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Prediction of leaf and internode development in wheat

R. M. WEIGHTMAN[1]*, E. J. M. KIRBY[2], R. SYLVESTER-BRADLEY[1], R. K. SCOTT[3], R. W. CLARE[4] AND A. GILLETT[3]

[1] *ADAS Arable Research Centre*, *Anstey Hall*, *Maris Lane*, *Cambridge CB2 2LF*, *UK*
[2] *The Studio*, *Blythburgh Road*, *Westleton*, *Saxmundham IP17 3AS*, *UK*
[3] *University of Nottingham*, *Faculty of Agriculture and Food Sciences*, *Department of Agriculture & Horticulture*, *Sutton Bonington Campus*, *Loughborough*, *Leicestershire LE12 5RD*, *UK*
[4] *ADAS Arable Research Centre*, *Rosemaund*, *Preston Wynne*, *Hereford HR1 3PG*, *UK*

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SUMMARY

Functions which predict rate of leaf emergence and final number of leaves, used in a model to predict the date at which growth stages occur, were tested in an experiment on winter wheat cv. Mercia grown with standardized husbandry at six sites in 1992/93, 1993/94 and 1994/95. A study of the number of detectable nodes on the culm and leaf length was also made.

The predicted rate of leaf emergence was mostly within 5% of the observed value. The difference between observed and predicted final number of leaves was mostly less than half a leaf but suspected errors in leaf counts resulted in some differences of more than two leaves.

Variable extension of the basal internode impaired confidence in the detection of nodes. The mean number of detectable nodes differed significantly among sites and between seasons from 3·7 to 4·8 but could not be related to sowing date or final number of leaves. Further information on factors affecting extension of the basal internode is desirable to standardize node detection and improve prediction of culm leaf appearance.

Culm leaves showed successively longer laminae up to the penultimate leaf. There was a significant relationship between length of the flag leaf and the final number of leaves, but it was positive in 1993/94 and negative in 1994/95. This may have been due to greater water stress in 1994/95.

INTRODUCTION

The development and growth of crop plants can proceed at contrasting rates, because they are driven by different environmental factors: development responds to temperature and daylength, whilst growth responds to radiation and water. But there are close interdependencies between the two processes. For example, (i) the double ridge stage signals floral initiation and also the cessation of tiller production, (ii) the emergence of successive leaves signifies further progress toward flowering, as well as governing the rate at which the photosynthetic canopy expands, and (iii) the start of stem elongation not only signals a step towards maturity, but introduces a large new sink for assimilate, which appears to increase growth rates (Green & Vaidyanathan 1987) and, perhaps in consequence, coincides with the start of tiller abortion. Internode extension also governs height, hence the propensity of the crop to lodge. Thus the numbers of leaves and internodes, the rates at which they are produced, and their eventual lengths are fundamental to understanding and predicting both development and growth.

In current commercial practice, the numbers of emerged leaves and internodes have been adopted to define development stages. For example, on the scale of Zadoks *et al.* (1974), principal stage 1 is based on the number of emerged leaves on the main shoot, and in later stages of development, when internodes of the culm extend, nodes become apparent and 'detectable nodes' are used to define principal stage 3. These stages provide a basis for instructions on the timing of agrochemical applications, so there would be useful commercial advantages arising from their successful prediction.

However, Kirby & Weightman (1997) report discrepancies between predicted and observed stages of development which they attribute to causes other than observer error. The predictions relied upon a close co-ordination between leaf emergence and development of the main shoot apex, stem elongation and flowering (Kirby 1990; Kirby *et al.* 1994). The

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* Present address: Dalgety Food Technology Centre, Station Road, Cambridge CB1 2JN, UK.

discrepancies may therefore arise either in the co-ordination of leaf emergence with other developmental events or in the prediction of leaf emergence (Baker *et al.* 1980; Miglietta 1991 *a*) and determination of the final number of leaves (Miglietta 1991 *b*; Kirby 1992).

In this paper, we re-examine current hypotheses to account for variation in leaf emergence, final number of leaves and the number of internodes found at six sites over three seasons where a single variety of winter wheat was grown with, as far as possible, standardized husbandry. A comparison between estimation of fractional leaf emergence, assessed by the 'Haun' method (Haun 1973) and by measurement, is also reported and there is an analysis of variation in leaf length and factors which may affect it.

MATERIALS AND METHODS

Sites and agronomy

Winter wheat (cv. Mercia) was sown at six sites in England and Scotland in 1992, 1993 and 1994, giving a total of 18 site-season combinations (Table 1). The cultivar Mercia has been grown widely in the UK since 1986, largely for use in bread-making; it exhibits a moderate vernalization requirement, is moderately sensitive to long days, is early to mature, is not a semi-dwarf (Worland *et al.* 1994), and is relatively low yielding (Anon. 1995). Details of the management of the plots is given in a previous paper (Kirby & Weightman 1997). Plots were generally sown after a non-cereal crop, fertilized to optimize yield and given a prophylactic fungicide programme with applications at stem extension, flag leaf emergence and ear emergence. All plots were treated with plant growth regulators and no lodging occurred.

Records of plant development

Measurements of leaf emergence began as near to 15 February as possible, with recordings at 4, 6 and 8 weeks after the first measurement and weekly thereafter until the flag leaf was fully emerged.

In February 1992, the main shoots of 20 plants were marked in each of five replications and the number of leaves which had fully emerged over the winter was counted. At each subsequent sampling date the number of fully emerged leaves (ligule visible) was recorded and the last fully emerged leaf was tagged with wire or cotton.

In 1993/94 and 1994/95 the procedure was changed to give information about intermediate stages of leaf emergence. Between 15 and 20 plants were marked in each of three replicates; ten per replicate were used for recording and the remainder were used as a reserve to replace plants which had died. At the first sample, the number of leaves which had emerged over the winter was estimated and the length of the emerging leaf, from tip to the ligule of the subtending leaf, was measured and marked to facilitate identification. At subsequent samplings, the number of fully emerged leaves was counted and the length of the emerging leaf measured and marked as before. The final length of the lamina of any leaves that had emerged since the last sampling was measured. Thus in retrospect, at any date, the length of the emerging lamina was expressed as a fraction of its final length and this was the 'number of emerged leaves' used for calculation of leaf emergence. This method is similar to that of Haun (1973) but the fractional length of the emerging leaf is based on its final length, rather than on the length of the subtending leaf. After full emergence of the flag leaf the final number of leaves produced on the shoot was recorded.

In 1992/93 and 1993/94, detectable nodes were identified according to Tottman (1987), taking care not to break the stem. The number of nodes was counted on 10 plants per replicate at most sample dates following the onset of stem elongation and the mean was recorded. Final number of nodes was estimated from those samples taken after the beginning of June. In 1995, a final count of detectable nodes (elongated internodes) was made using the plants marked for leaf counts (Fig. 1).

Weather data and estimation of thermal time

Daily maximum and minimum temperatures were measured at meteorological stations situated within 1 km of the experimental plots. Thermal time (base 0 °C) was calculated using the Meteorological Office technique (Form 3300, Kirby & Weightman 1997).

Development functions

The model to predict growth stages described by Kirby & Weightman (1997) is based on functions to predict rate of leaf emergence and final number of leaves.

Rate of leaf emergence (L) was calculated by the function of Baker *et al.* (1980, corrected version):

$$L = a + bR \qquad (1)$$

where the coefficients a and b depend on variety. For Mercia, a was set to 0·0109 and b to 0·026 (Kirby 1994). The rate of change of daylength at seedling emergence (R) was calculated using the photoperiod function described by Keisling (1962).

Final number of leaves (f) was calculated from:

$$f = \alpha + \beta V + \gamma D \qquad (2)$$

where a, β and γ are variety coefficients, set to 9·3, 0·00604 and $-0{\cdot}088$ respectively for Mercia. V is accumulated thermal time from sowing to full vernalization and D is the daylength at the time of full

Table 1. *Details of sites and sowing dates*

Site	Code	Latitude (°N)	Sowing date		
			1992	1993	1994
ADAS Boxworth, Cambridgeshire	BW	52·2	1 Oct	18 Oct	6 Oct
University of Edinburgh	ED	55·8	7 Oct	2 Nov	30 Sep
ADAS Gleadthorpe, Nottinghamshire	GL	53·2	17 Oct	28 Oct	10 Oct
Harper Adams Agricultural College, Shropshire	HA	52·8	2 Oct	28 Sep	5 Oct
ADAS Rosemaund, Hereford	RM	52·1	16 Oct	23 Oct	23 Sep
University of Nottingham, Sutton Bonington, Leicestershire	SB	52·8	7 Oct	2 Nov	6 Oct

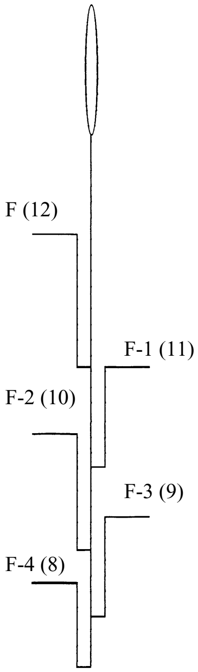

Fig. 1. Diagram to illustrate the leaf numbering conventions used in this paper. The plant illustrated has a final leaf number of 12 and four detectable nodes. F (12), etc represent the leaf numbers, numbering from the flag leaf (F) downwards and (12) from the first leaf upwards.

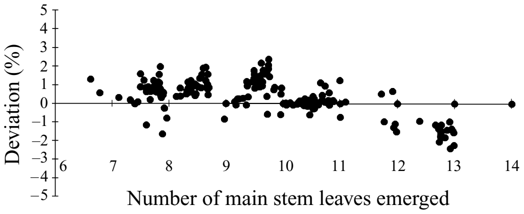

Fig. 2. Deviations (%) between measurements and Haun (1973) methods of estimating number of emerged leaves for Boxworth (BW), 1994/95. See text and Eqn (3) for more detail.

vernalization (Kirby 1992). Full vernalization was defined as the time when plants had experienced 50 vernalization days. Vernalization was estimated on a daily basis using a function which assumed that the temperatures between 0·5 and 8 °C were fully effective and that temperatures $< -0{\cdot}5$ and > 12 °C were ineffective. The contribution of temperatures between $-0{\cdot}5$ and 0·5 and between 8 and 12 °C were estimated by linear interpolation (Kirby 1992).

RESULTS

Leaf measurement versus Haun score

In most recent papers which estimate rates of leaf emergence, the Haun (1973) method of leaf numbering has been used. Leaf length data from the experiment described in this paper could be used to calculate number of emerged leaves by the Haun method.

At each sample the length of the exserted portion of the emerging leaf was expressed as a fraction of the length of the fully emerged leaf immediately basal to it. If the length of the exserted portion of the emerging leaf exceeded that of the subtending leaf, the fraction was given a value of 0·9.

The percentage deviation between the estimates was calculated as:

$$(NH - NL)/NL \times 100 \qquad (3)$$

Table 2. *Observed and predicted final number of leaves and difference between observation and prediction. The mean difference and root mean square of the difference* (R.M.S.D.) *are shown*

	BW*	ED	GL	HA	RM	SB	Mean	R.M.S.D.
			Predicted					
1992/93	11·6	10·3	10·6	11·2	10·8	11·2		
1993/94	10·7	9·9	10·4	11	10·7	10·4		
1994/95	13	11·9	12·3	12·8	13·9	13		
			Observed					
1992/93	11·4	9·8	10·2	12·0	11·0	10·9		
1993/94	10·7	9·3	10	10·3	10·5	10·1		
1994/95	12·7	9·2	10			13		
			Observed − predicted					
1992/93	−0·2	−0·5	−0·4	0·8	0·2	−0·3	−0·1	0·5
1993/94	0·0	−0·6	−0·4	−0·7	−0·2	−0·3	−0·4	0·4
1994/95	−0·3	−2·7	−2·3			0	−1·3	1·8
Mean	−0·2	−1·3	−1·0	0·1	0·0	−0·2	−0·6	
R.M.S.D.	0·2	1·6	1·4	0·8	0·2	0·3		1·0

* For site codes, see Table 1.

Table 3. *Observed and predicted rate of leaf emergence (leaves (100 °Cd)*$^{-1}$*). The differences (observed − predicted) are shown as absolute values and as percentages of the observed. The mean difference and root mean square of the difference* (R.M.S.D.) *are shown for the percentage differences*

	BW*	ED	GL	HA	RM	SB	Mean	R.M.S.D.
			Predicted					
1992/93	0·92	0·92	0·97	0·92	0·94	0·93		
1993/94	0·94	1·03	0·98	0·92	0·95	1·00		
1994/95	0·92	0·90	0·92	0·92	0·92	0·92		
			Observed					
1992/93	0·80	0·99	0·84	0·84	0·85	0·64		
1993/94	0·92	1·17	0·97	0·83	0·94	0·94		
1994/95	0·86	0·86	0·93			0·88		
			Observed − predicted					
1992/93	−0·12	0·07	−0·13	−0·08	−0·09	−0·28		
1993/94	−0·02	0·14	−0·01	−0·09	−0·01	−0·06		
1994/95	−0·06	−0·04	0·01			−0·04		
			Observed − predicted as % of observed					
1992/93	−15	7	−16	−10	−11	−44	−15	21
1993/94	−2	12	−1	−11	−1	−6	−2	7
1994/95	−7	−4	1			−5	−4	5
Mean	−8	5	−5	−10	−6	−18	−7	
R.M.S.D.	10	8	9	10	8	26		14

* For site codes, see Table 1.

where NH and NL are the number of emerged leaves estimated by the Haun (1973) method and the method described in this paper, respectively.

Except for the flag leaf, the final length of a leaf was longer than that of its subtending leaf. Therefore NH was expected to be greater than NL, resulting in positive deviations between the two methods. For example, at Boxworth, 1995 (Fig. 2) a positive bias can be seen in lower leaves, but there were a significant number of negative values (48 out of a total of 210 observations) particularly for the upper leaves. The majority of these negative values represent the emergence of the flag leaf which was smaller in length than its subtending leaf. The other negative deviations in lower leaves could be as a result of operator error in leaf measurement. These results suggest the leaf measurement method of scoring leaf emergence would overestimate phyllochron slightly.

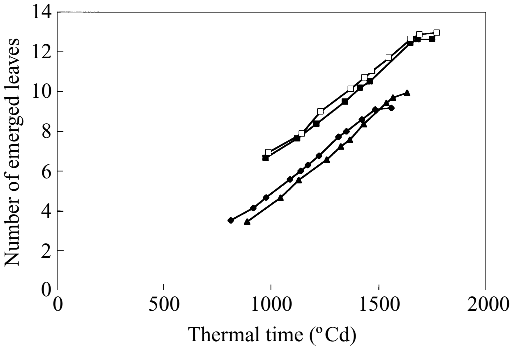

Fig. 3. Number of leaves *v.* thermal time from sowing for BW (■), ED (◆), GL (▲) and SB (□), 1994/95.

Regarding the magnitude of the deviations, the only difference between the two methods would be in the fractional part of the leaf number. In the extreme case for this data-set, where the length of a leaf was never more than 135% of its subtending leaf, the maximum difference between the fractional parts was *c.* 0·3. This meant that the maximum deviation varied from about 5 to 2% for leaves 4 and 10 respectively. The differences between the Haun method and the leaf measurement method recorded here were generally very small. There were only three deviations < -2% and three deviations $> +2$%, all deviations being within the range −3 to +3% (Fig. 2). For the other four sites in 1995 (see Table 1 for codes used), similar variation was observed, with few deviations either $> +5$%; (SB, 1; HA, 1; GL,1; and ED, 1), or < -5% (SB, 0; HA, 5; GL,0; ED, 0).

Leaf emergence and final number of MS leaves

Counts of final number of leaves on the main shoot were on average 0·6 leaves fewer than the number predicted (Table 2). Only at HA and RM in 1992/93 were there more leaves observed than predicted. At ED and GL in 1995, the difference between observed and predicted was more than two leaves.

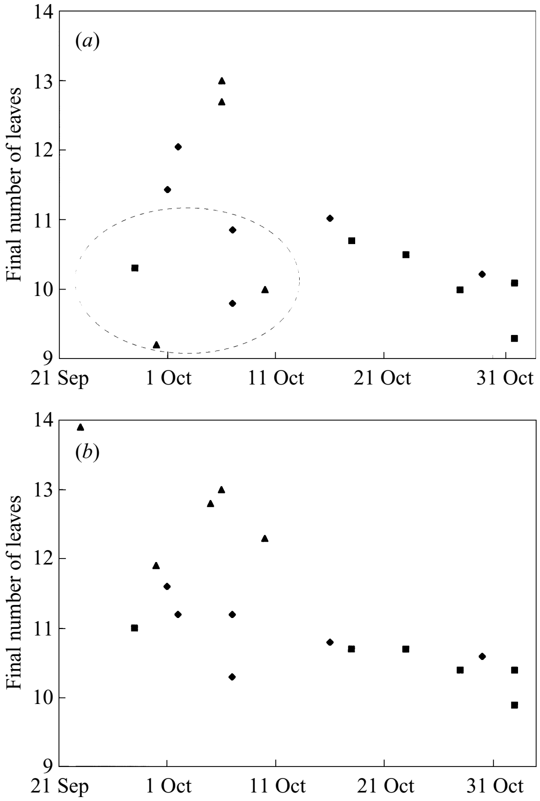

Fig. 4. (*a*) Observed and (*b*) predicted final number of leaves in 1992/93 (◆), 1993/94 (■) and 1994/95 (▲). The observed points within the dotted ellipse are those for ED, 1992/93, HA, 1993/94 and ED and GL 1994/95. Note that in 1994/95 there were no observations for two sites (Table 7) and that BW and SB had the same sowing date and predicted final number of leaves.

The rate of leaf emergence on the main shoot was also generally lower than that predicted (Table 3). The differences were particularly large in 1992/93. In this season the method of measuring leaf emergence was different from that used in the two following seasons and from that used to derive the coefficients for the model and the data for this season were not considered further. In all cases in 1993/94 and 1994/95 the plot of emerged leaves *v.* thermal time showed only a linear trend (e.g. Fig. 3). The variation accounted for by linear regression was always >99%. In 1993/94 and 1994/95, the difference between observed and predicted rates of leaf emergence ranged from +0·0014 to −0·0009 leaves °Cd^{-1} or, expressed as a percentage of the observation, from +12 to −11%. Most of the predictions were within 5% of the observation (Table 3).

Inspection of the graph of numbers of emerged leaves *v.* thermal time for 1994/95 showed a difference in the pattern of leaf emergence amongst the sites (Fig. 3). The lines for BW and SB in which the difference between observed and predicted final number of leaves was −0·3 and 0 respectively were separated, at any thermal time, from ED and GL by about two leaves. (The difference in final number of leaves was > 2 at both sites.) The intercept on the x-axis ($-a/b$) which is the calculated thermal time at which leaf emergence begins is set to 180 °Cd in the model. The calculated values for BW, ED, GL and SB were 225, 429, 534 and 209 °Cd respectively. This suggests that at ED and GL two leaves which emerged early in the season were missed from the leaf count.

Both observed and predicted final number of leaves declined as sowing became later (Fig. 4). This was less obvious for the observed number of leaves, due to

Table 4. *Mean temperature (10 day periods, from date of sowing) for sites sown before 11 October*

	1992/93				1993/94	1994/95					
Decade	BW*	ED	HA	SB	HA	BW	ED	GL	HA	RM	SB
1	11·2	7·2	10·3	5·8	10·7	10·1	9·3	8·9	9·6	9·9	9·1
2	6·9	4·0	5·9	6·7	7·7	10·4	8·3	9·9	9·7	10·3	10·2
3	6·3	5·6	5·5	7·6	5·5	9·9	8·0	10·4	9·4	10·8	9·9
4	9·0	4·8	9·0	6·6	5·7	10·4	7·7	9·3	10·4	8·7	10·6
5	4·9	4·6	4·5	6·7	1·5	10·3	9·0	6·4	10·2	8·3	10·5
Mean	7·7	5·2	7·0	6·7	6·2	10·2	8·5	9·0	9·9	9·6	10·1

* For site codes, see Table 1.

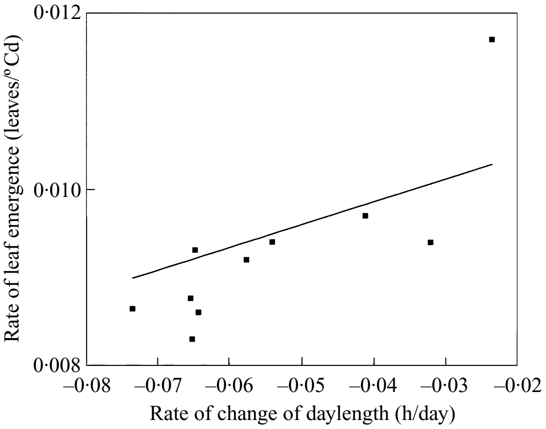

Fig. 5. Observed (■) and predicted (——) values of rate of leaf emergence *v.* rate of change of daylength. The point in the top right hand corner is Edinburgh (ED), 1993/94.

four cases in which sowings before 10 October exhibited < 10·5 leaves; these include the anomalous points for ED and GL. With sowings before 10 October, the predicted and observed final number of leaves at BW and SB for 1994/95 exceeded those for the 1992/93 and 1993/94 sowings during this period. In 1994/95 the mean daily temperatures in the 50 days following sowing were, with the exception of ED, generally > 9 °C, whereas in the other two seasons the temperatures were lower (Table 4). This would extend the period to full vernalization, increasing final number of leaves as predicted by the model function (Eqn (2)).

The predicted rate of leaf emergence is a linear function on the rate of change of daylength at seedling emergence (Fig. 5). Rate of change of daylength depends on day of the year and latitude. Because of the variation in sowing date in 1993/94 and 1994/95 and, to a lesser extent, site latitude, rate of change of daylength at seedling emergence varied from $-0·07$ to $-0·02$ h d^{-1}. With the exception of ED in 1993/94, the trend of the observed rates of leaf emergence is consistent with prediction (Fig. 5). The regression of the observed response of rate of leaf emergence (L) *v.* rate of change of daylength (R), excluding ED 1993/94, is:

$$L = 0·01053 + 0·026R \qquad (R^2 = 0·54)$$

The response coefficient (0·026 leaves °Cd^{-1} h^{-1} d^{-1}) is the same but the 'a' coefficient is smaller than that used in the model function (Eqn (2); 0·01053 cf. 0·0109 leaves °Cd^{-1}).

Table 5. *Mean number of detectable nodes*

Site*	1993	1994	1995	Mean
BW	5·0	4·2	4·1	4·4
ED	4·8	4·1	3·7	4·2
GL	4·2	4·0	4·0	4·1
HA		4·3	4·2	4·3
RM		4·3	4·8	4·6
SB	4·8	4·6	4·7	4·7
Mean	4·7	4·3	4·3	4·4

* For site codes, see Table 1.

Number of elongated internodes

The mean numbers of detectable nodes are shown in Table 5. In 1995, when plants from all sites were measured by one operator, recognition of the lowermost node presented some difficulty. For a proportion of the plants the lowermost internode was *c.* 10 mm long, but nodal roots arising from the proximal and distal nodes made identification and accurate measurement difficult. Shoots with nodes of this type were classified separately as 3+, 4+ and 5+ shoots (compared, for instance, to '3 nodes' where the lowest node was clearly > 10 mm). The overall frequency distribution of shoots using this classification is shown in Fig. 6.

For comparison with the 1993 and 1994 data and for further analysis, the frequency of plants with 3

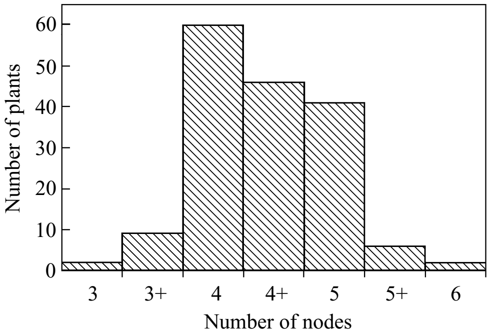

Fig. 6. Frequency distribution of number of nodes, all sites, 1995 (for explanation of 3+, 4+ and 5+, see text).

Table 6. *Frequency of number of elongated internode classes and mean number of nodes in 1995*

Site*	Number of nodes 3	4	5	6	Mean
BW	1	22	5	0	4·1
ED	8	22	0	0	3·7
GL	1	26	1	0	4·0
HA	1	21	8	0	4·2
RM	0	6	12	2	4·8
SB	0	9	21	0	4·7

* For site codes, see Table 1.

and 3+ nodes were added to give a 3 node (4 internode) class and the 4+ and 5+ classes were similarly amalgamated (Table 6). Generally, at any site in 1995, only two classes of node numbers were found. There were significant differences (χ^2; $P < 0{\cdot}001$) among sites.

Leaf length and position

Measurements of maximum leaf length in 1994 and 1995 were examined in order to study the relationships between final leaf number and leaf length and between leaf length and its position on the main stem. At each site, the final numbers of leaves of each of the (*c.* 30) shoots were summarized and the frequency of the number of leaves in each final leaf number class tabulated (Table 7). The range in final number of leaves at each site complicated the comparison between sites across seasons. It was therefore decided that the modal final leaf number (M) was the best summary of observations to use for the study of these relationships. At most sites there were 3–4 final leaf number classes present, the exception being GL in 1995, at which only two classes were recorded.

After determining M, individual leaves could be compared by either numbering up from the bottom or alternatively down from the flag leaf (F; Fig. 1). It is clear from these data that there is a strong pattern in leaf size with position on the shoot relative to F-1, whereby an increase in leaf size was observed from F-n to F-1, followed by a subsequent reduction in size from F-1 to F. This trend in leaf size with leaf position was little affected by site or season. The exceptions were at ED in 1994 and BW in 1995 where some environmental stresses in water or N uptake may have been responsible for the small sizes of both F and F-1.

In each season there was a strong correlation between the length of F and M. However, between seasons, the coefficients reversed in sign (Table 8), being positive in 1994 and negative in 1995. The 1994 data suggested that larger leaves are produced with

Table 7. *Frequency of final number of leaves, mean and modal final number of leaves*

Site*	Final number of leaves 8	9	10	11	12	13	14	Mean	Mode
				1994					
BW			9	20	1			10·7	11
ED	2	19	6	3				9·3	9
GL		1	27	2				10·0	10
HA		3	16	9	2			10·3	10
RM	1	3	8	15	3			10·5	11
SB		1	26	3				10·1	10
				1995					
BW				1	9	19	1	12·7	13
ED	6	14	8	2				9·2	9
GL		1	29					10·0	10
SB					6	18	6	13·0	13

* For site codes, see Table 1.

Table 8. *Leaf length (mm) based on modal number of leaves (Mode), correlation between flag leaf length and length of other leaves (F:F−n) and correlation between length of F and modal number of leaves 1994 and 1995*

	BW*	ED	GL	HA	RM	SB	Mean length	F:F−n
				1994				
F-7			76		80	93	83	
F-6	100	84	79	107	102	99	95	0·59
F-5	122	88	96	113	118	118	109	0·78
F-4	153	115	131	133	144	158	139	0·76
F-3	169	149	144	163	189	198	169	0·78
F-2	187	185	179	208	235	215	202	0·78
F-1	215	183	218	220	250	234	220	0·99
F	178	138	179	185	212	203	183	
Mode	11	9	10	10	11	10		
Correlation between length of F and modal final leaf number								0·72
				1995				
F-7	112			117			114	
F-6	125		114	119		117	119	
F-5	134	92	120	123		133	121	−0·54
F-4	156	96	149	138		152	138	−0·46
F−3	189	130	174	162		180	167	−0·60
F−2	195	156	178	174		197	180	−0·61
F−1	193	208	199	198		213	202	0·57
F	148	194	196	190		186	183	
Mode	13	9	10	12		13		
Correlation between length of F and modal final leaf number								−0·63

* For site codes, see Table 1.

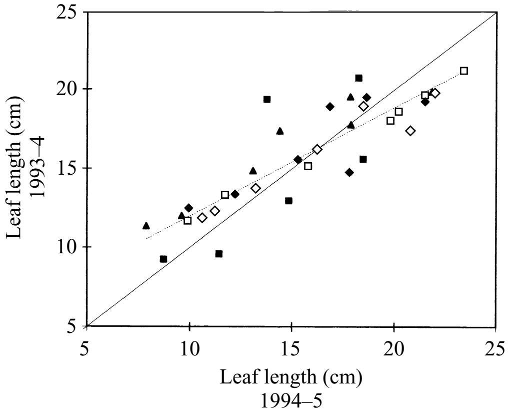

Fig. 7. Length of leaves F-6, F-5…F in 1993/94 *v.* comparable leaf length in 1994/95. The 1:1 ratio is the solid line (——) and the dashed line (----) is the fitted regression (see text for details). BW, (◆); ED, (■); GL, (▲); HA, (◇) and SB, (□).

larger values of M, but in 1995 the two sites with the largest values for M (BW and SB) had the smallest flag leaves. When leaf length in 1993/94 (y) was plotted *v.* leaf length in 1994/95 (x), there was a significant departure from a 1:1 ratio (Fig. 7):

$$y = 5{\cdot}11 + 0{\cdot}688x \qquad (R^2 = 0{\cdot}77)$$

The lower leaves (F-6, F-5, F-4) were longer in 1994/95 than in 1993/94, but for leaves F-3 or F-2, F-1 and F (Table 8), the reverse was true. When the data for ED (■, Fig. 7) were excluded this effect was more obvious:

$$y = 5{\cdot}85 + 0{\cdot}646x \qquad (R^2 = 0{\cdot}87)$$

When the leaves are numbered acropetally on the same shoots, the pattern in leaf size is less clear (Table 9). However, the possibility of predicting leaf size, working upwards from the base of the plant, may provide a useful tool for crop modelling, when final leaf number is not known. In Table 9 it can be seen that the general pattern in leaf size with position on the shoot is maintained (with maximal leaf size at F-1 or F-2) but between seasons, these occur at different absolute leaf numbers. In contrast, when numbered downwards from the flag leaf, the length of which did not differ between seasons (Table 8), the effect of site and season is much less pronounced.

Since the pattern in leaf size was so clear within a shoot when numbered in relation to F, a relative description of leaf sizes was sought. Leaf length was expressed as a proportion of the length of F-1, this generally being the largest leaf (in 9 observations out of 11), so that most other leaves had a value < 1 (Table 10). The effect of season was much clearer, with the flag leaf being fairly uniform in relative size in 1994 (ED 0·75, and the other five sites 0·83–0·86)

Table 9. *Leaf length (mm) based on modal number of leaves (Mode) with successive leaves numbered from base of plant upwards*

Leaf	BW*	ED	GL	HA	RM	SB
			1994			
3			76			93
4		88	79	107	80	99
5	100	115	96	113	102	118
6	122	149	131	133	118	158
7	153	185	144	163	144	198
8	169	183	179	208	189	215
9	187	138	218	220	235	234
10	215		179	185	250	203
11	178				212	
12						
Mode	11	9	10	10	11	10
			1995			
3						
4		92	114			
5		96	120	117		
6	112	130	149	119		
7	125	156	174	123		117
8	134	208	178	138		133
9	156	194	199	162		152
10	189		196	174		180
11	195			198		197
12	193			190		213
13	148					186
Mode	13	9	10	12		13

* For site codes, see Table 1.

Table 10. *Ratio (based on modal number of leaves) of length of individual leaves to length of F-1 (penultimate leaf) numbered in relation to the flag leaf (F)*

Leaf	BW*	ED	GL	HA	RM	SB	Mean
			1994				
F-7			0·35			0·40	0·37
F-6	0·46		0·36	0·48	0·41	0·42	0·43
F-5	0·57	0·48	0·44	0·51	0·47	0·50	0·50
F-4	0·71	0·63	0·60	0·60	0·58	0·68	0·63
F-3	0·78	0·81	0·66	0·74	0·76	0·85	0·77
F-2	0·87	1·01	0·82	0·95	0·94	0·92	0·92
F-1	1·00	1·00	1·00	1·00	1·00	1·00	1·00
F	0·83	0·75	0·82	0·84	0·85	0·86	0·83
			1995				
F-7	0·58			0·59			0·58
F-6	0·65		0·57	0·60		0·55	0·59
F-5	0·69	0·45	0·60	0·62		0·63	0·60
F-4	0·81	0·46	0·75	0·69		0·71	0·68
F-3	0·98	0·62	0·87	0·82		0·85	0·83
F-2	1·01	0·75	0·89	0·88		0·93	0·89
F-1	1·00	1·00	1·00	1·00		1·00	1·00
F	0·77	0·93	0·98	0·96		0·88	0·90

* For site codes, see Table 1.

compared with 1995 which had a wider range in relative flag leaf size (small values; BW 0·77, SB 0·88, and large values; GL 0·98, HA 0·96).

DISCUSSION

Leaf measurement

Measurement of lamina length of emerged and emerging leaves on a marked plant allowed a measured estimate of the proportion of an individual leaf which had emerged. However, when it is not possible to return to the same plants, other methods have to be used in order to estimate the proportion of the leaf emerged such as that proposed by Haun (1973). Such methods have been used previously to gather the data which have been used in building models of crop development. Thus it was important to establish whether deviations between predicted and actual rates of leaf emergence were, in part, due to differences in measurement procedure. In general the deviations based on the Haun method were small ($< 6\%$) compared with the method used in this paper. Thus, compared with other potential sources of error (e.g. observer error in determining final number of leaves emerged), these differences should have only trivial influence on the estimates of rate of leaf emergence. It should be noted, however that the analysis presented here does not fully examine the method of Haun (1973) as it would be applied in the field when different plants are visited on each sampling occasion.

Final number of leaves and leaf emergence

Variation in the observed final number of leaves on the main shoot was partly explained by response to sowing date which is consistent with other experiments (Kirby *et al.* 1985*a*). At least two of the anomalous observations (ED and GL, 1994/95) appeared to be due to misidentification of the position on the shoot of emerging leaves when counts began in the spring, probably because of damage by frost or disease to over-wintering leaves. Accurate counts of leaves on autumn-sown crops normally necessitates some form of leaf tagging (Kirby & Appleyard 1987).

Amongst plants sown before the middle of October, those in 1994/95 (excluding ED and GL) had greater final numbers of leaves than those in trials sown in the two previous seasons. This appeared to be due to the higher temperatures experienced by the crops sown in 1994/95 compared with 1992/93 and 1993/94 (Table 4).

Generally, the final number of leaves was predicted to within less than half a leaf and, with the exceptions noted above, in all cases within 0·8 leaves. The generally negative difference (more leaves were predicted than observed) indicates that the coefficients used in Eqn (2) may need revision for Mercia.

The observed variation in rate of leaf emergence was generally explained by the hypothesis that such variation is a function of rate of change of daylength (Fig. 5; Baker *et al.* 1980). With the exception of the sowing at ED in 1993/94, all points were near to or below the predicted trend. Comparison of the coefficients of the function (Eqn (1)) used to predict leaf emergence rate with those of the calculated linear regression of the observed rate *v.* thermal time indicate that the '*a*' term of the equation may be too large.

It should be noted, however, that the differences between observed and predicted values for both leaf emergence and final number of leaves may have been related to differences in the conditions in the experiment described in this paper and those in which the coefficients were estimated. The data used to determine the coefficients generally came from plots in which seedling depth, plant spacing and population were controlled, in some cases by hand sowing. In other cereals, plant population is known to affect both rate of leaf emergence and final number of leaves (Kirby & Faris 1970), high populations reducing the magnitude of both characters. The deviations were to some extent self correcting in the calculation of growth stages; for example, calculation of stage 39 is the quotient of final number of leaves and rate of leaf emergence. Even if the coefficients of both parameters were overestimated, the estimated thermal time might be similar. Therefore any revision of the coefficients should embrace all parameters, possibly including the number of detectable nodes (see below).

Number of detectable nodes

The number of nodes on the culm is an element in the model to predict growth stage and nodes were counted to check the assumption in Eqn (4), Kirby & Weightman (1997). The apparently simple task of counting nodes was complicated by the definition and measurement of the lowest internode. The criterion proposed in Materials and Methods was difficult to apply. Reference to the attempts of others to find a criterion showed that the definition of the first internode has been a problem from the time that the use of detectable nodes (growth stages 31, 32, etc) were recommended for herbicide and growth regulator application. In their discussion of the topic, Tottman *et al.* (1985) came to the conclusion that the 'first (lowermost) node' was defined by a subtending internode of 20 mm or more. In a subsequent paper, Tottman (1987) redefined the 'first node detectable' as when the subtending internode was 10 mm or more long.

Measurements of the length of the lowermost internode showed that it was more variable than the more distal internodes (Kirby 1994). The amalgamation of the 3 and 3+, etc node classes in the 1995 analysis implies that a definition of the lowermost internode of 20 mm or more is a more satisfactory criterion.

Table 11. *Temperature, sunshine hours and rainfall for Boxworth in 1994 (season 1993/94) and 1995 (season 1994/95) to illustrate the contrast between the seasons. Mean daily temperature (°C) and mean daily hours of sunshine are shown for 7-day periods from 1 April to 1 June. The mean daily temperature, mean daily hours of sunshine and total rainfall (mm) are also shown for the whole period. These dates roughly correspond to the period from growth stages 30–39, that is from the period when the culm leaves (typically F-3 – F) were emerging*

	1994		1995	
Period ending	Temperature	Sunshine hours	Temperature	Sunshine hours
7 April	5·5	5·4	9·1	5·6
14 April	6·7	5·4	7·1	8·2
21 April	12·7	4·0	8·7	4·9
28 April	11·5	8·5	11·5	3·8
5 May	11·5	7·4	12·7	7·4
12 May	11·4	7·1	7·5	5·4
19 May	11·0	3·1	12·0	5·7
26 May	11·6	0·3	14·9	6·5
1 June	12·9	8·8	13·2	6·2
Mean over period	10·5	5·5	10·8	6·0
Rainfall	135		32·2	

In 1995 there were significant differences among sites, the mean number varying from 3·7 to 4·8 nodes (Table 6). The differences among sites in 1993 and 1994 were not analysed, as frequency data were not recorded, but the ranges of variation were similar (Table 5). The greatest mean number of nodes was found in 1993, although there were no records for two sites. SB had consistently the greatest number of nodes and GL the least. The overall mean was 4·4 and most sites had a modal number of nodes of four (5 elongated internodes, Eqn (4), Kirby & Weightman (1997)), confirming that this number is most generally applicable for the model.

Variation in number of detectable nodes must be predicted if growth stage estimation is to guide the timing of agrochemicals such as fungicides. For example, growth stage 31 bore a different relationship to flag leaf or ear emergence in a culm with three or four detectable nodes (GL) compared to one with mostly five detectable nodes (SB). Kirby *et al.* (1985*b*) and Kirby (1994) saw the variation to be related to date of sowing and therefore possibly to the final number of leaves. For the data from this experiment there was no significant correlation, either with date of sowing or with final number of leaves ($r = 0{\cdot}43$, 12 D.F.). Investigation of factors, other than daylength and vernalization, which affect the final leaf number, such as plant population (Kirby & Faris 1970) and N (Longnecker *et al.* 1993) might provide the information necessary to predict the final number of detectable nodes.

Leaf length and position

The data show that the relative sizes of individual leaves are interrelated when numbered from the flag leaf basipetally. This simple relationship might become a useful component of a predictive scheme for canopy structure; the sizes of leaves appear to be related to their final leaf position. However, environmental factors (water or nitrogen limitation) may mean that the relationship does not hold in stressed crops. Gallagher *et al.* (1979) found that rate of leaf extension depended on temperature, but slowed when bright sunshine caused fast transpiration, which reduced leaf water potential.

Water stress did not affect the duration of leaf growth and therefore reduced final leaf size. It is possible that crops which produce large leaves use more water early in the season, subsequently exacerbating the effect of a dry spell during stem extension and so reducing the size of the last two or three leaves in conditions such as those which occurred in 1994/95 compared with 1993/94 (Table 11).

Moisture stress and high temperatures were particularly prevalent in 1995 and it may be that environmental factors influenced the final size of the leaves, even though their 'potential' size may have been related to final leaf number. The difference between ED and the other sites may be related to different stress levels, e.g. water stress. However, errors in leaf numbering (discussed above) in the second season may also have obscured this effect.

Given the difficulties in ensuring that growth stage observations are made with satisfactory accuracy (Kirby & Weightman 1997), modelled predictions should reduce the need for crop inspection and enable improvements in commercial wheat production. The functions used here predicted rate of leaf emergence and final number of leaves within *c.* 5% of the observed values (ignoring anomalous results). We judge that this level of precision would not generally be bettered by in-field inspection but that, in either case, applications of a fungicide (for example), would often be mistimed in relation to emergence of the specific culm leaf for which they were intended. Thus further development of either approach must prove worthwhile.

In addition, the predicted values for both characters were bigger than the observations. Possible errors in counts of number of leaves may have inflated the discrepancies and care should be exercised in identifying dead leaves when inspecting over-wintered crops. But also, a re-calibration of the functions for leaf emergence and final number of leaves appears to be necessary for Mercia.

There was variation amongst sites in the number of detectable nodes on the culm, but no relation was found with sowing date or final number of leaves. There was some indication that it was affected by site. Further investigation of extension of the basal internode is desirable to standardize node detection and improve prediction of culm leaf appearance.

The pattern of leaf lamina length with leaf position on the culm was similar in two seasons but the relation of flag lamina length to final number of leaves changed between 1993/94 and 1994/95. This was possibly due to the very dry conditions in the latter season. Further investigation is needed to establish functions to predict leaf size.

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