Field Studies of Cereal Leaf Growth

I. INITIATION AND EXPANSION IN RELATION TO TEMPERATURE AND ONTOGENY

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ABSTRACT
Measurements of leaf initiation, appearance, and expansion are presented for winter wheat and spring barley crops. For winter wheat, these processes occurred during periods of several weeks when fluctuating temperatures influenced process rates. Analysis of these measurements was facilitated by plotting variables against the time integral of temperature above an appropriate base temperature (0 °C), here called thermal time with units of °C d. Leaf primordial number and appearance stage increased linearly with thermal time for both winter wheat and spring barley which initiated 12 and 9 leaves respectively. When plotted against thermal time 90% of laminar and leaf length growth and 80% of laminar width growth was satisfactorily described by a straight line for both species. This enabled an average extension rate and duration of linear growth to be defined for each leaf. When expressed in thermal time, wheat leaves had a similar duration of linear growth (210 °C d; s.d. 30 °C d) with insolation exerting a negligible influence. The first seven barley leaves had a shorter duration of linear growth (151 °C d; s.d. 8 °C d). For wheat, final leaf length and laminar width increased with leaf number and were not apparently associated with changes in apical development stage. Changes of barley leaf dimensions with leaf number were more complex.

INTRODUCTION
The importance of leaf area in controlling plant dry matter growth rate has long been appreciated (Gregory, 1921). During the early part of the growing season the growth rate of many crops is directly related to the radiation intercepted by their leaf surfaces (Shibles and Weber, 1966; Biscoe and Gallagher, 1977). Furthermore, the total amount of dry matter produced by a number of crops is almost proportional to the total amount of radiation they intercept (Duncan, Shaver, and Williams, 1973; Monteith, 1977). However, few field experiments have investigated the effects of environmental factors on leaf area expansion. Some studies showed that leaf area expansion rate was positively correlated with temperature (Bull, 1968; Monsi and Murata, 1970), whereas others showed a negative correlation (Gregory, 1926; Tinker and Jones, 1931). The effect of other weather factors has not been consistently detected. This is probably because, using destructive harvests, small day to day changes in leaf area are impossible to detect (Gallagher, Biscoe,
and Saffell, 1976). During longer periods, the effects of varying sunshine, rainfall, temperature, and humidity are likely to be confounded.

A field study of barley and wheat leaf expansion was therefore attempted with the following objectives:

1. to describe leaf area expansion from initiation to ligule appearance with special reference to the effects of weather and ontogeny;
2. to determine which organs contribute to leaf expansion measured by rules or auxanometers and the relevance of such measurements of leaf extension to crop leaf area expansion;
3. to investigate the short term response of cereal leaf extension rates to weather and plant water status using auxanometers in the field.

The results of these investigations are reported in this and three following papers.

MATERIALS AND METHODS

Crops, site, and seasons

The crops were grown on the Nottingham University farm on a site whose edaphic and climatic characteristics have been described previously (Biscoe, Clark, Gregson, McGowan, Monteith, and Scott, 1975; Gallagher, Biscoe, and Scott, 1975). The barley (Hordeum distichum var. Proctor) was sown on 18 March 1972 at a density of 15 g seed m⁻² field giving an establishment of about 425 seedlings m⁻². A 20:10:10 fertilizer was applied to the seedbed to give 5 g N m⁻². Further details about cropping and weather were given by Biscoe, Scott, and Monteith (1975). The winter wheat (Triticum aestivum var. Huntsman) was sown on 30 October 1974 at a density of 12 g seed m⁻² field giving an establishment of about 280 seedlings m⁻² on a field next to the 1972 barley crop. A 33:0:0 fertilizer was applied on 1 May 1975 to give about 10 g N m⁻². Weather conditions during the growth of this crop were described by Gregory, McGowan, and Biscoe (1978). Weeds were controlled by a chemical spray in both crops.

Crop measurements

Details of the sampling and measurements of barley leaf growth were given by Gallagher, Biscoe, and Scott (1976). For the wheat, four replicate samples, each consisting of plants from 0.5 m of row in each of two adjacent rows, were brought back to the laboratory at weekly intervals from 5 November 1974 to 29 April 1975 after which samples were taken twice weekly. The numbers of tillers and plants in each sample were counted. Two plants of modal size from each replicate were retained and six of these were used for measurement and dissection. Similar observations as for barley were made but the tillers in the axils of the second and third leaves were also measured from their emergence until 1 May when rapid tiller death was evident. Because of difficulty in unrolling delicate, young laminae, reliable measurements of width could only be made once it was greater than about 2 mm. When rapid extension began, the variation associated with measurements of leaf dimensions was large with coefficients of variation sometimes as high as 50%. Williams and Rijven (1965) reported similar variation in their controlled environment experiments. Final organ dimensions were estimated from at least 30 organs and the coefficients of variation were about 5%. The distance from the tip of the youngest emerged lamina to the last emerged ligule and laminar width at this point were also measured on wheat. Main stem leaf appearance stage was calculated as the arithmetic mean of the youngest leaf appearing on each culm measured. Throughout this paper the term leaf refers to lamina and sheath.

Thermal time

One problem in analysing field measurements of leaf growth is the wide range of temperature experienced during the growing season as temperature is known to affect cereal leaf growth and appearance rates (Friend, Nelson, and Fisher, 1962; Watts, 1973). In particular, the growth of the wheat occurred over a wide range of daily and weekly mean temperatures (Gregory et al., 1978). To separate effects of temperature from ontogeny, and to enable the growth pattern of different leaves to be compared, plant variables were plotted against 'thermal time' rather than chronological time.
Thermal time is similar to accumulated temperature and a convenient unit is the Celsius degree day (°C d). In this study thermal time ($t'$) was calculated from

$$t' = \sum_{i=1}^{n} (\bar{T}_i - T_b)$$

where $\bar{T}_i$ is daily mean temperature, $T_b$ is a base temperature, and $n$ is the number of days temperature observations. This calculation of thermal time is justified provided that two conditions are met:

1. the temperature response of the growth and development rates being studied is linear over the range of temperature experienced;
2. daily temperature variation is not symmetrical about $T_b$ and temperatures do not fall below $T_b$ for a significant part of many days during the growing season.

Preliminary measurements of barley and wheat leaf extension rates indicated that the first of the above conditions held. In addition, a literature survey showed temperate cereal germination rates (Irwin, 1931), root growth rates (Valovich and Grif, 1974), and development rates (Pohjonen, 1975) to respond linearly to temperature over the range experienced in the field and that $T_L$ was within 1 °C of 0 °C. As temperatures fell below $T_b$ for only very short periods, the second condition was also met. Because mean temperature from 5 cm below to 2 m above the soil surface differed only slightly over periods of several days (Gallagher, 1976) air temperature readings were used to calculate thermal time.

Irradiance has also been shown to affect grass leaf morphology (Friend et al., 1962; Silsbury, 1970). However, total radiation incident on the plants during the growth of any particular leaf was substantially greater than the maximum shown to affect leaf morphology in controlled environments and was therefore assumed unimportant in determining the leaf growth pattern.

**RESULTS AND DISCUSSION**

**Leaf initiation and appearance**

Figure 1A shows the total primordial number of the wheat main stems plotted as a function of time. The rate of primordial initiation increased gradually, contrasting with Kirby's (1974) results for spring wheat which showed two distinct and constant primordial initiation rates; the slower associated with leaves and the faster with spikelets. However, when temperature differences during primordial initiation were accounted for by plotting primordial number against thermal time, two distinct phases of leaf and spikelet initiation were recognizable (Fig. 1B). The leaf primordial initiation rate, normalized to 10 °C was 0.16 (±0.006) primordia d$^{-1}$. This is less than half the rate of 0.37 primordia d$^{-1}$ reported by Kirby (1974) for spring wheat in the field when mean temperature during leaf initiation was about 8 °C. In Kirby's experiment, however, day length was about 14.5 h, compared with 8.0 h for the winter wheat. The barley leaf initiation rate of 0.4 primordia d$^{-1}$ could be calculated only approximately because few measurements were made during this phase. Nevertheless, the rate is close to Kirby's (1974) value for spring wheat measured at the same time of year.

When plotted against time, wheat leaf appearance rate slowed during mid-winter and increased during spring (Fig. 2A). This slowing of leaf appearance rate during winter is typical of cereals (Hoogland, 1964). However, if changes in temperature were accounted for by plotting leaf appearance stage against thermal time, a constant leaf appearance rate equivalent to 0.09 (±0.001) leaves d$^{-1}$ at 10 °C resulted (Fig. 2B). At constant temperature a steady rate of leaf appearance is therefore to be expected and this has been found for wheat, ryegrass, and maize (Friend et al., 1962; Silsbury, 1970; Brouwer, Kleinendorst, and Locher, 1973).
Both primordial numbers and leaf appearance stage of the wheat crop were regressed against thermal time using a range of base temperatures above and below 0 °C. The residual variation always started to increase rapidly with base temperatures greater than +3 °C and less than −3 °C. These calculations, therefore, supported the use of a base temperature of 0 °C. For the barley crop, mean weekly temperature during leaf growth ranged only between 7.9 and 11.7 °C and leaf appearance stage increased linearly with time. Mean temperature during leaf appearance was 9.5 °C and the corresponding appearance rate was 0.12 (±0.003) leaves d⁻¹, comparable to the value of 0.09 obtained for the wheat normalized to 10 °C (Fig. 2b). Kirby (1973) reported a leaf appearance rate of 0.18 (±0.004) leaves d⁻¹ for barley sown at the end of March. Kirby's faster leaf appearance rate was probably due to later sowing and below average temperatures during germination. These factors delayed the start of leaf appearance until towards the end of April when photoperiod was 1.25 h longer and temperature about 2.5 °C higher than for the Sutton Bonington crop where leaf appearance began early because of high temperatures during germination. The lower sowing density of Kirby's crop was associated with ten leaves per plant, rather than nine as at Sutton.
Bonington, and larger leaf numbers are associated with faster leaf appearance rates (Kirby and Faris, 1970).

**Length growth**

When plotted against thermal time the pattern of laminar extension was very similar to that described for wheat by Williams and Rijven (1965) (Fig. 3). The slope of the lines for wheat showed that the relative laminar extension rate \( r_L \) increased to a maximum, attained before leaf emergence, and then gradually declined until maximum length was attained (Fig. 3A). For the laminar length of barley, the shape of the growth curve was similar to that for wheat but an increasingly large fraction of growth occurred before leaf appearance. The flag leaf lamina was very short and extended almost entirely within the sheaths of the preceding leaves (Fig. 3B).

The period of declining \( r_L \) accounted for between 80 and 90% of laminar extension in both wheat and barley and when laminar length was plotted on a linear scale it was conveniently described by a straight line (Fig. 4). The regression lines in Fig. 4 were calculated using all points greater than 0.1 final laminar length \( L (F) \) and up to the last point which was less than 0.9 \( L (F) \) (cf. Dennett, Auld, and Elston, 1978). A steady rate of leaf extension at constant temperature has been shown for leaves of *Lolium perenne* (Wilson, 1975), maize (Grobbelar, 1962), and *Festuca arundinacea* (Robson, 1972). Detailed considerations of growth also indicate that a steady increase of leaf length may be expected when cell extension
FIG. 3. The change with thermal time in length of laminae 1 (○), 2 (△), 3 (□), 4 (▽), 5 (◇), 6 (●), 7 (▲), 8 (◇), 9 (▽), 10 (◆), 11 (○), and 12 (□) for (a) wheat and (a) barley (nine leaves only) main stems. Arrows mark the time of 50% leaf appearance and 'V' on the abscissa indicates the time of initiation of primordia 4–12 (wheat only).
predominates (Richards, 1969). A linear description of laminar length increase enables \( L(F) \) to be described simply as

\[
L(F) = (\tilde{R}_L \times D_L) + L(i)
\]  

(2)

where \( \tilde{R}_L \) is the mean laminar extension rate during the linear phase, \( D_L \) is the duration of that phase \((0.9 \ L(F)/\tilde{R}_L)\) and \( L(i) \) is the laminar length at the beginning of linear growth \((0.1 \ L(F))\). This formal description of laminar extension is essentially the same as that used successfully to describe leaf growth in \( Lolium \) sp. (Edwards, 1967) and \( Populus euramericana \) (Pieters, 1974).

While leaf lengths were plotted against thermal time, a linear growth phase also accounted for about 85% of total extension in both wheat and barley. This allowed leaf extension to be expressed in terms of a mean extension rate \( \bar{R} \) and growth duration \( D \) just as for laminae (equation 2).

**Width growth**

The width of leaves wider than 2 mm increased steadily with thermal time in both wheat and barley. Accordingly, a straight line was used to describe the final 80% of laminar width growth (Fig. 5). No comparable measurements of the width growth of either cereal or grass leaf laminae appear to have been made. The laminar width of \( Populus euramericana \) measured by Pieters (1974) also increased steadily with time at constant temperature and he inferred linear increase in cell size.
Temperature

Because of the inherent variability of dissection measurements of leaf length (see above) extension rates between individual harvests could not be calculated accurately and only the variables $\hat{R}$ and $D$ (equation 2) were studied in relation to temperature. Because mean temperatures during the growth of individual barley leaves varied by only $\pm 2.0 \, ^\circ C$, the barley measurements were not analysed. Changes in $\hat{R}$ were associated mainly with the pattern of change of leaf length with leaf number and analysis therefore concentrated on the effects of temperature on $D$.

Results for a wide range of biological processes show that the reciprocal of process duration is frequently a linear function of temperature (e.g. Braune, 1971; Pohjonen, 1975). Figure 6 shows $1/D$ plotted against mean temperature during the linear extension phase. A straight line described the response well ($P < 0.01$). The
Ontogeny

Figure 7 shows changes in final leaf dimensions with leaf number for the barley and the wheat. In wheat the penultimate lamina was longest (Fig. 7A). This contrasts with Borrill's (1959) results, obtained from glasshouse and laboratory experiments, showing that the laminae of several species of grass and of wheat became progressively shorter after floral initiation (defined by the appearance of double ridges). The pattern of final laminar length with leaf number for barley contrasted with that for wheat (Fig. 7). Laminar length increased to a maximum achieved at the time of double ridge formation, and then declined in a similar fashion to that shown in growth rooms by Kirby and Eisenberg (1965) and in the field by Kirby and Faris (1970). This contrast between wheat and barley was also evident when leaf lengths were compared (Fig. 7); wheat leaf lengths increased until the flag leaf whereas those of barley increased until leaf 5 and then decreased.

For wheat, the increase of final leaf length with leaf number was largely accounted for by faster leaf extension per unit thermal time during the linear growth phase as $D$ was similar for all leaves (mean 210; s.d. 30 °C d). The behaviour of barley was more complex. $D$ for leaves 2–7 was very similar (mean 151; s.d. 8 °C d) but both leaf 8 and leaf 9 had a growth duration of about 220 °C d.
Final laminar width increased from leaf 4 onwards in wheat (Fig. 7A). This increase in leaf width may reflect an increase in apical dome size while these leaves were being initiated as shown for wheat (Kirby, 1974), rice (Yamazaki, 1963), and maize (Abbe, Randolph, and Einset, 1941). There is a general correspondence between laminar length and width for wheat (Fig. 7) but it is not as close as that reported for *Populus euramericana* (Pieters, 1974). For barley, final laminar width increased from leaves 1 to 7 but decreased again in leaves 8 and 9 as did laminar width in the comparable density of Kirby and Faris (1970). This pattern of change of laminar width is associated neither with changes in apical dome size (Kirby, 1977), nor changes of laminar length (Fig. 7A and C).
Unfortunately, no measurements of cell number or dimensions at the end of expansion could be made in this work as these would have shown whether faster leaf growth rates were due mainly to more, or to larger cells. In various circumstances both cell numbers (Uchimya and Takahashi, 1973; McCree and Davis, 1974) and cell size (Borrill, 1959; Friend and Pomeroy, 1970) have been found to be primary determinants of laminar length.

CONCLUSIONS
Throughout this work the use of thermal time allowed calculations of the rate and duration of various processes during periods of chronological time when temperature varied considerably. The concept of thermal time therefore appears to be useful for analysing experimental results where significant temperature variations occur during the developmental or growth processes being measured. However, the need remains to validate further the shape of the temperature response curves for physiological processes as the use of thermal time implies a linear response of process rate from the base temperature, at and below which the process stops.

Despite the importance of cereal leaves in intercepting radiation and providing assimilate for the developing ear and for grain growth, very little seems to be known about the factors which determine their numbers and size in the field. The techniques outlined in this paper for quantitative studies of barley and wheat leaf expansion should prove useful for investigating effects of environment and genotype on leaf size. Measurements of cell number and size in the mature leaf are also needed to distinguish processes of cell division and expansion.

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LITERATURE CITED
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