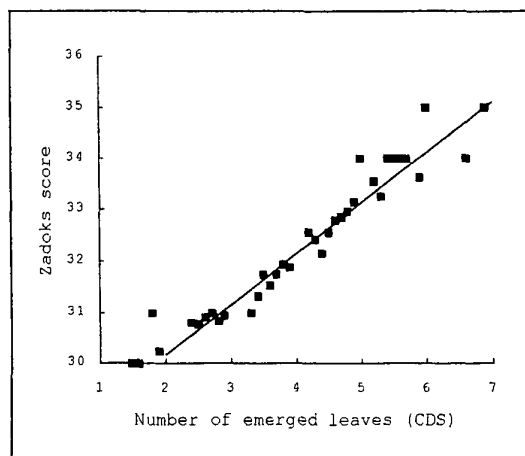


Fig. 7.4. Zadoks growth stage score vs. number of emerged culm leaves. The line was fitted by regression.

The greatest deviation from the linear trend was seen for Zadoks 30; this was related to the high variability of the length of the first elongated internode. When the proportion of plants at a particular Zadoks stage was examined in relation to the number of emerged culm leaves it was found that an internode generally did not rate a score before the associated leaf was fully emerged and almost all plants had completed a further stage by the time that the next distal leaf was fully emerged. For example, for Anstey Hall 1991-92 wheat, < 2% of the plants with 3 - 3.9 leaves received a Zadoks 33 score and only a few plants with more than five leaves had not achieved or

passed stage 33 (Fig. 7.5). Generally about half the plants had achieved a Zadoks score when the leaf above the associated leaf was half emerged (e.g. CDS 4.5 in Fig. 7.5).

#### Internode final length

The length of internode 1 was more variable than that of internode 2 and 3 (Table 7.2). In most trials observations ceased before it was certain that more distal internodes had completed elongation, but these also appeared to have lower coefficients of variation.

The frequency distribution curves for internode 1 (Fig. 7.6) showed that for ADAS 1992 plants the highest frequency of internode length was < 10 mm and in all groups the distributions were strongly skewed to the shorter internode categories.

For Anstey Hall 1991-92 internode 1 final length declined with increasing number of culm leaves. Sowing date did not affect internode 1 length at Anstey Hall 1991-92. There was no difference in

Table 7.2. Mean length of internodes 1 and 2 (mm), standard error of the mean (S.E.) and coefficient of variation (CV, %)

	ADAS			Anstey
	1990	1991	1992	Hall
<b>Internode 1</b>				
Mean	16.6	24.1	21.7	29.9
S.E.	0.5	0.47	0.54	0.97
CV	52	57	65	59
<b>Internode 2</b>				
Mean	44.5	67.7	64.7	90.3
S.E.	1.48	1.08	0.97	2.00
CV	27	36	30	24

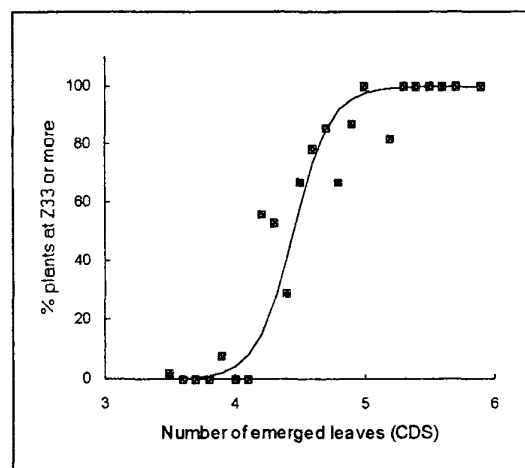


Fig. 7.5. Zadoks growth stage 33 or more vs. number of emerged culm leaves for Anstey Hall 1991-92. The line is a logistic curve to show the trend.

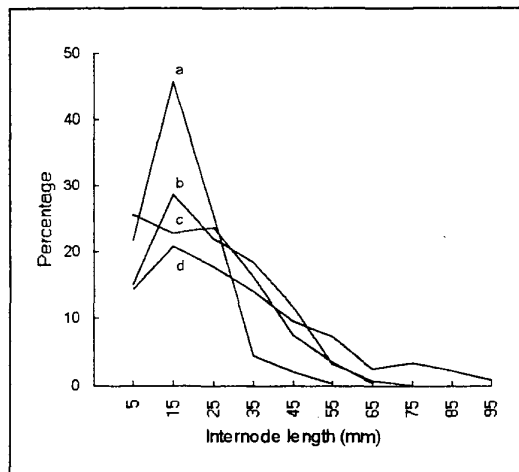


Fig. 7.6. Frequency distribution (%) of internode length. Categories are 0 to 9 (5), 10 to 19 (10) and so on. ADAS 1989-90, a; 1990-91, b; 1991-92, c; Anstey Hall 1991-92, d.

internode 1 length or variability between 'early' and 'late' sowing (plots sown before or after the middle of October) in the three years of ADAS data.

Table 7.3. Mean length (mm) of internode 1 and coefficient of variation (CV %) for culms with 5, 6 or 7 leaves at Cambridge

Number of culm leaves	Mean	CV
5	42.2	52
6	32.0	52
7	17.7	57

The frequency distributions for internode 2 and the more distal internodes were normal (Fig. 7.7).

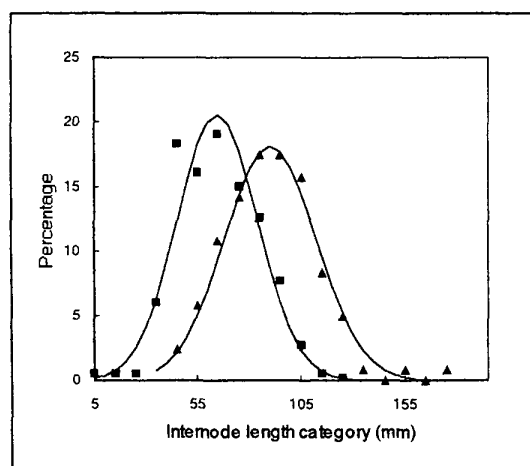


Fig. 7.7. Frequency distribution (%) of length of internode 2. Categories coded as Fig. 7.6. ADAS 1991-92, observed values, ■; normal distribution, left. Cambridge 1991-92, observed values, ▲; normal distribution, right.

#### Number of leaves on the culm

In the Anstey Hall 1991-92 trial the number of

Table 7.4. Mean number of culm leaves for Anstey Hall 1991-92 and for another sowing date experiment at Anstey Hall, spring 1991

	Number of leaves
Anstey Hall 1991-92	
17 September	6.2
15 October	6.1
21 November	5.8
3 February	
Anstey Hall 1991	
7 February	5.2
7 March	5.1

culm leaves varied between five and seven with a mode was six culm leaves. There was a significant decline ( $\chi^2 = 86$ , 9 d.f.,  $P < 0.005$ ) with sowing date in the number of culm leaves (Table 7.5). There were significant differences between cultivars.

A reduction in the number of culm leaves is consistent with data from a spring-sown sowing date experiment at Anstey Hall, 1991. The mean number of leaves was 5.1 and although there was no significant difference between sowings in this experiment there were fewer than Anstey Hall 1991-92 (Table 7.4) the mean for which was 6.0.

#### Relationship to ear development

In each of the of wheat groups, Zadoks growth stage 30 was first detected at the double ridge stage and more than 50 % of plants had attained this stage by the glume or lemma stages. Virtually all plants were at Zadoks growth stage 30 by floret stage (Table 7.6). Fifty per cent or more of plants at the lemma or floret stage had an internode 10 mm or more long (Table 7.6).

When classified by sowing date there was some indication that a Zadoks stage occurred at a more advanced apex stage in late sowings. At Anstey

Table 7.5. Percentage of plants at or past Zadoks growth stage 30 or 31 at each apex stage for each group. Bold figures show when 50% or more had achieved a stage

Apex stage	1989-90	ADAS 1990-91	1991-92	Anstey Hall 1991-92
Zadoks 30 or greater				
Double ridge	17	5	1	6
Glume	<b>74</b>	34	33	<b>54</b>
Lemma	94	<b>80</b>	<b>88</b>	43
Floret	100	99	100	92
Terminal spikelet	100	100	100	99
Zadoks 31 or greater				
Double ridge	2	1	0	1
Glume	24	5	6	21
Lemma	<b>54</b>	34	37	14
Floret	87	<b>75</b>	<b>77</b>	<b>68</b>
Terminal spikelet	95	97	94	99

Table 7.6. Percentage of plants at or past Zadoks growth stage 30 or 31 at each apex stage for Anstey Hall 1991-92 sowing dates. Bold figures show when 50% or more had achieved a stage and blank cells indicate no plants were found at that stage

Apex stage	Sowing date				
	17 Sep	15 Oct	21 Nov	3 Feb	16 Mar
Zadoks 30					
Double ridge	7	5	3	12	0
Glume	<b>90</b>	<b>64</b>	38	24	0
Lemma	67		<b>56</b>	22	0
Floret	100	100	82	<b>79</b>	<b>100</b>
Terminal spikelet	98	100	100	100	100
Zadoks 31					
Double ridge	1	1	0	0	0
Glume	<b>60</b>	18	8	0	0
Lemma			22	11	0
Floret	66	<b>87</b>	<b>67</b>	42	<b>67</b>
Terminal spikelet	98	100	100	<b>100</b>	100

Hall 1991-92 there was a significant difference ( $P < 0.01$ ) amongst the sowing dates (Table 7.6). In sowing 1 (17 September) 90% of plants at glume stage had attained or passed Zadoks growth stage 30, whereas in sowings 4 (3 February) and 5 (16 March) no plants attained Zadoks growth stage 30 until floret stage. (In sowing 5, fewer plants were scored because of more rapid development of cultivars with a low vernalization response and some cultivars with a strong vernalisation response did not reach Zadoks growth stage 30 during the course of the experiment.) Amongst the ADAS experiments, in which all sowing were made before the New Year, only ADAS 1989-90 showed a response to sowing date ( $P < 0.025$ ) and Zadoks 31 occurred at an earlier apex stage in plants sown before 10 October than those sown later.

There was no difference between cultivars in the stage at which a Zadoks stage was attained.

## Discussion

Studies of leaf and internode based on an analysis of length versus time or thermal time have shown that the growth of these organs is a highly integrated process (Gallagher 1979; Kirby 1988). By expressing the number of emerged leaves on the basis of culm leaves it was possible to examine internode growth as a function of leaf emergence. The analysis confirmed that the growth of internodes is integrated with leaf emergence and that stem growth is an ordered and predictable phenomenon in terms of emerged culm leaves. Response curves based on data from wheat grown in the field at different sowing dates (Anstey Hall

1991-92) and a glasshouse experiment (Kirby 1988) were all virtually identical (Fig. 7.3, a and b). Malvoisin (1984, Fig. 5) plotted log internode length against foliar stage (equivalent to emerged leaves) and found an ordered sequence of elongation with each successive internode having a similar relative growth rate and growth duration.

Data from ADAS wheat plants showed a broadly similar pattern of internode length versus number of emerged culm leaves, but at first the internodes were longer than in Anstey Hall 1991-92 (Fig. 7.4). Possible reasons for this may be differences in management, such as the application of growth regulator or herbicide or differences in handling after sampling, when ADAS plants may have been exposed to high temperature while in transit via the Post Office to Margaret Appleyard. Such difference in detail did not obscure the general pattern and the phase of rapid internode elongation was similar in terms of emerged culm leaves.

The largest deviations from the general trends of Zadoks score or internode length versus number of emerged culm leaves was seen for the first elongated internode, the growth of which determines the attainment of stage 30. Over all groups about 20 % of internode 1 were shorter than 10 mm. Thus some elongating internodes might score stage 30 and then, with continued growth, stage 31, while others would not. This gave a variable transition from stage 30 to 31. The shift from stage 31 to 32 and between the more distal internodes always occurred when another internode elongated as all or almost all of internodes 2 and above were longer than 20 mm at maturity.

The variation in final length of internode 1 was related to the number of culm leaves (Table 7.3). Some variation was due to differences among the cultivars included in the groups. Variation in sowing depth, which may arise from the variable penetration of the seed drill, was associated with variation in number of leaves in other experiments (Kirby 1993) and other factors such as plant density contribute to variation in number of leaves (Kirby & Faris 1970).

The number of elongated internodes on the culm varies depending on variables such as variety, depth of sowing and date of sowing. The trend for date of sowing recorded at Anstey Hall 1991-92 and Anstey Hall 1991 was consistent with the results from an experiment in which the number of elongated internodes declined from 6.2 to 4.8 in a series of sowing dates from 3 September to 3 December, respectively (Kirby *et al.* 1985b). For the spring variety Tonic sown on 4 April and 12 May 1993 the number of elongated internodes was 4.2 and 4, respectively (E.J.M. Kirby 1993, unpublished data), also confirming the trend. In these trials the final number of leaves was 8.3 and 7.3, respectively. The change in the number of elongated internodes is probably associated with the final number of leaves, but there was insufficient data from properly structured experiments to test this hypothesis or derive a prediction function.

The relationship between stem elongation and apex stage for winter-sown wheat are well established and are consistent with several other published results (e.g. Tottman 1977), although

there was some indication that spring sowing may delay stem elongation relative to apex stage. This was confirmed by data from late sowings, referred to in the previous paragraph in which stem elongation did not start until after the terminal spikelet was recorded.

## Conclusions

There is a very strong relationship between stem elongation and emerged leaves which was consistent over several environments.

The most variable part of the system is the timing of the beginning of stem elongation (Z30). This is an important indicator of plant development for some agronomic treatments and as such may require further investigation.

The number of elongated internodes (culm leaves) was variable and prediction might be possible. The value used in the template was 6, typical of plants sown at the normal time (middle of September until end of October).

There was a very strong correlation between Zadoks stage 3 scores ( $Z$ ) and number of emerged culm leaves ( $CDS$ ), summarised as:

$$Z = 28.2 + 0.981 CDS$$

To transform predicted number of emerged leaves to  $CDS$ ,

$$CDS = e - (f - n)$$

where  $e$  is the number of emerged leaves,  $f$  = final number of leaves and  $n$  is the number of culm internodes (6).

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## 8. References

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## 9. Appendix

### Contents:

1. List of functions
2. Model structure
3. Nomogram

### 1. List of functions used in the template to predict number of emerged leaves, final number of leaves and relationship between number of emerged leaves and shoot apex and stem development.

#### Vernalisation effectiveness

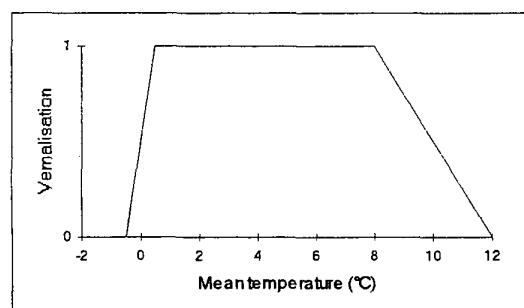


Fig. 9.1. Relationship between vernalisation effectiveness and temperature used to model vernalisation.

Vernalisation effectiveness is assessed on a daily basis using daily mean temperature, e.g. if the mean temperature is  $> 0.5$  and  $< 8$  °C, the plant experiences one vernalisation day (see Kirby 1992).

#### Time to full vernalisation

Winter varieties; 50 vernalisation days ( $F_v50$ ).  
Spring varieties; 20 vernalisation days ( $F_v20$ ).  
(See Kirby 1992.)

#### Thermal time

A method given by the Meteorological Office (Form 3300) is used to calculate thermal time ( $Tt$ ):

if both maximum ( $T_{\max}$ ) and minimum temperature ( $T_{\min}$ )  $>$  base temperature ( $T_{\text{base}}$ )

$$Tt = 0.5(T_{\max} + T_{\min}) - T_{\text{base}}$$

but if maximum temperature  $>$  base temperature and minimum temperature  $<$  base temperature then

i) if mean temperature  $>$  base temperature

$$Tt = 0.5(T_{\max} - T_{\text{base}}) - 0.25(T_{\text{base}} - T_{\min})$$

ii) if mean temperature  $<$  base temperature

$$Tt = 0.25(T_{\max} - T_{\text{base}})$$

#### Photoperiod

Photoperiod ( $P$ ) is calculated using the method given by Keisling (1962). No correction is made with reference to leap years:

$$P = \frac{2}{15} \arccos[\cos \alpha \sec \phi \sec \delta - \tan \phi \tan \delta]$$

where

$\alpha$  = zenithal distance in degrees of the sun ( $96^\circ$  for civil twilight),

$\phi$  = latitude in degrees (positive in the northern hemisphere)

and

$\delta$  = declination of the sun in degrees.

The equation relating declination of the sun to time of year is:

$$\delta = \arcsin\{0.39779 \sin \lambda\}$$

where

$$\lambda = M + 1.916 \sin M + 0.02 \sin 2M + 282.565$$

and

$$M = 0.9856t - 3.251$$

where  $t$  is the day of the year (days after 31 December).

## Seedling emergence

Thermal time to seedling emergence was estimated by:

$$T = 131 + 0.76 D$$

where  $T$  is thermal time to emergence ( $^{\circ}\text{Cday}$ , base temperature  $0^{\circ}\text{C}$ ) and  $D$  is sowing depth in millimetres.  $D$  is taken as 40 mm,  $T = 161^{\circ}\text{Cday}$ .

## Number of emerged leaves

The rate of change of daylength model is used. The number of emerged leaves is estimated by:

$$L = (t - 180) b$$

where  $L$  is the number of emerged leaves and  $t$  is thermal time (base temperature  $0^{\circ}\text{C}$ ). (See Section 4 for the reason why  $180^{\circ}\text{Cday}$  is used for winter crops sown at the normal time and the factors which affect this constant.)

$b$  is a function of rate of change of daylength ( $D$ ) at seedling emergence.

$$b = \alpha + \beta D$$

$$\beta = 0.0359.$$

$\alpha$  varied amongst varieties (Table below).

Table 9.1. Variety values of  $\alpha$  in the above equation

Variety	$\alpha$
Avalon	0.0112
Beaver	0.0100
Hereward	0.0093
Mercia	0.0109
Riband	0.0099
Soissons	0.0104
Tonic	0.0099

## Final number of leaves

The final number of leaves on the main shoot ( $L$ ) is estimated by:

$$L = a + bt + cp$$

where  $t$  is thermal time for full vernalisation and  $p$  is photoperiod at full vernalisation.  $a$ ,  $b$  and  $c$  are

constants, the values of which are given in the Table below.

Table 9.2. Coefficients  $a$ ,  $b$ , and  $c$  in the equation, above

Variety	$a$	$b$	$c$
All winter	9.9	0.00593	-0.109
Avalon	9.9	0.00591	-0.075
Beaver	10.5	0.00514	-0.104
Mercia	9.3	0.00604	-0.088
Riband	9.4	0.00551	-0.075
Tonic	16.8	0.00137	-0.589

## Shoot apex development

Number of emerged leaves at double ridge stage is estimated by:

$$L = -2.82 + 0.814f$$

and for the terminal spikelet stage:

$$L = -1.04 + 0.845f$$

where  $L$  is the number of emerged leaves, counted by the Haun method and  $f$  is the final number of leaves.

## Stem elongation

Zadoks principal growth stage 3 is estimated by:

$$Z = 28.2 + 0.981 CDS$$

where  $Z$  is the Zadoks growth stage and  $CDS$  is the number of emerged culm leaves.

To transform predicted number of emerged leaves to  $CDS$ ,

$$CDS = e - (f - n)$$

where  $e$  is the number of emerged leaves,  $f$  = final number of leaves and  $n$  is the number of culm internodes.

The number of elongated internodes varies and may depend on time of sowing and final number of leaves. For winter wheat sown at normal time it is taken as 6.

## Inputs

The flowchart illustrates the progression of rice growth stages, categorized by Zadoks principal growth stages, and the factors influencing each stage. A central vertical bar represents the timeline of growth.

- Seedling emergence (Zadoks principal growth stage 0):** Determined by **Thermal time**.
- Number of emerged leaves (Zadoks principal growth stage 1):** Determined by **Seedling emergence**.
- Rate of leaf emergence:** Determined by **Photoperiod (Rate of change)**, **Thermal time**, and **Variety**.
- Number of elongated internodes (Zadoks principal growth stage 3):** Determined by **Rate of leaf emergence**.
- Final number of leaves:** Determined by **Photoperiod**, **Thermal time**, and **Variety**.
- Culm leaves (Flag leaf) (Zadoks principal growth stage 3):** Determined by **Final number of leaves**.
- Number of culm internodes (6):** Determined by **Variety** (indicated by a dashed arrow).
- Ear emergence (Zadoks principal growth stage 5):** Determined by **Number of culm internodes (6)**.
- Anthesis (Zadoks principal growth stage 6):** The final stage shown.

Photoperiod is estimated from latitude and day of the year.

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### 3. Nomogram to predict Zadoks growth stages 30 - 55 and emergence of culm leaves.

The nomogram is an example of how the template might be adapted to predict Zadoks growth stages as an aid to spray treatments and similar operations. It is based on developmental relationships described in the template for stem elongation (Section 7). It assumes that some crop monitoring or development prediction has been done to detect the onset of stem elongation (growth stage 30, 'ear 1 cm').

Table 9.3 is a table of daily mean temperatures. In the example these are one year's records for Cambridge 1992, but in practice a long term average would be more appropriate. During the period of stem elongation mean temperature rarely

falls below 0 °C and therefore thermal time (base temperature 0 °C) can be accumulated by summing daily values.

Table 9.4 gives phyllochron values (number of degree days for a leaf to emerge) for some varieties. These are calculated from Table 9.1 for latitude 52° (Cambridge) for the mid point of each period.

Table 9.5 is an outline table giving equivalent stages, including the stages based on counting down from the flag leaf. The columns 'estimated +' and 'Predicted date' are completed by a user. The observed stages were those recorded in the Anstey Hall 1992-92 experiment.

#### USING THE NOMOGRAM

1. Find out when Zadoks growth stage 30 occurs by monitoring plant development or prediction (or both methods, combined).
2. Select the appropriate phyllochron value from Table 9.4 and calculate the 'estimated+' thermal times to each stage in Table 9.5. (e.g. Stage 31:  $1.2 \times P (125) = 151$ .)
3. Starting at the date when Zadoks growth stage 30 was observed, sum the daily mean temperatures in Table 9.3 noting the dates when the sum is equal to or greater than the estimated thermal times in Table 9.5. (In the example the accumulated thermal time is filled in and the dates of the stages are circled. In practice the sums could be added up on a calculator and the dates noted from the thermal time sum shown by the calculator display.)

Nomogram to predict Zadoks growth stages (Z30 - Z55) and culm leaf emergence.

Table 9.3. Daily mean temperatures

Date	Daily mean temp.	Accumul. thermal time	Date	Daily mean temp.	Accumul. thermal time	Date	Daily mean temp.	Accumul. thermal time	Date	Daily mean temp.	Accumul. thermal time
Feb	temp.	time	Mar	temp.	time	Apr	temp.	time	May	temp.	time
1	2.0		1	7.2	7.2	1	7.2		1	9.9	
2	2.7		2	6.5	13.7	2	5.1		2	8.5	
3	5.9		3	9.4	23.0	3	5.8		3	8.7	
4	6.1		4	10.0	33.0	4	5.0	278.2	4	10.3	
5	7.8		5	8.4	41.4	5	6.6		5	11.3	
6	8.1		6	8.9	50.2	6	7.4		6	13.2	
7	3.9		7	9.2	59.4	7	8.0		7	15.4	
8	4.7		8	9.7	69.1	8	11.6		8	11.3	
9	6.0		9	6.2	75.3	9	9.3		9	9.4	
10	4.7		10	9.5	84.8	10	9.0		10	8.0	
11	7.0		11	6.5	91.3	11	9.9		11	10.1	
12	10.0		12	9.7	101.0	12	10.4		12	13.3	656.2
13	6.2		13	10.0	110.9	13	7.8		13	15.2	
14	6.5		14	5.5	116.4	14	8.1		14	19.4	
15	7.2		15	6.2	122.6	15	5.9		15	17.5	
16	4.1		16	8.9	131.4	16	5.5		16	16.5	
17	3.1		17	10.7	142.1	17	7.1		17	11.3	
18	2.7		18	11.1	153.2	18	12.5		18	11.3	
19	2.3		19	8.5	161.6	19	11.9	408.7	19	16.4	
20	4.2		20	12.5	174.1	20	11.1		20	16.8	
21	4.9		21	9.8	183.9	21	11.9		21	16.8	
22	5.4		22	9.1	and	22	11.0		22	16.7	
23	8.5		23	6.6	so	23	11.5		23	17.5	
24	6.5		24	6.8	on	24	10.5		24	18.5	
25	4.5		25	6.8	,	25	11.9		25	18.8	
26	6.7		26	6.6	.	26	12.8		26	18.7	
27	10.5		27	5.6	.	27	11.4		27	17.8	
28	6.4		28	6.5	.	28	9.8		28	18.9	
29	9.6		29	8.6	.	29	8.0		29	16.6	
			30	5.9	.	30	8.7	527.1	30	17.0	
			31	8.9	↓				31	15.7	

Nomogram to predict Zadoks growth stages (Z30 - Z55) and culm leaf emergence.

Table 9.4. Phyllochron values (P) calculated for latitude 52°

	Late Sep.	Early Oct.	Late Oct.
Mercia	118	117	115
Riband	134	132	130
Soissons	125	124	122
Tonic	134	132	130

Late Sep. : 15 - 30 September

Early Oct. : 1 - 15 October

Late Oct. : 16 - 31 October

Table 9.5. Sample prediction

Field: *Amstey Hall* Variety: *Soissons* Sowing date: *17 Sept.*

P =

Stages			Calculation		Predicted date	(Observed date of Z stage)
No. of emerged culm leaves	'Flag leaf' stage*	Zadoks growth stage	Thermal time from Z30 formula	estimated +		
3	4	31	1.2 x P	150	18 Mar	16-Mar
4	3	32	2.2 x P	275	4 Apr	6-Apr
5	2	37	3.2 x P	400	19 Apr	19-Apr
6	1	39	4.2 x P	525	30 Apr	27-Apr
		(43-53)				
Ear emergence		55	5.2 x P	650	12 May	

\* 'Flag leaf' stage: leaves numbered from flag leaf downwards i.e. 1= flag leaf fully emerged = Zadoks growth stage 39.

+ thermal time calculated using the appropriate value for phyllochron (P) from Table 9.4.