THE ENVIRONMENTAL CONTROL OF DEVELOPMENT IN WINTER WHEAT

by

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ABSTRACT

1. The relevance of studies of development in crop-weather investigations is reviewed and the aims of the present work are outlined.
2. The procedures used in studying development in field crops of winter wheat are described. The developmental progress of the plants was ascertained by frequent dissections.
3. Primordium initiation at the stem apex is strongly dependent upon apex temperature, which could be accurately estimated from standard meteorological screen temperatures. Like numerous other complex biological processes, initiation has a markedly linear response to temperature: the number of primordia initiated is therefore in direct proportion to accumulated temperature (thermal time). To calculate this requires estimation of the base temperature (T_b).
4. The linear dependence upon temperature of the initiation rates of leaves, spikelets and florets (R_l , R_s and R_f) was evident. Spikelets were initiated faster than leaves; rate changed at a distinct inflexion point, usually at about the end of leaf initiation but sometimes later. $T_b = 0^oC$ for leaves but was higher for spikelets and florets. The shift in T_b apparently occurred because R_s and R_f were strongly influenced by the daylength at inflexion point. When temperature was corrected for daylength influence, $T_b = 0^oC$ for each developmental phase. Inflexion point timing apparently depended upon interaction between vernalisation before crop emergence and photothermal time afterwards.

5. Leaf appearance rate in thermal time was linear but apparently influenced by the direction and magnitude of daylength change at emergence, with a possible secondary effect of current daylength. Leaf extension was strongly related to temperature. The gradient of lamina size up the stem appeared to be ontogenetically determined.
6. Compared with early-sown or fully-fertilised crops, floret survival and grain yield was lower in those sown late or inadequately fertilised, probably on account of their smaller amount of growth per unit of developmental time.

List of Symbols and Abbreviations

c.v.	coefficient of variation
^{o}Cd	degree Centigrade days (thermal time units)
D	a duration (subscripts: l, s, f, initiation of leaves, spikelets, and florets; e, linear phase of leaf extension)
D.A.S.	days after sowing
D.R.	double ridges
F_f	fraction of maximum floret number fertile
F_g	fraction of fertile florets bearing grain
L.A.	leaf appearing
L.A.S.	leaf appearance stage
Ll (f)	final length of lamina
max.	(subscript): a maximum
min.	(subscript): a minimum
M.S.	main stem
N	a number (subscripts: l, s, f, leaves, spikelets, and florets; e, ears)
Nfe	a total number of florets per ear (subscripts: f, fertile; g, grain-bearing)
Ns_f	number of spikelets with fertile florets
Nf_f	number of florets per fertile spikelet
Ng_e	number of grains per ear
R	a rate (subscripts: l, s, f, initiation of leaves, spikelets and florets; a, leaf appearance; e, leaf extension)
$R(^{o}Cd)^{-1}$	a rate in thermal time
S_f	fraction of maximum spikelet number fertile
T	temperature (subscripts; a, air; s, soil)
T_b	base temperature for a process

$\overline{W}_g$	mean weight per grain
ϕ	daylength (includes civil twilight)
ϕ_b	base daylength for a process
ϕ_{inf}	instantaneous daylength at the point of inflexion of initiation rate
$d\phi/dt$	rate of change of daylength

I INTRODUCTION

(i) Weather and Crop Yield

From antiquity, farmers have realised that there is a link between the weather and the yield of their crops. The elucidation of this relationship has been one of the aims of agricultural science from its inception and as one of the classic studies of the 19th century states, "It is, in fact, the distribution of the various elements making up the season, their mutual adaptations, and their adaptation to the stage of growth of the plant, which throughout influence the tendency to produce quality or quantity".

When Lawes and Gilbert wrote this in 1880 they hoped that their analysis of yield data, gathered since 1843 from the continuous crops of wheat on the Broadbalk field at Rothamsted, would go far to show how yield was affected by weather. Yet despite having copious records perhaps uniquely suitable for the purpose, they were unable to reach firm conclusions. Neither did anything more definite emerge from computer analysis of over 60 years' results obtained from continuation of the Broadbalk experiment. (Buck, 1961).

The fact that yields alone have not been very helpful in understanding how crop growth is influenced by weather is not altogether surprising, because "Yield is an ultimate expression or integration of plant development" (Doughty & Engledow, 1928). The word 'development' is used here in a precise sense to describe events that go hand in hand with plant growth. The distinction between growth and development is important.

(ii) Crop Growth and Development

The word 'growth' is generally taken to mean an increase in size, as in the growth of a seedling to become a mature plant.

It is distinct from development, which means the orderly sequence of morphological stages that the plant passes through before reaching maturity. If a plant grows without advancing its progress towards maturity at the same time, then no matter what its increase in size it cannot be said to have developed.

Much of the work on field crops has been devoted to measuring their growth. Study of growth is important in discovering how dry matter is distributed among the parts of the plant and in particular how the distribution affects commercial yield. A wide range of temperate and tropical crops has been studied but cereals have received special attention because of their great importance to man.

A problem in studies of field-grown plants is that the variability of their metrical attributes is large, which necessitates the taking of many samples if precise estimates of the attributes are to be made. If many treatments are being studied it is impracticable to make complicated and time-consuming measurements. The growth analysis methods due to Gregory (1917) and to West, Briggs and Kidd (1920) do not require complicated measurements and therefore have been widely used to study crop growth. Despite their basis of simple observations they have been very informative. Essentially, conventional growth analysis is concerned with how dry matter is produced and used; it is an indirect way of studying the plant's carbon economy. In recent years more direct methods have been used. One line of inquiry has examined the uptake and fate of carbon-14 by leaves enclosed in chambers (e.g. Ryle & Powell, 1976). A second line of investigation has been the use of micrometeorological techniques to study fluxes of carbon dioxide to and from the crop stand (e.g. Monteith, 1962; Biscoe, Scott & Monteith, 1975). Dry matter production, therefore, has been extensively

studied by both conventional and newer approaches. Techniques have also been devised for the measurement of very short-term changes in stomatal aperture and water status, and together with studies of dry matter production have given deeper insights into crop growth processes. Even so, because such work has not been fitted into a framework of development it is still not sufficiently clear how weather influences yield.

It is surprising to find, therefore, that compared to the effort expended on studies of weather and crop growth, the response of plant development to weather has been little investigated. In view of the important relationship of development to yield, stressed some years ago by Doughty and Engledow (see (i)), this lack of attention is both unwarranted and unfortunate. Very often much information about development could have been obtained in the course of growth analysis work.

When development has been studied in the field, observations have often been confined to outwardly visible "growth stages" (e.g. brairding, leaf sheaths erect, etc.). The developmental significance of such stages is uncertain in the absence of a knowledge of concurrent events at the shoot apex. Nevertheless, attempts have been made to relate simple phenological observations to weather, for example the time to flowering in different seasons. For temperate cereals Nuttonson (1956) made a more ambitious and extensive phenological study of crops grown in a wide range of latitudes, but his work provides little detailed information about the course of plant development in relation to weather. In recent years there has been more detailed work on the development of crop plants, but it has mostly been done in growth rooms. The development of a plant in an artificial environment may well differ from what happens in nature: the implications of this uncertainty will be examined next.

(iii) Development in Artificial and Natural Environments

The development of crop plants has been extensively studied in controlled environments. For cereals, development has been found to be strongly regulated by temperature (Friend, 1965; Rahman& Wilson, 1978) including vernalisation (Rawson, 1970; Wall & Cartwright, 1974); by photoperiod (Rawson, 1971; Lucas, 1972), and by light (Friend, 1965). Other work has explored the interaction of weather factors with mineral nutrient supply (Holmes, 1973).

Despite the prominence given to growth room work, results have rarely been used to explain the outcome of field experiments. It seems logical to attempt such an exercise, but it is an unfortunate fact that extrapolation from growth rooms to the field is fraught with difficulty. Evans (1963) has emphasised that, in nature, "Plant development may well have become geared to the natural sequence of changes in the environment . . . if plants are grown throughout in an unchanging environment, or are subjected to abrupt changes in photoperiod, temperature, etc., the results may be misleading." In a particularly apposite remark, Evans reminds us that ". . . the plant may possibly perceive and react to more environmental components and combinations than we can at present think of." The behaviour of plants in pots may not be relevant in the highly competitive conditions of a field crop (Watson, 1963) and in any case the quality and intensity of light in growth rooms is a continuing source of uncertainty (Huxley & Summerfield, 1976).

It is clear that any attempt to comprehend how yield is affected by weather should be based on study in the field of a plant's development to maturity from its earliest stages, for only in this way is it possible to reach conclusions that can be applied with confidence to field crops. Remarkably, few such studies have been made. Those by Kirby (1974) and

Gallagher, Biscoe & Scott (1976) are almost unique in the way development was followed long enough and in sufficient detail to give a complete qualitative and quantitative description. Even these pioneering investigations do not provide enough information for a full understanding of how the development of a temperate cereal in the field is regulated by the weather that the crop experiences. Fuller understanding would be possible if detailed, relevant measurements were made, using the same criteria throughout, on the same variety in several seasons.

The emphasis given to investigations of crop growth in the field has already been outlined. The abundance of reports from such work highlights the paucity of development studies in the field, which are essential for an understanding of how yield is determined.

(iv) Scope of Field Study of Development

Yield obviously depends upon the number and weight of grains per unit area of crop. The number of grains can be expressed in terms of the morphological components of which it consists and Engledow (1925) proposed a simple algebraic statement of this form:

$$Y = p.e.n.g$$

in which yield, Y, is considered as the product of p, the mean plant population per unit area; e, the number of ears per plant; n, grain number per ear, and g, the mean weight per grain. Since then many other field studies have acknowledged the importance of accurately measured yield components (e.g. Bremner, 1969; Pearman, Thomas & Thorne, 1977), reflecting the importance for yield of the number of sites on each plant at which grain may arise. Study of yield components at harvest, however, does not reveal how they depend upon development.

The number of grain sites, as well as of leaves, depends upon the degree and duration of activity of the stem apex, but most of our

knowledge of apical behaviour has come from work done in controlled environments and so does not necessarily mirror what happens in the field. While it is true that Kirby (1974) found that the course of apical development was the same in both environments, this result was obtained with spring wheat and it is by no means certain that a winter variety would behave naturally in growth rooms. Indeed, the vernalisation response alone almost guarantees that it would not.

There is a need to investigate the progress of events at the stem apex in field-grown plants during the entire life of the plant, and to relate apical development to weather. Such a study should examine the extent to which different weather variables regulate the number of leaves, spikelets and florets. It should also try to identify the factors governing leaf expansion and unfolding: leaf area is crucial to plant growth, and each leaf unfolded marks a step along the road to maturity.

A further objective in studying development in the field is the need to be able to make reliable correlations between the plant's outward appearance and its stage of apical development. The publication of more precise scales (e.g. Zadoks, Chang & Konzak, 1974) for describing cereal growth stages has stimulated some work (e.g. Tottman, 1977) aimed at making such correlations more accurate, but additional knowledge is still needed. Programmes for growing cereals which have recently proliferated all stress that the right materials must be applied at the right stage of plant development: calendar date is an unreliable guide (see Appendix II). Even in conventional husbandry systems it has been realised for some years that mis-timed applications of fertiliser or herbicide are at best ineffective and at worst detrimental to yield (e.g.) Scragg, 1952).

(v) Aims of the Present Study

It was decided to study the development of a temperate cereal in the field. Winter wheat was chosen because this crop is very important in human nutrition and because there was already some information about the plant from work done at Sutton Bonington. The main objectives of the work described in this thesis were as follows:

(a) To make a detailed investigation of the course of initiation and subsequent development of primordia at the stem apex of winter wheat grown in field crops, from the time of sowing until just after anthesis.

(b) To determine as far as possible how weather variables influence the initiation of primordia and the change from vegetative to reproductive development.

(c) To examine how weather variables influence the expansion and unfolding of leaves. Apart from the relevance of these processes to crop progress it is appropriate to study them in conjunction with apical development because there is evidence that the apex is involved in their control (Watts, 1972; Peacock 1975).

(d) To explore the relevance of plant development to yield determination.

II CROPS, TREATMENTS, SAMPLING & TECHNIQUES

(i) Crops, Seasons and Treatments

The same cultivar of winter wheat (*Triticum aestivum* L., 'Maris Huntsman') was studied in all the investigations reported here; the work described was done on plants from crops which (except in 1977/8) were grown following usual agronomic practice. Edaphic and climatic characteristics of the site, on the Nottingham University farm at Sutton Bonington, were described by Biscoe, Clark, McGowan, Monteith & Scott (1975).

(a) 1975/6 season

A seed-bed dressing of 20:10:10 (N:P:K) fertiliser was applied to the field on 1st September 1975 at 125 kg ha^{-1} (25 kg ha^{-1} N). On 4th October seed was sown at 167 kg ha^{-1}. Two adjacent plots each 30 x 100m were then marked out: one received subsequent applications of fertiliser (the +N treatment); the other did not (the 0N treatment). The +N plot was given 315 kg ha^{-1} of 20:10:10 NPK (63 kg ha^{-1} N) on 4th April 1976 and 190 kg ha^{-1} of 33:0:0 (63 kg ha^{-1} N) on 6th May. Both plots were treated with 490 l ha^{-1} of herbicide mixture (CMPP + 2, 4-D appropriately diluted) on 5th April.

(b) 1976/7 season

The crop was grown on a field adjacent to that used in 1975/6. Seed was sown on 31st October 1976 at 174 kg ha^{-1}. The farm manager judged that there was no need for a seed-bed dressing of fertiliser, and made no application until 5th May, when the crop was given 380 kg ha^{-1} of 33:0:0 NPK (125 kg ha^{-1} N). By this time considerable nitrogen deficiency was apparent. Herbicide mixture of the same composition as in 1975/6 was sprayed on 2nd May.

Heating cables were installed under part of the crop in order to study the effects of soil warming on plant development. The plot size of 6 x 9.5m was dictated by cable length, power supply and the proposed sampling procedure. An adjacent plot of equal size provided control plants. The cables, each of 0.5 kW heating capacity (Autogrow Ltd. Northumberland), were buried before the crop was sown and were placed about 20 cm deep with about 20 cm between runs. This distribution was chosen to give even heating (Canham, 1964) and to raise the temperature at the soil surface by 4-5^{o}C above ambient (Peacock, 1975).

Stage of apical development was the guide for the timing and duration of heating, which was started on 21st March 1977 after maximum leaf number appeared to have been reached and ended on 15th May when the stem apex was about to rise above the soil surface. Soil temperature was measured by diodes at depths of 1, 5 and 10 cm in the heated plot and at 1 cm in the control plot. During most of the period of heating, the mean depth of the stem apex below the soil surface was about 2 cm. LVDT auxanometers of the type described by Gallagher, Biscoe and Saffell (1976) were used to measure hourly rates of leaf extension in both plots.

(c) 1977/8 season

The sowing dates of the crops of previous seasons fell within a period covering only a few weeks in autumn. To examine further the effect of daylength on development, plantings were made on dates well outside that range.

Small trials were planted in a field no more than 0.5 km from those used previously and having comparable soil and aspect. In previous seasons the irregular spacing of plants in the rows in crops sown by the farm drill had caused some difficulties in sampling:

to overcome this problem as far as possible, a more precise drill - the Øyjard - was used instead. To suit the drill, each plot was 1.5 x 15m. There were 9 plots altogether and 3, chosen at random, were sown on each of 3 dates: 11th October, 2nd December 1977 and 6th March 1978. To ensure an adequate plant population, seed was sown at 256 kg ha^{-1}.

Because the plots were not part of the farm crop the timing of fertiliser application was not decided by farm management. Instead, application rates and timings were based on plant development as revealed by dissection. Nitrogen was applied as a split dressing, half at maximum tiller number and half at maximum spikelet number. Herbicide mixture was applied after DR but before maximum spikelet number. Details of all applications are shown in Table 2-1.

Table 2-1

Fertiliser and Herbicide Application in 1978

	Application Date		
	N1*	N2*	Herbicide Mixture
Sowing			
OCTOBER	9th March	28th April	7th April
DECEMBER	28th April	20th May	5th May
MARCH	20th May	1st June	24th May

*N1 and N2 refer to dressings of 33:0:0 (N:P:K) fertiliser each of 60 kg ha^{-1}

In addition to the records from the three seasons described above, some were available from crops of the same cultivar grown on one of the sites in 1973/4 and 1974/5.

(ii) Sampling

(a) 1975/6

A major problem in sampling was that not all attributes to be studied had the same variance. For example, the number of primordia per MS apex was far less variable (c.v. = ca. 5%) than the number of tillers per plant (c.v. = ca. 25%). Leaf length had a large variance during fast extension (c.v. = ca. 40-45%) but a small variance in mature leaves (c.v. = ca. 10%). Ideally, enough samples would be taken to estimate the most variable attributes to within 10% of the mean or less (cf. Misselwitz, 1975) but this is impracticable.

Immediately after the crop had emerged, a preliminary investigation was made to ascertain the size and number of samples that would be needed to give a standard error of 10% of the mean or less in estimates of plant population. The results showed that 6 samples each consisting of a 0.5m length of two adjacent rows would be sufficient. Because plant population is one of the more variable attributes (c.v. = ca. 20% in the crops studied), and because 6 samples of that size could be taken at each harvest without exhausting the supply of plants, each plot was divided into 6 blocks of equal size.

Plants were harvested at intervals determined by their rate of development and harvests were of two kinds. A 'TD' harvest consisted of 0.5m of two adjacent rows: the plants were dug up and tillers were counted on all of them, a sub-sample being used for dry weight, leaf growth and dissection observations. In the interval between TD harvests, a small sample of plants was taken for leaf growth and dissection observations only: this was called a 'D' harvest. In each TD harvest, plants were dug up at a randomly chosen spot in each block of the two treatments. A 'D' harvest consisted of 10 plants removed from a discard area of 1m diameter around the

TD sample position. Until the beginning of March, alternating TD and D harvests were made fortnightly; during March TD was weekly and D fortnightly, and from the start of April onwards a TD harvest was taken at the beginning of each week and a D harvest at the end.

(b) 1976/7

Each plot was divided into 6 blocks as before, but owing to the small size of the plots and the total number of samples required during the season, all samples were of 10 plants. Samples of this size gave errors of 10% or less in apical development measurements made in 1975/6. TD and D harvests followed the same pattern as in 1975/6 but both were taken weekly once soil warming had begun.

On several occasions, 6 samples of 0.5m lengths of adjacent rows were dug up at random points in the crop outside the experimental plots. These samples were necessary to make more accurate estimates of tiller numbers and plant population than those obtained from the small samples within the plots.

(c) 1977/8

As in 1976/7, small samples were dictated by the small plots and the total number of harvests required. For consistency with the previous seasons, 6 samples were taken from the plots of each sowing date: on each harvesting occasion 10 plants were removed at two random points in each plot. In the October and in the December sowing TD and D harvests were made at the same intervals as in the 1975/6 crop, but in the March sowing, plant development was faster and so TD and D harvests were made weekly.

Estimates of plant population were made by digging up lengths of rows as before.

(iii) Observations and Techniques

(a) Meteorological Observations

1. Field measurements

Details of the computer-controlled data-logging system used in the 1974/5 wheat crop are given in Biscoe, Clark, Gregson, McGowan, Monteith & Scott (1975) and Gallagher (1976) detailed the micrometeorological measurements that it recorded. The same instrumentation was used in the crops grown in 1975/6 and 1976/7.

2. Standard records

Standard records from an official climatological station were available for all seasons (cf. Gallagher, 1976). Neither of the sites referred to in the present work was more than 1km away from the station and both were due north of it.

Because temperature is particularly relevant in crop growth and development studies, Gallagher investigated thoroughly the extent to which temperatures recorded in the standard meteorological screen represent those that the crop experiences. He found that there was very good agreement between them, particularly for periods longer than a few days, so that screen temperatures could be used with confidence in an analysis of the response of a crop to the temperature regime of the field environment. (Chapter 3).

(b) Plant Observations

1. Tiller counts

The tiller in the axil of the coleoptile was designated T_c and that in the axil of a foliage leaf was given a number corresponding to the leaf, e.g. T_1 was the primary tiller in the axil of leaf 1. When a leaf was removed in dissection (b.5) a note was made of the tiller that it subtended. A tiller was defined as having emerged when the tip of its prophyll had grown out of the sheath of the

subtending leaf. Generally, the only tillers to emerge were those in the axil of the coleoptile and of the leaves up to 3 or 4. The tiller in the axil of leaves 5 and 6 rarely grew to more than 5 or 6 mm long, and in the axil of succeeding leaves remained a small mound visible only with a microscope. Even under the microscope no bud was visible in the axil of leaves higher than 7 or 8, according to season. The total counted, including T_c and up to the smallest bud visible, was the plant's tiller bud complement.

2. Dry weight

In 1975/6 and 1976/7, 6 modal plants from each TD sample were divided into main stem (MS) and the classes (T_c, T_1, etc.) of primary tillers. Within each sample, the MS and each primary tiller class was bulked separately for weighing. All material was dried for 48 h in a forced-draught oven at 60-65° C. These results are not reported.

3. Green area

In 1976/7 only, plant green area was measured. A Patton electronic planimeter was used to determine the leaf and stem area of the MS and of each class of tiller. Green area was always measured on the plants used for dry weight determination.

4. Leaf extension

The construction and performance of LVDT auxanometers designed for the accurate measurement of leaf extension has been described by Gallagher, Biscoe & Saffell (1976). In 1976/7, 8 auxanometers linked to the data logger were used to monitor continuously the response of hourly leaf extension rates to soil and air temperatures: four were sited in the warmed plot and four in the control.

5. Dissection observations, methods and criteria

At every harvest, two modal plants of each sample were reserved for dissection, one of them being intended as a standby in case the first was damaged during manipulation.

Figure 2-1

Stem apex of a plant from the October 1977 sowing, dissected on 20th December 1977. The plants ultimately had 12 leaves. The primordium of the tenth leaf (10) has begun to differentiate; that of the flag leaf (12) has just been initiated. The apical dome (see text) lies above primordium 12: l & d are its length and diameter, respectively.

Figure 2-2

Stem apex of an October-sown plant at the end of March 1978, showing double ridges (DR). In each pair of ridges the lower one (L) corresponds to a leaf, in the axil of which a spikelet will develop from the primordium forming the upper ridge (U). Thirteen spikelet sites are present.

Figure 2-3

A spikelet from the same sowing at an early stage of floret initiation (early May). Lower and upper glume primordia (G1 & G2) are at the base of the spikelet; above, florets 1 & 2 have been initiated, and floret 3 is not yet big enough to be rated as present (see text).

Figure 2-1

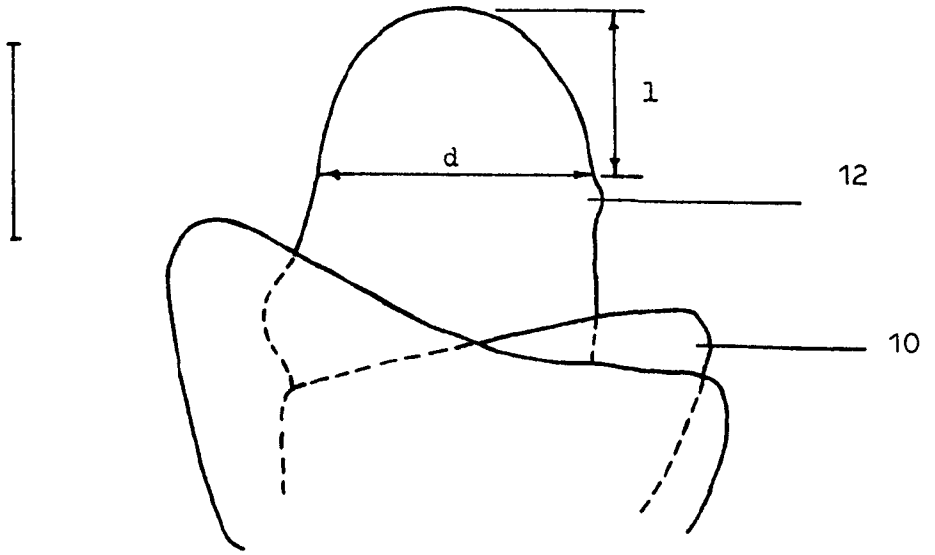


Figure 2-2

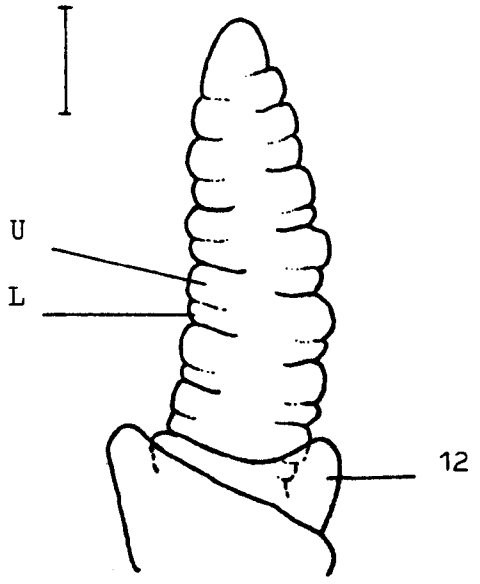
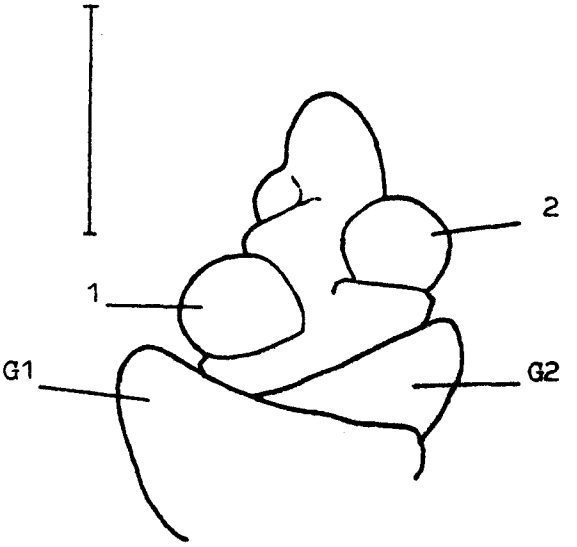


Figure 2-3



The scale line is 0.1 mm

Dissection always followed the same procedure. First, leaf appearance stage (Chapter 5) was noted and the number of emerged tillers counted. Second, the leaves were removed one by one until a leaf about 1 mm long was reached. As each leaf was removed its length from tip to ligule was measured by rule. Laminar width was measured at about half way along the length. Length was easily measured on all leaves down to 1 mm long, but width could not be reliably estimated on any less than about 3 mm wide. Dissection was continued under the stereomicroscope (x32) once a leaf less than about 5 mm long was reached. In 1976/7 only, sheath length and width was also measured. After removal of the leaf about 1 mm long, there remained a series of smaller ones that had begun differentiation, and these merged acropetally into primordia in which no differentiation was apparent: the whole series ended with the primordium most recently initiated (Figure 2-1). Following Kirby (1977) a primordium was considered as present when it bulged beyond the imaginary line extending along the smooth flank of the apical dome. The apical dome is defined as that part of the apex lying above the most recently initiated primordium (Figure 2-1). Dome length and width (Figure 2-1) was measured in 1976/7, using a monocular microscope fitted with an eyepiece graticule. Because there was no visible difference between leaf and spikelet primordia at the time of their initiation, primordium number was recorded as the total (N_p) produced by the apex. This number included the primordia present in the seed and was given by adding together the number of leaves 1 mm or more long and the number of smaller leaves and undifferentiated primordia.

Spikelet development was first apparent when double ridges (DR) began to form (Figure 2-2), by which time several undifferentiated primordia had accumulated at the apex (Chapter 3). When florets began

to develop, the number of florets in each of the odd-numbered spikelets was counted. A floret was rated as present when it bulged beyond the primordium of the lemma subtending it (Figure 2-3). Once the glumes at the base of the spikelet had grown so large as to conceal the florets, dissection and counting were confined to the ninth spikelet, which lies in the region of the ear where development is most advanced and where the resulting grains are the largest of all.

In 1975/6 and 1976/7, the development of the MS and T_1 was studied, and dissection and leaf measurement were both done on each. In 1977/8, only the MS was studied and no leaf measurements were made.

(c) Measurement of development

The initiation of primordia is an orderly sequence of distinct ontogenetic events; it has already been stated that the plant's progress through such a series of well-marked morphological stages is development (Chapter 1). The initiation of each primordium constitutes a unit of developmental time.

Major developmental units in the plant's life history (see Appendix I) constitute developmental phases. For example, the period during which leaf primordia are formed is the vegetative initiation phase. Development is slow when a phase takes a long time and fast when it takes a short time: the inverse of the phase duration gives the development rate.

A study of apical development requires a suitable scale for estimating development rate. Scales intended for agronomic purposes (Chapter 1) are inappropriate for the present work and in any case they would be too coarse a measurement of developmental time. A simple scale for estimating development can be obtained by giving each distinct stage of apical differentiation a number: numerical

scales of this kind were used by Aspinall and Paleg (1963), Langer and Hanif (1973) and others. They were derived for use in growth room experiments and often concentrate on the stages after DR. They do not necessarily measure development rate even under constant conditions. In any case the long span of developmental time before DR is either represented by only one or two numbers, or is omitted, so these scales are of limited use when the progress of apical development is followed from shortly after sowing, as in the present work.

A scale of chronological time may be used but is inadequate since it does not allow for changes in development rate caused by variations in the weather. Because temperature has a strong influence on development rate, a scale of time corrected for temperature was used and is described in Chapter 3.

(iii) Calculating and Statistical Procedures

(a) Mean temperature

Mean daily air temperature, $\overline{T}_a$, was calculated from the meteorological screen minimum ($T_{min.}$) and maximum (T_{max}):

$$\overline{T}_a = \frac{T_{min} + T_{max}}{2}$$

To calculate thermal time above a series of base temperatures (Chapter 3) a computer programme was used which estimated the diurnal course of air temperature by fitting a modified sine curve to the daily screen temperatures. Details of the programme (TEMPSUM) and the assumptions made in developing it are given in Gallagher (1976).

(b) Curve fitting procedures

In many of the graphs presented, y is a linear function of x: linear regressions were fitted using a standard least squares procedure.

In some relations it was apparent that there were two straight lines, with a change in slope at a point of inflexion (Chapter 4). It was easy to see within which region this point lay but difficult to decide on the appropriate break-point of the data to be included in fitting each line. To overcome the difficulty a "broken-stick" procedure was used: for a specified selection of breaks of the data this fitted the two straight lines to all the points in the data set. Changing the break position by one data point at a time, the two lines were found that gave the smallest mean square deviation from the regression for the whole data set. The intersection of the two lines so fitted gave the required point of inflexion.

Polynomial regressions were fitted using a least squares procedure derived by the Nottingham Algorithm Group (cf. Gallagher, 1976). Significant quadratic components in a regression could be tested; the quadratic component was taken as being significant if the variance estimate of the second degree polynomial was less than 60% of the variance of the first degree polynomial.

III INITIATION OF PRIMORDIA

I: DESCRIPTION OF THE SYSTEM AND BASIS OF ANALYSIS

(i) The Shoot Apex and Primordium Initiation

When the cereal grain is sown, the shoot apex of the embryo plant already carries leaf primordia initiated during grain development in the ear. Their number is a characteristic of the species, varying from two in oats to five or more in maize (Bunting and Drennan, 1966). Following imbibition and the resumption of cell activity, additional primordia are initiated by the apical dome in acropetal sequence. The earlier primordia of this series become leaves and the later ones the sites where spikelets are initiated during reproductive development. Details of cereal primordium morphology and histogenesis are given by Sharman (1945) and Barnard (1955).

(a) Ontogenesis at the apex

In the descriptive terminology of Sharman (1945) the apical dome tissues consist of three cell regions. The surface layer (hypodermis) and underlying dermatogen each form a shell one cell thick; within these layers is the central core (corpus). The first structural sign of leaf inception is a periclinal division in one or two cells of the hypodermis on the flank of the apical dome, followed by a similar division in an immediately adjacent dermatogen cell. From this localised site, further divisions spread laterally, forming a crescentic primordium thickest at the point of origin and tapering to either side (Barnard, 1955). As in other Gramineae, the primordia of wheat are laid down in two opposite ranks whose members alternate. The time between the initiation of successive primordia is a plastochron. In a variable number of the basal leaves, a tiller

bud arises in the axil of the young leaf about 3 plastochrons after it is initiated. Following initiation, each foliage leaf primordium continues growing both upwards and sideways, so that it soon overtops and ensheaths the developing apex. This rapid expansion of each leaf primordium characterises the vegetative phase.

After a variable number of primordia destined to become leaves have been initiated, there are changes that signal the onset of reproductive development. The shoot apex elongates: primordia are produced faster but their further development is arrested so that a succession of undifferentiated ridges accumulates: morphologically these are leaf primordia but they do not develop further.

Instead, periclinal divisions occur in cells of the peripheral corpus tissue between two ridges: concurrent divisions occur in the hypodermis and dermatogen, with meristematic activity extending transversely around half the axis circumference (Barnard, 1955). These divisions result in the appearance of another lateral ridge of tissue - the spikelet primordium - subtended by the original leaf primordium of arrested development (Fig. 2-1). Each spikelet is thus an axillary structure morphologically equivalent to a tiller bud. Because of the shape and position of the spikelet primordia at this stage is known as <u>double ridges</u> and many workers take it as the true beginning of floral initiation (but see Kirby, 1974, and Chapter 4). The apical dome continues to initiate single ridges, which pass very quickly to the double ridge stage. Doubling begins in the mid-region of the embryo inflorescence. When it starts about half the final number of spikelet primordia have been initiated (Chapter 4 (ii)) and once begun it spreads rapidly towards the inflorescence base and tip. The upper ridge of each pair develops further to become a spikelet and obliterates the lower member. The number of spikelets

cannot increase further once a terminal spikelet has formed: the resulting completed inflorescence is termed the ear. In the mature ear the lower member of each ridge pair survives as a vestigial subtending prominence in the basal spikelets. At the first spikelet node it forms a distinct narrow encircling flange, the collar, which sometimes reveals its nature by developing far enough to become a small leaf.

The apical dome of the spikelet itself has the same tissue organisation as that of the vegetative apex. It initiates two sterile basal glumes followed by a succession of lemmas, in a pattern like that of leaves on the main axis. Glumes and lemmas are indeed modified leaves, having the same histogenetic origin from the spikelet apex as leaves have from that of the main axis. (Barnard, 1955). In the axil of each lemma a floret primordium is initiated: floret and spikelet are thus both axillary to a modified leaf primordium.

The spikelet positions where double ridges first appeared are also the first to start initiating florets. Each spikelet primordium rapidly differentiates the floral parts: first the palea, then lodicules, stamens, and finally the carpel. When stamens form in the most advanced florets, spikelet number reaches its maximum as a terminal spikelet is initiated. Because of this the wheat spike is usually said to be determinate, in contrast to barley where a terminal spikelet is wanting and the spike is thus indeterminate. But Fisher (1973) argues that wheat too is truly indeterminate, because the apical meristem remains projecting beside the last-formed floret of the terminal spikelet.

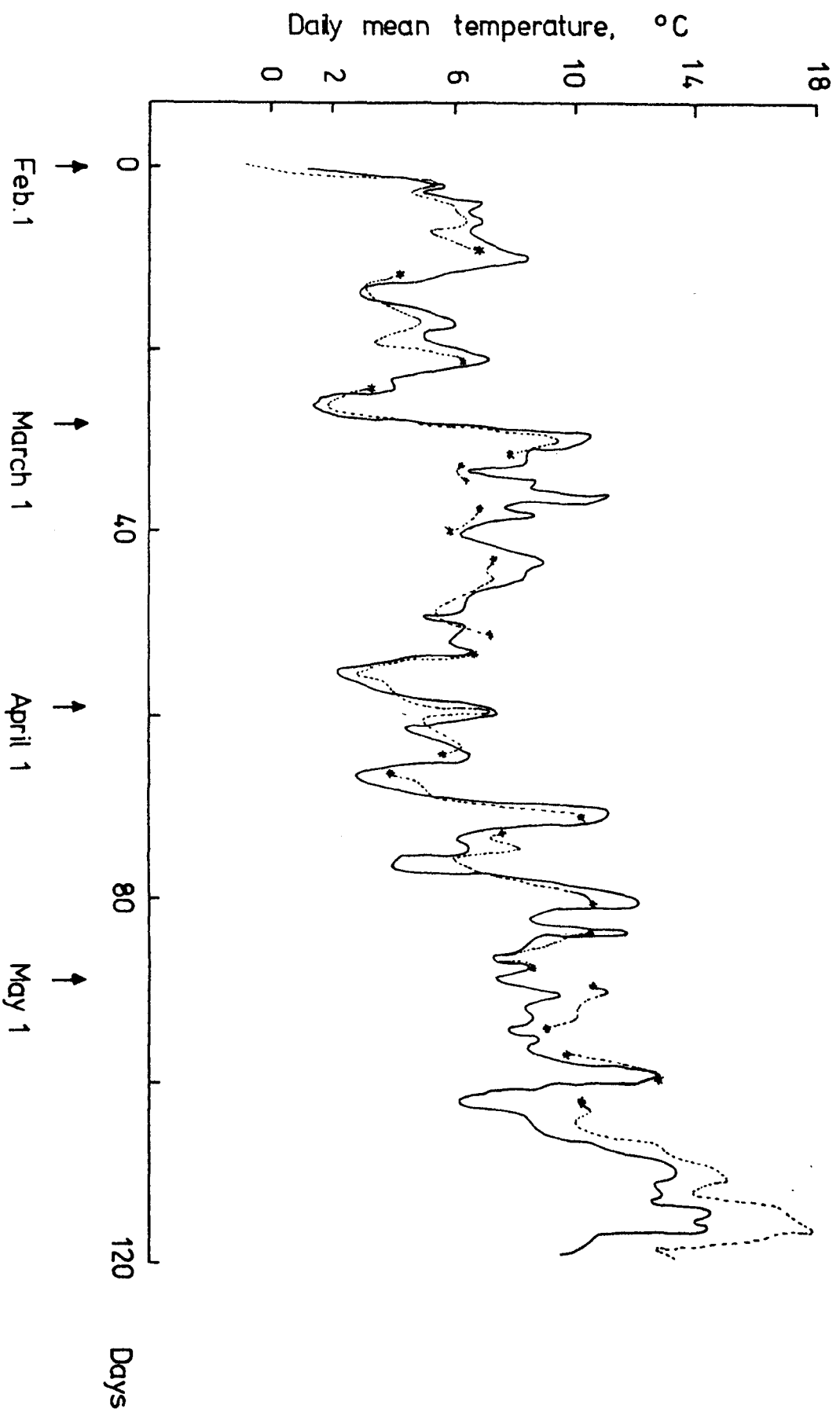
(ii) Initiation in the Field: Temperature Relationships

Primordium production is an end product of processes strongly dependent on temperature; because temperatures change rapidly and continuously in the field, initiation rate varies with time. Field measurements on spring cereals presented by Kirby (1974, 1977) and Gallagher et al. (1976) showed this effect, but the present study investigated a winter variety which developed over a wider temperature range and the effect of temperature on initiation rate was more evident (Chapter 4). Because initiation rate responds to the temperature at the plant apex (Watts, 1972; Peacock 1975) that is where temperature should be measured, as in work reported by Gallagher (1975).

In this study the nearest appropriate temperature available was a continuous record by diodes at 1 cm. depth. While apical primordia were being initiated, the apex was about 2-3 cm below the soil, emerging above the surface at about the time that floret initiation was ending. The record was reliable only during the latter half of the 1976/7 season. If, as found by Gallagher, daily mean temperatures at shallow soil depths corresponded closely to the mean air temperature recorded at 2 m. height in the screen at the nearby meteorological site, then screen temperatures would be a good estimate of those experienced by the apex.

Figure 3-1 shows that the daily mean soil temperature at 1 cm was close to the mean screen temperature and for periods of several days, agreement was even better. The fact that the mean difference between soil and air temperature is small implies little net exchange of sensible heat between the atmosphere and the ground - a useful feature of our maritime climate but not a general rule.

Figure 3-1 The relationship of daily mean temperature recorded in the screen (2m) at the meteorological site (solid line) with daily mean of hourly averages in soil (1 cm) recorded by soil diodes at the field site (pecked line). Breaks in the soil temperature record were caused by incomplete data on some days and are shown by a gap and asterisks.


Daily mean temperature, °C
0
2
6
10
14
18
0
40
80
120
Days
Feb. 1
March 1
April 1
May 1

An accurate estimate of apical temperature was important; initiation of primordia is strongly dependent upon temperature, and a comparison of the progress of initiation in different seasons was to be based on the degrees of temperature per day effective for the initiation process. Before this could be done two fundamental points had to be considered; first, the relation of initiation to temperature; and second, the determination of the lower threshold temperature for the initiation process - its base temperature, T_b. The shape of the temperature response of the rates of developmental processes such as primordium initiation will now be dealt with.

(a) Temperature relations: principles

Simple in vitro biochemical reactions proceed at a rate R_n related exponetially to temperature by the Arrhenius equation:

$$\log_e R_n = \frac{-E}{R\theta} + \log_e B$$

where R_n is the rate of reaction at a thermodynamic temperature θ, R is the gas constant, E is the activation energy for the reaction and B is a constant.

Reviewing the problem of shape of the response to temperature for rates of growth and development in vivo, Gallagher (1976) concluded that the Arrhenius equation often did not provide a satisfactory description, for many reports showed that the rate/temperature relationship was linear rather than exponential.

There is considerable evidence for the linear relation of rate to temperature, for both primordium initiation and for other developmental processes in crop plants as well. From controlled environment work, a linear relationship with temperature was apparent for leaf initiation in maize (Coligado and Brown, 1975) and for spikelet initiation and leaf appearance rates in wheat (Friend, Helson and Fisher, 1962; Friend, Fisher and Helson, 1963; Halse and

Weir, 1974). More relevantly to the present study, many field measurements also reveal a linear dependence of rates on temperature. The time from emergence to heading in wheat, oats and rye (van Dobben, 1962); from emergence to flowering in peas (van Dobben, 1962; Balvoll and Bremer, 1965) and in spinach (Boswell, 1934) all show a linear dependence of rate on temperature: this is true also for leaf appearance rates (Peacock, 1975, 1976; Thomas and Norris, 1977).

In older work temperature responses were described in terms of 'cardinal points', i.e. minimum, optimum and maximum temperatures for the process concerned. Though such descriptions are often for rates of growth (e.g. Leitch, 1916) the concept is equally applicable to rates of development. Leitch presented a temperature response curve for the growth of pea roots. The curve showed distinct cardinal points: from a couple of degrees above the minimum temperature, and up to the optimum, at which growth was fastest, the growth rate increased almost linearly with temperature. A linear relationship between development rate and temperature may be described within the cardinal points concept. Figure 3-2 shows Leitch's curve as a pecked line with the linear portion emphasised by a solid line. The linear relation is assumed to hold over most of the temperature range (A-B) which the plant normally experiences. Temperatures will not often go outside this range, so the amount of a developmental process occurring will, other things being equal, be directly proportional to the sum of mean temperatures measured over fixed periods, e.g. hours or days (cf. Arnold and Monteith, 1974). To initiate each number of a developmentally identical series (e.g. leaf primordia) will thus require an equal sum of temperature. Calculation of temperature sums requires a knowledge of the minimum temperature at which development stops.

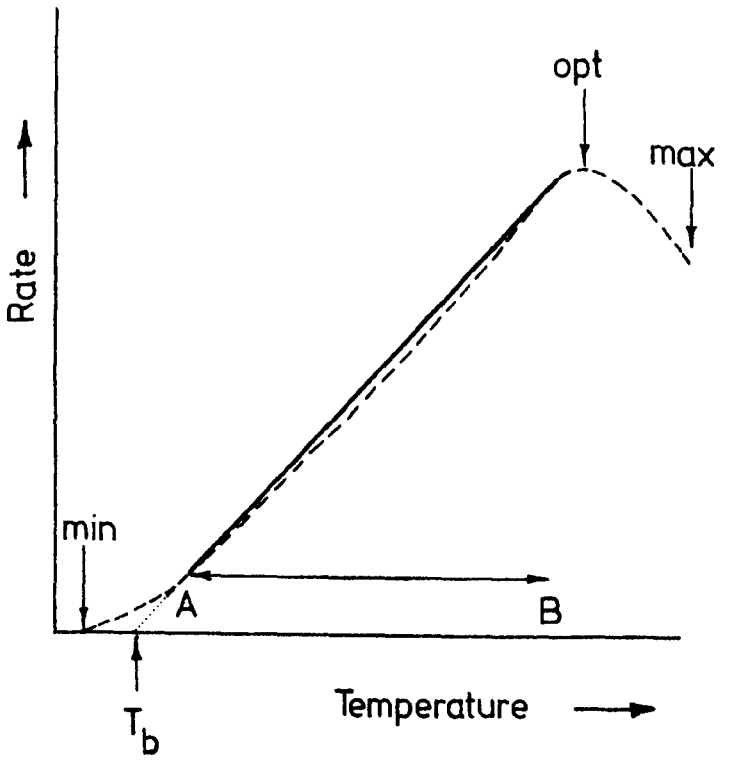


Figure 3-2 The response of process rate to temperature in terms of the 'cardinal points' concept. The pecked line is Leitch's (1916) curve for extension rate of pea roots vs. temperature. Over much of the temperature range (A-B) the response may be considered linear and a base temperature, T_b, may be found by extrapolation. See text for further details.

Near the minimum, development rates are so slow that it is difficult to measure them accurately enough to observe directly the temperature at which development ceases. But, if the development rate response is truly linear, a small extrapolation downwards on the graph will cut the x-axis at a temperature very close to the physiological minimum (cf. Campbell et al., 1974). This intercept is termed the base temperature for the developmental process concerned and has the symbol T_b. Only temperatures above the base value are effective in promoting the developmental process. The summation of effective temperature has been given a variety of names, e.g. accumulated temperature; growing degree-days; heat units. Commenting on this diversity, Gallagher (1976) suggested that to emphasise its components it should be called "thermal time" and given units of degree Centigrade days (^{o}Cd), a useful notion which is adopted here.

On some days in the field it is too cold for any development to take place because the temperature never rises above the base. Hence, thermal time cannot be calculated accurately without a continuous temperature record. An accurate estimate of T_b is also essential and methods for determining T_b are now considered.

(b) Methods for determining base temperature

The base temperature for growth or development, or for both, has been determined for a number of crop plants: Iwata (1974) summarised the information available. An objection to some of the reported values of T_b is that the criteria for choosing the stated value are not given (e.g. Katz 1952; Robertson, 1973). Other workers detail exactly why a given value was chosen for T_b, as in Boswell (1934); Madariaga and Knott (1951); Hoover (1955); Reader (1975), and Gallagher (1976). Nearly all of this published work was done on crops in North America. In the continental climate of America, the

relationship between plant, soil and air temperatures may differ appreciably from that which obtains in our own maritime climate (see (ii)). This uncertainty may mean that the methods for determining T_b used by the American workers are not really suitable for use in our climate. Nevertheless, some of the methods in these reports were tested by application in the present work.

Usually, in determining T_b the thermal time accumulated above a series of postulated bases is calculated between either sowing or emergence and a later developmental event such as flowering. This procedure can be repeated for a range of sowings or locations or both. The base temperature can then be defined as the value of T_b giving the least variability in thermal time for the developmental period concerned.

The similarity among published methods for determining T_b was emphasised by Arnold (1959), who pointed out that the methods really differed only in the statistic chosen as an estimate of the variability of thermal time. Some used standard deviation, some the coefficient of variation (c.v.), and others used both. He concluded that the most appropriate criterion was to find the base temperature value that minimised the coefficient of variation between thermal time sums, and that that value should be taken as T_b. Some of the methods that workers have used to determine T_b are now dealt with.

1. Boswell (1934): Spinach (Spinacia oleracea)

For the time from emergence to flowering in spinach, Boswell calculated a thermal time sum using a series of bases. He also calculated an exponential index sum for the same period: this he did by multiplying mean daily temperature by an exponent derived from the Arrhenius equation. The thermal time sum consistently gave the lower c.v. between sowings: the lowest

c.v. was given by a T_b of 36.5°F, so this temperature was taken as the appropriate base. Because the thermal time sum gave a lower c.v. than the corresponding exponential index sum, this suggests that the relation of development rate to temperature was linear and not exponential.

2. Madariaga and Knott (1951): Lettuce (Lactuca sativa)

These workers investigated T_b for the growth of lettuce. They noted that the c.v. fell as the base for accumulating temperature was lowered. Their guide for the eventual choice of T_b was the minimum temperature at which lettuce plants appeared to grow in the field.

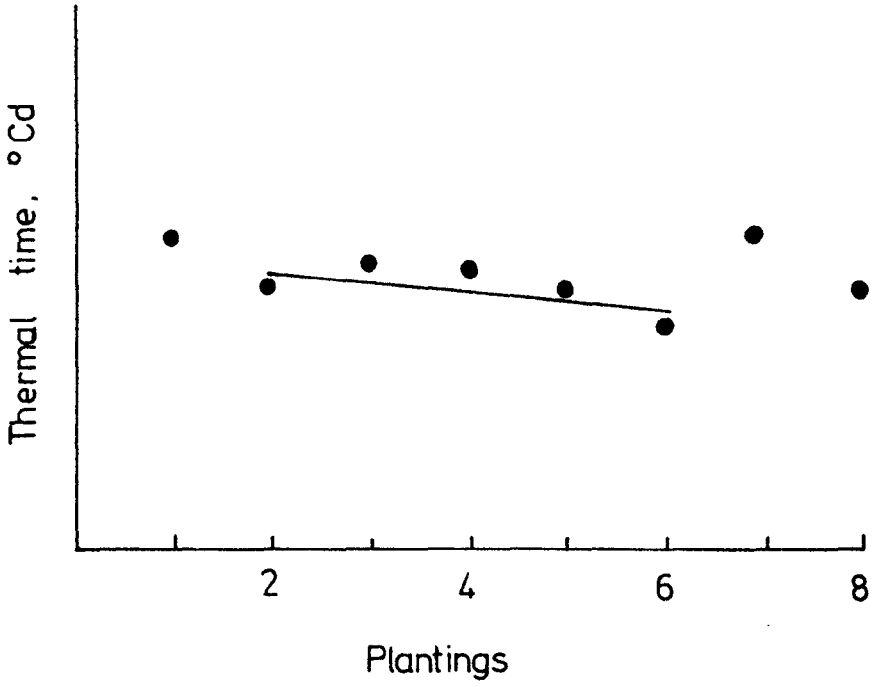
3. Hoover (1955): Southern pea (Vigna sinensis)

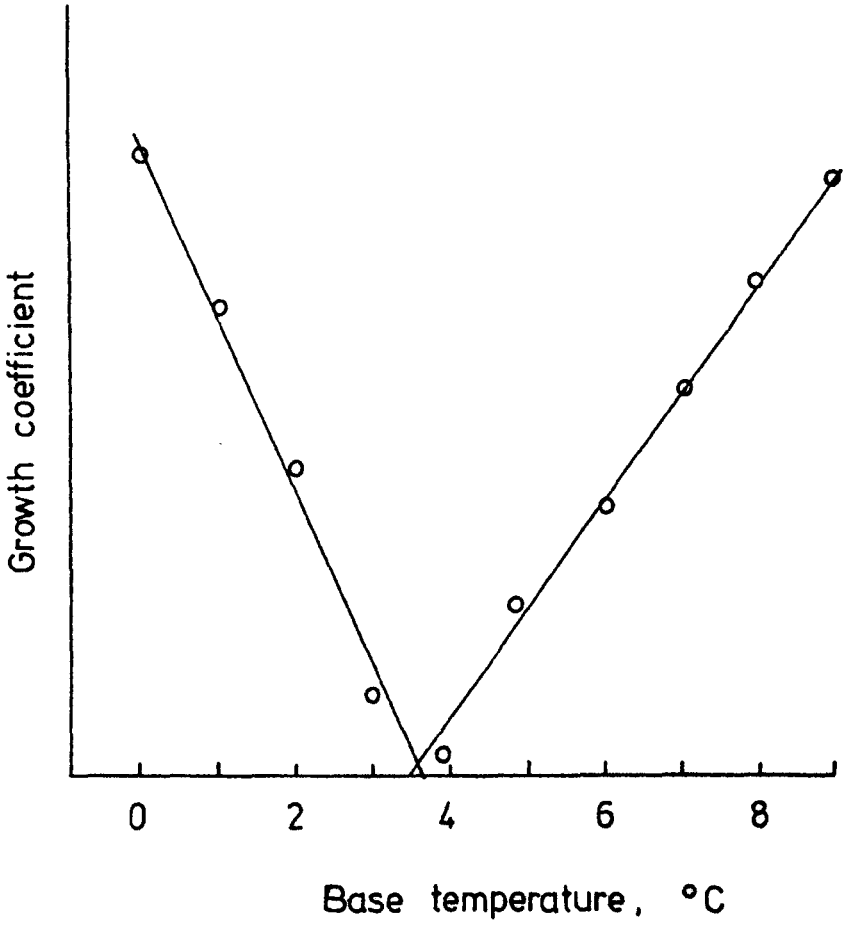
In a series of eight plantings, Hoover calculated the thermal time from sowing to flowering; for each putative base temperature, he then plotted the thermal time sum for each planting against an x-axis of planting date, and fitted a linear regression to the five points "which deviated the least from linearity" (Figure 3-3a). The slope of this line was the "grown coefficient" for that base temperature and it was negative for temperatures below T_b and positive for those above. After they had been plotted against bases, a line was drawn through the negative and positive coefficients, as shown in Figure 3-3B, to give an x-axis intercept which was taken as T_b for field conditions. There are several uncertainties in Hoover's method: the validity of fitting a line to only five of the eight points is questionable; it is not clear if the selection was made objectively or not; and the success of his procedures probably depended on the fact that daylength and mean temperature both increased with planting date.

Figure 3-3 Diagrams to illustrate the method of Hoover (1955) for finding T_b.

(a) Determination of "growth coefficient". Thermal time taken for completion of the same developmental stage in the different plantings is plotted against planting order; the growth coefficient is the slope of the line fitted to the five consecutive points deviating the least from linearity.

(b) Each growth coefficient is plotted against its base temperature. When two lines are drawn as shown, their intersection indicates T_b on the x-axis - in this hypothetical example, T_b = ca.3.5°C.


Thermal time, °Cd
2
4
6
8
Plantings


Growth coefficient
0
2
4
6
8
Base temperature, °C

4. Reader (1975): Dogwood (Cornus florida)

The method used in this work involved temperature summation during different periods before the flowering date. For each period a temperature sum was calculated above each of a range of bases, and for each postulated base the c.v. of the sums for the various periods was found. Reader's rather tortuous procedure was apparently necessitated by the wide geographical area of the study and by uncertainty about when the process that controlled flowering date began. She does not state what developmental phase was thoughtto be identified by the results obtained. Her method is inappropriate to the present study and is not considered further.

5. Arnold (1959): Maize (Zea mays)

Arnold used a regression of mean temperature against mean rate of development. With only one development observation (silking) in each sowing, he was nevertheless able to estimate a mean rate. When this was plotted against mean temperature, T_b was the intercept on the x-axis for zero rate. The method is, of course, especially suitable for use with detailed data on development, as in the present study.

6. Gallagher (1976): Wheat (Triticum aestivum)

To determine T_b for the appearance rate of wheat leaves, Gallagher fitted a least-squares linear regression to leaf appearance data plotted against thermal time above each of a series of postulated base temperatures. The chosen T_b was that minimising residual variation about the fitted line.

For a range of base temperatures, the **principle of** Gallagher's method was tested for the ideal case of a uniform rate of leaf appearance in **thermal** time, using actual

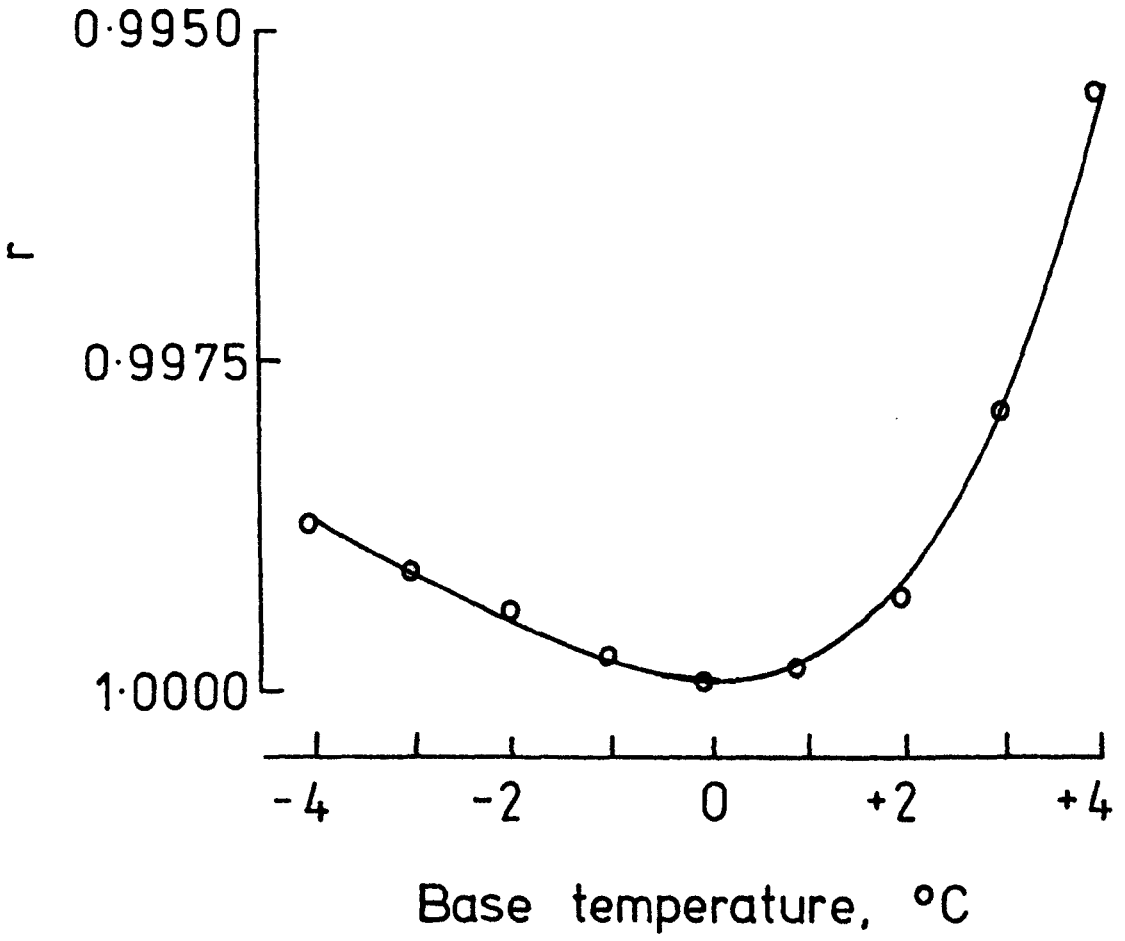


Figure 3-4 Distribution of values of the correlation coefficient, r, from an ideal case test of Gallagher's (1976) method for finding T_b. (See text for details). The base temperature chosen as T_b is that which minimises the residual variation (i.e. when r is largest): T_b in this case is therefore 0°C.

meteorological data and an assumed T_b value of $0^{\circ}C$. The line fitted to leaf appearance rate in thermal time calculated above T_b was the one that minimised the residual variation (Figure 3-4).

(iii) Quantitive Analysis of Development

There are differences between cereal varieties in the number of vegetative and reproductive primordia initiated (Cooper, 1956; Austin & Jones, 1974). Within a variety, these numbers vary appreciably between different crops and depend on factors such as sowing date, weather and nutrition, which influence the course of the developmental processes responsible for organ initiation.

From his data on spring wheat, Kirby (1974) proposed that organ initiation should be analysed quantitatively; each developmental phase can be described in terms of a mean rate and a duration. If $\overline{R}$ is the mean rate of organ initiation during a developmental phase and D is the phase duration, then the number (N) of organs initiated during that phase is given by:

$$N = \overline{R} \times D$$

This is the essence of Kirby's scheme. The next chapter will show how it can be used in an assessment of the effects of environmental factors on development in the field.

IV INITIATION OF PRIMORDIA II : EXPERIMENTAL EVIDENCE

(i) Introduction

By studying the whole course of primordium initiation, it should be possible to find the relative importance of weather factors within and between seasons in the control of leaf, spikelet and floret numbers. Rate of initiation in the field varies with time because of temperature fluctuations, but the data can be analysed by taking temperature into account. To do this T_b has to be accurately estimated so that the daily temperature effective for development can be calculated and accumulated to give thermal time sums.

(ii) Time and Temperature Relationships

(a) Event correlations in the field

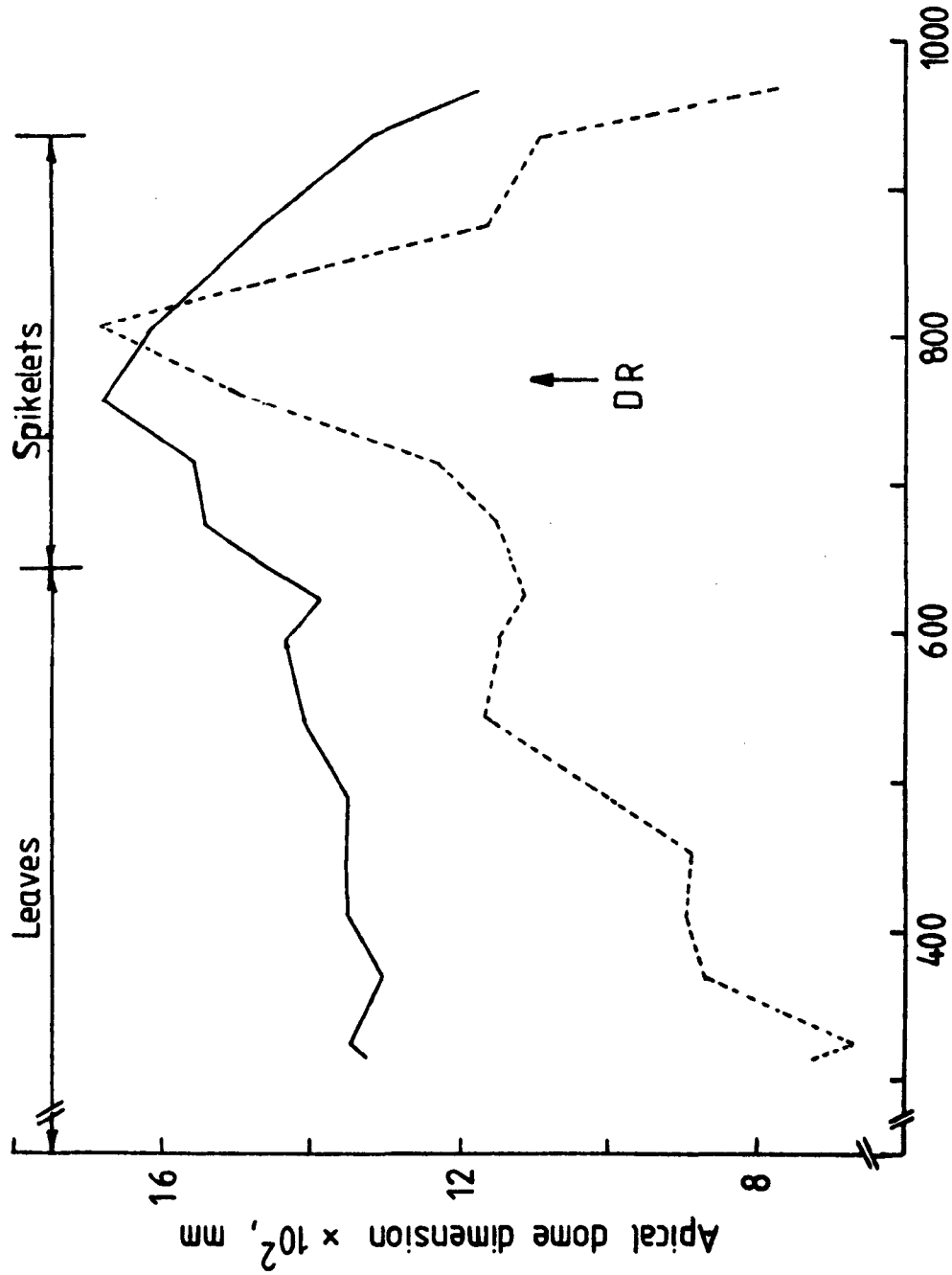
As expected, the same developmental phase lasted for different times in different sowings, depending mostly on how warm or cold the season was. For example, from sowing dates in the same month in different seasons (31.10.76 and 11.10.77) the dates when leaf initiation ended were widely separated (9.3.77 and 17.12.77 respectively) because average temperature differed in the two cases. This emphasises that chronological time is unreliable as a guide for assessing plant development (Appendix II). Relative timing of events in the plant's life history is best considered in terms of developmental time.

Reproductive development was considered to have begun when leaf initiation ended (see (iii)(b)). At this time the number of leaves appeared (Chapter 5) varied little between sowings, averaging 4.7 (range, 4.25-5.15). Tiller bud initiation had stopped by this time. Double ridges occurred when on average 51.5% (range, 49-52% of the final spikelet number was present (comparable with figures given by Kleinendorst, 1974, and Kirby, 1977) and this coincided with

Figure 4-1 Changes in size of the apical dome during primordium initiation. The leaf and spikelet initiation phases are indicated; DR is the time when double ridges were first seen.

- - - - - Dome length

——————— Dome diameter


Leaves
Spikelets
DR
16
12
8
400
600
800
1000
Apical dome dimension × 10², mm
Thermal time, °Cd since sowing

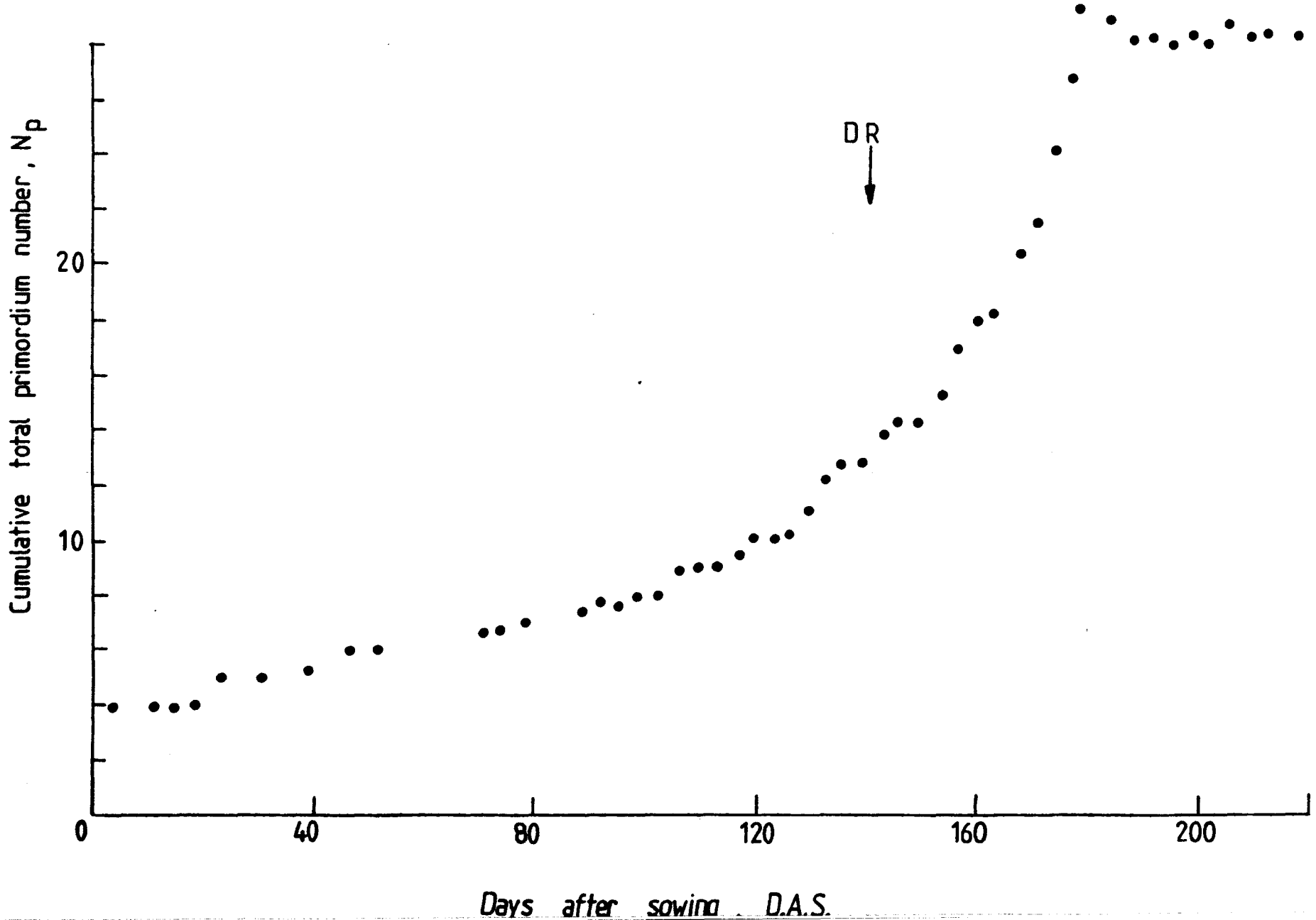
the maximum emerged tiller number. Floret initiation began at 85.4% (range, 75-92%) of final spikelet number, and ended when the flag leaf appeared. Terminal spikelet formation followed soon after the start of florets (Chapter 3), and the stem began to extend at about the same time. An overall difference of 5 months in sowing date was reduced to little more than one month in the timing of anthesis. Evidently wheat is able to make a substantial compensation for late sowing or slow early development, probably by perceiving daylength.

The size of the apical dome changed systematically with the progress of initiation. Its length and width both increased slowly during leaf initiation and more rapidly when reproductive development started; size was greatest at the time of double ridges. From then it became progressively smaller until the terminal spikelet was initiated (Figure 4-1). This pattern has been observed in spring wheat (Kirby, 1974) and in spring barley (Kirby, 1977; Fletcher & Dale, 1977) and corresponds to the frequently reported observation that the spikelets most advanced in development are in the mid-ear region. These are laid down when dome size is greatest, and when initiated are the largest of all primordia (Kirby, 1974, 1977).

(b) Estimation of T_b

When the total number of leaf and spikelet primordia (Np) produced on the main stem since sowing is plotted against chronological time (days after sowing, D.A.S.), there are changes of initiation rate with time because temperature fluctuates (Figure 4-2). If initiation rate responds linearly to temperature (Chapter 3), and if T_b is known accurately and does not change with developmental phase (cf. Balvoll & Bremer, 1965), then a plot of Np against thermal instead of chronological time should be linear.

Figure 4-2 The increase of primordium number in chronological time. DR is the first appearance of double ridges.


Cumulative total primordium number, N_p
20
10
0
40
80
120
160
200
DR
Days after sowing . D.A.S.

Several methods for finding T_b were tested. Using daily observations of screen temperature (T_a) a calculation was made, with the TEMPSUM programme (Chapter 2) of the accumulated temperature above bases ranging from -5° to $+5^{\circ}C$. This range was chosen as the extremes of the values revealed by a literature search. A test was made of minimisation of the coefficient of variation ($c.v._{min}$) between temperature sums to estimate T_b for the whole phase of leaf initiation - that is, from sowing to flag leaf primordium initiation - and the methods of Hoover (1955) and Gallagher (1976) were also tested. In a test of Arnold's method (1959) the reciprocal of leaf initiation phase duration ($1/D_1$) was plotted against the mean temperature for the phase ($\overline{T}_a,1$).

Source of method; and T_b selection criterion	Indicated T_b value $^{\circ}C$
Various sources;	0
$c.v._{min}$	
Hoover (1955);	
"Growth coefficient"	0
and x - intercept	
Arnold (1959);	
x - intercept on plot	0.75 + 1.1
of rate vs. temperature	
Gallagher (1976);	0 (3 seasons)
smallest residual variation	1 (3 seasons)
	2 (1 season)

Table 4-1 The distribution of T_b values indicated by testing some published methods for its determination. These are values obtained using leaf initiation data only

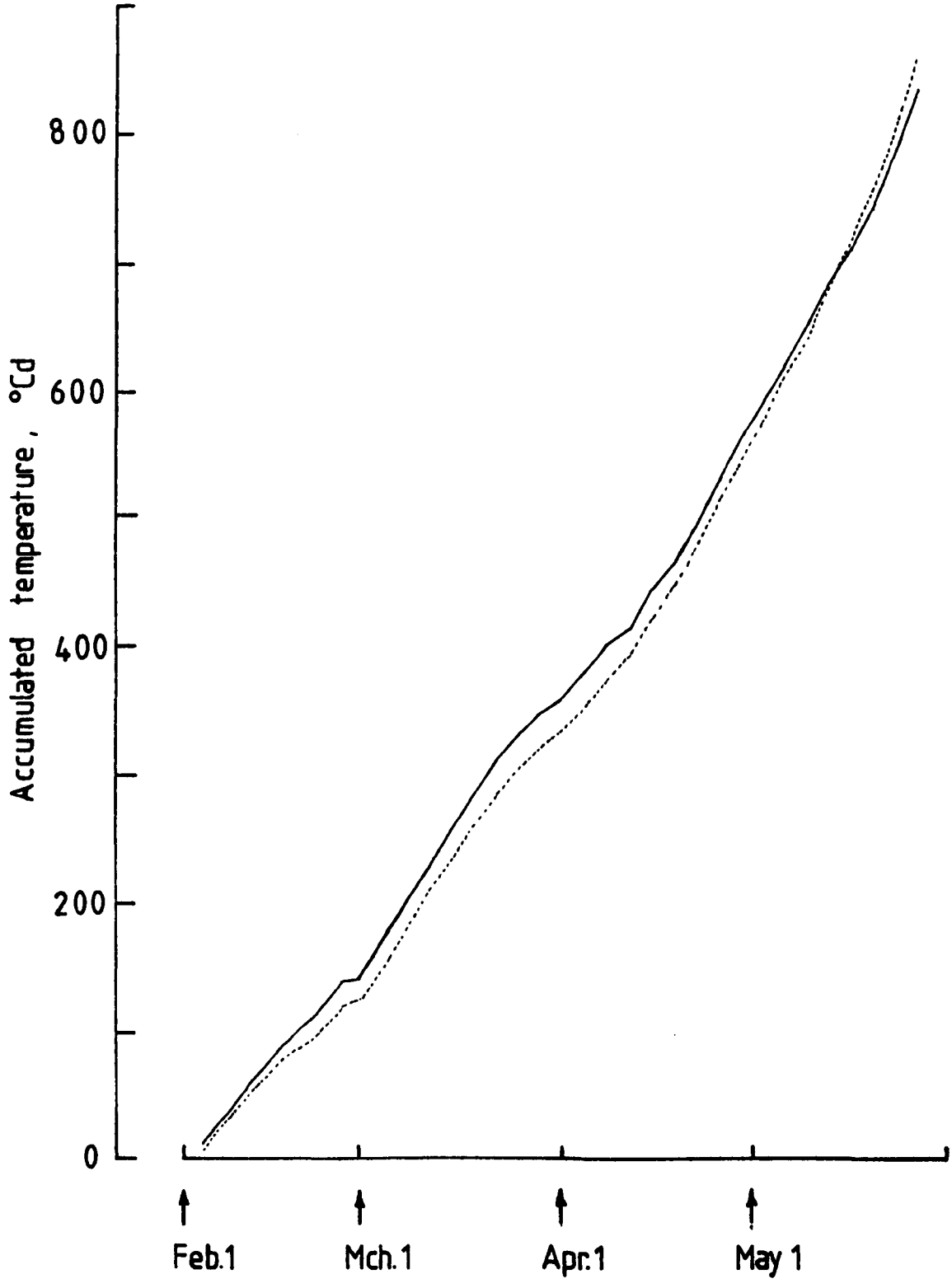


Figure 4-3 Thermal time accumulated above 0°C base temperature for each harvest during February - May inclusive (1976/7 crop). Calculated from daily mean screen temperature (———) and daily mean of hourly averages in soil at 1 cm (- - - - -) measured by diodes.

The value of T_b according to each method is shown in Table 4-1, and is generally close to 0°C. In the smallest residual variation method the statistic changed so little for a range of two or three degrees that its differences there may not have been significant. Hoover's method was successful only if the x-axis was in order of increasing mean temperature during the phase. Its success in his case, therefore, probably depended on the consistent increase of mean temperature with sowing date. However, when it was successful in the present work, it indicated a value of T_b very close to those obtained by the other methods tested.

Little work of similar detail to the present study is available for comparison, but for wheat Gallagher (1976) found that leaf appearance had a T_b of 0°C. Crop emergence takes place during early leaf initiation: it depends upon leaf appearance and so probably has a similar T_b. The time from sowing to emergence from data of Irwin (1931) and Barnard (1936) appeared to have a T_b of 1.3°C; these workers used soil temperatures. The weight of evidence, therefore, is that, at least for early development and for leaf appearance, T_b in wheat is 0°C, and this value was adopted in the subsequent analysis (Figure 4-3). There appear to be few, if any, reports in the literature of 0°C being chosen as the appropriate base in wheat, in other temperate cereals, or in any other crops. However, Salter (1960) found that 0°C was the appropriate T_b for leaf initiation in cauliflower, and Keatinge et al. (1979) showed that leaf extension in rye grass occurred at all temperatures above freezing point.

(c) Initiation in thermal time

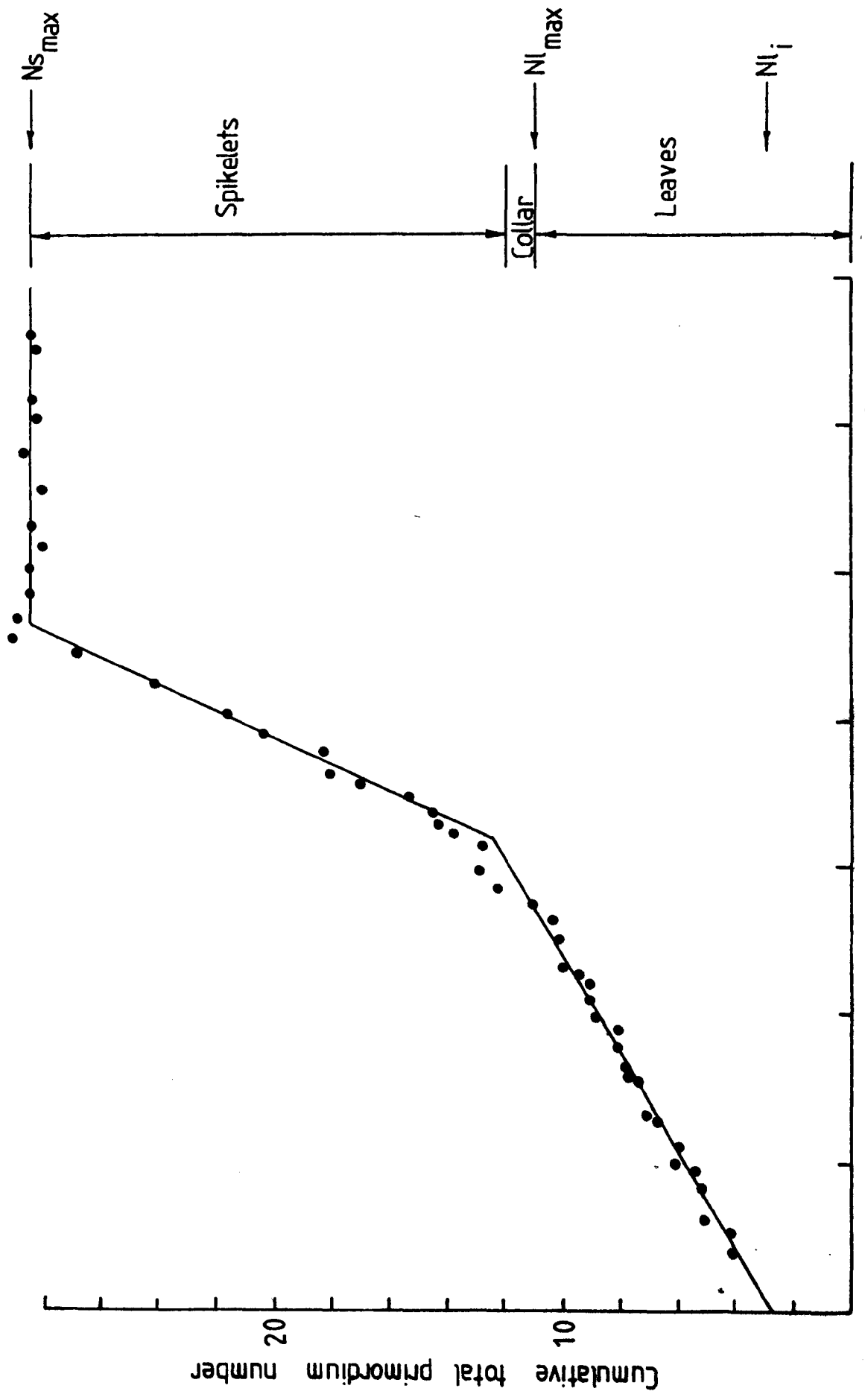
As expected, a plot of Np against thermal time with a 0°C base (Figure 4-4) removed the short-term fluctuations of rate and was linear. The plot against chronological time (Figure 4-2) showed that

Figure 4-4 The increase of primordium number in thermal time (T_b = 0°C), showing correspondence of the fitted lines with developmental stages. Nl_i = primordium number present in the grain; Nl_{max} and Ns_{max} = maximum leaf and spikelet numbers, respectively. DR = first appearance of double ridges.

The equations of the lines are:

Leaves: $y = 2.850 + 0.016x$

Spikelets: $y = -22.912 + 0.055x$


Cumulative total primordium number
10
20
400
800
1200
Thermal time since sowing, °Cd
Spikelets
Collar
Leaves
Ns max
Nl max
Nl i

a conspicuous rate increase began when primordia that became spikelet sites started to be initiated. If that increase was caused by a rise in temperature it too should have been removed by plotting against thermal time. It was not; instead, it was more clearly emphasised because the plot was well fitted by two straight lines with a distinct inflexion point. Figure 4-4 shows that the difference of rates in terms of thermal time corresponded to the initiation phases of primordia destined to become leaves and spikelets respectively. There were variations in this correspondence and these are discussed later. Similar increases of rate can be seen for both winter and spring wheats from work in controlled environments (Sunderland, 1961; Aspinall & Paleg, 1963; Rawson, 1970; Holmes, 1972) and in the field (Kirby, 1974): in all of these experiments a linear relationship described initiation rate in thermal time for both phases. The likely cause of the increase in rate seems to be enhanced hormone production (Holmes, 1972).

Because straight lines fitted the points so well, their intercepts with maximum leaf and spikelet numbers (Nl_{max} and Ns_{max}) fixed the ending of each development phase in thermal time. From the temperature record it was easy to find how many days corresponded to a given thermal time period, and so phase durations could be estimated accurately. With durations and organ numbers known, mean rates could be calculated accurately for leaf, spikelet and floret initiation, and related to $\bar{T}_a$, the mean air temperature recorded at the meteorological site.

(iii) Relation of Temperature to Initiation Rate

(a) Leaf primordia

To calculate leaf initation rate from phase duration (D_1) and organ number, the leaf primordium number present at sowing (Nl_i) was subtracted from the final leaf number (Nl_{max}). Mean rate, $\bar{R}_1$, was

then given by:

$$\bar{R}_1 = \frac{(Nl_{max} - Nl_i)}{D1}$$

Seeds soaked overnight were dissected to determine Nl_i. Three primordia were present; in his 1926 monograph Percival states that in wheat there are "two or three". Nl_i is the y-axis intercept in Figure 4-4. Calculated values of $\bar{R}_1$ ranged from 0.062 to 0.134 d^{-1}. Regression of $\bar{R}_1$ against $\bar{T}_{a,1}$ showed the expected linear relationship (Figure 4-5) and T_b was 0.75 $\pm$ 1.1°C.

Since Nl_{max} was either 11 or 12 in all sowings except that of December 1977, where it was 10, a given rate would always result in a similar duration: D_1 necessarily depended upon $\bar{R}_1$.

(b) Spikelet and floret primordia

When primordia of basal spikelets were initiated they were indistinguishable from the immediately preceding primordia that became foliage leaves, and could be identified only retrospectively. All primordia initiated after that of the flag leaf became spikelets, so that reproductive development may be considered as beginning when leaf initiation ended. Collar primordium initiation was taken as the start of spikelet initiation, and terminal spikelet formation as the end-point. This approach was adopted by Kirby (1974) but has not been widely used: most workers consider reproductive development to begin at the double ridge stage.

Duration of spikelet initiation was thus readily defined, but a complication in the calculation of a mean rate ($\bar{R}_s$) arose because in two sowings the first few spikelets were initiated at a rate in thermal time characteristic of leaves (Figure 4-6), in contrast to the pattern already noted, where all spikelets were initiated at the faster rate. To overcome the problem $\bar{R}_s$ was calculated using the

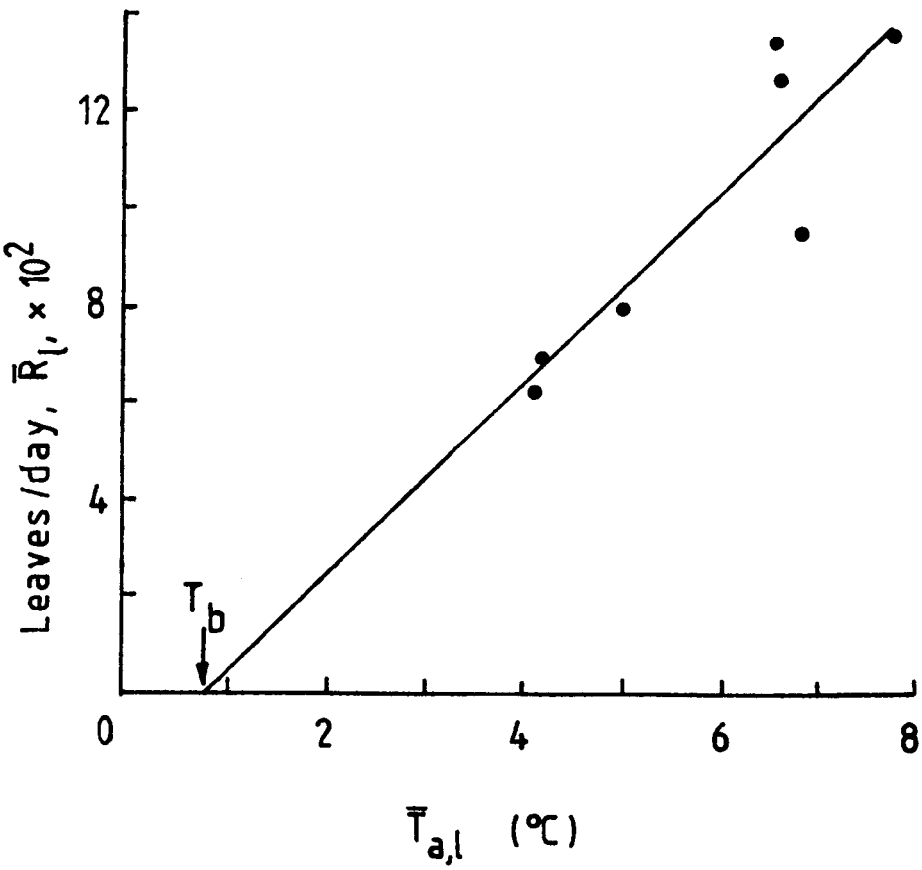
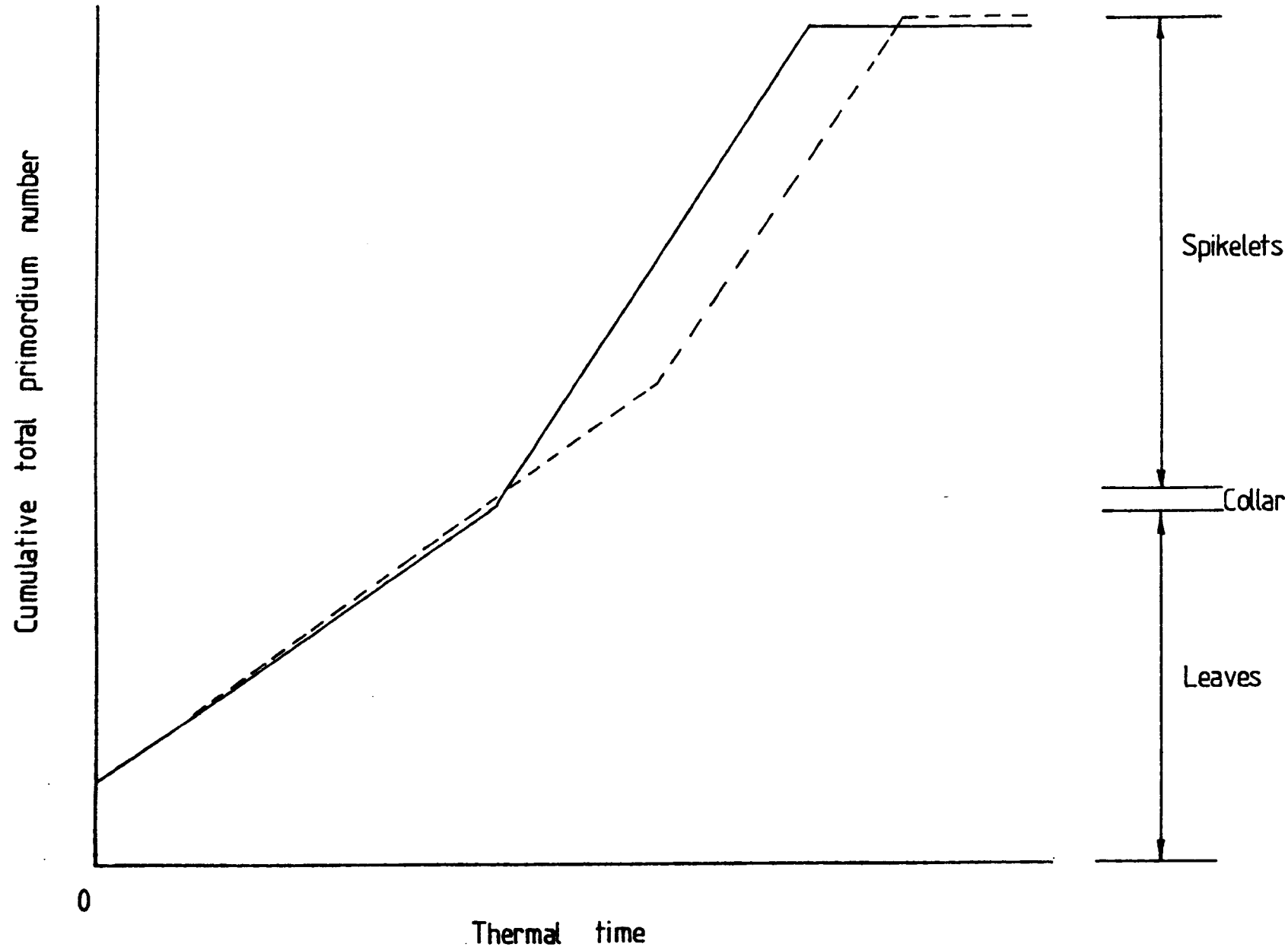


Figure 4-5 The relation of mean daily rate of leaf initiation ($\bar{R}_1$) to mean daily temperature ($\bar{T}_{a,1}$) during the leaf initiation phase. The base temperature, T_b, is 0.75 ± 1.1°C and the equation of the fitted line ($p < 0.01$) is:

$$y = -0.014(\pm 0.022) + 0.019(\pm 0.004)x$$

Figure 4-6 Comparison of primordium number increase in thermal time in contrasting sowings. For a crop sown in early October (- - - - -) the mean temperature during leaf initiation ($\overline{T}_{a,1}$) was 7.8°C. The other line (———) is for data from an early November sowing ($\overline{T}_{a,1}$ = 4.0°C). Note the difference in inflexion point timing in relation to spikelet initiation. The October sowing had 12 leaves and the November one had 11.


Cumulative total primordium number
0
Thermal time
Spikelets
Collar
Leaves

duration (D_s) and mean temperature ($\overline{T}_{a,s}$) from inflexion point to terminal spikelet formation and the spikelet numbers at those times (Ns_{inf} and Ns_{max}):

$$\overline{R}_s = \frac{(Ns_{max} - Ns_{inf})}{D_s}$$

Rates ranged from 0.21 to 0.75 spikelets d^{-1}. In figure 4-7 $\overline{R}_s$ is seen to be linearly related to $\overline{T}_{a,s}$ ($p<0.01$); the indicated T_b is 2.7 $\pm$ 0.7°C, and thus T_b was not significantly different for leaves and spikelets ($p<0.05$).

The range of variation in Ns_{max} between sowings (16.7 $\pm$ 0.2 to 20.3 $\pm$ 0.6) meant that D_s was inevitably strongly dependent upon $\overline{R}_s$. Both $\overline{R}_s$ and D_s were, therefore, apparently strongly influenced by temperature. Floret initiation rate, $\overline{R}_f$, was also correlated with the mean temperature ($\overline{T}_{a,f}$) for the initiation period (Figure 4-8). The correlation was significant ($p<0.05$); the relationship was not well fitted by a straight line, but one was fitted and showed T_b to be 3.1 $\pm$ 2.1°C, an estimate that is obviously unreliable. Nf_{max} was almost constant, so D_f depended strongly upon $\overline{R}_f$.

(iv) Thermal Time Relations of Initiation Rate

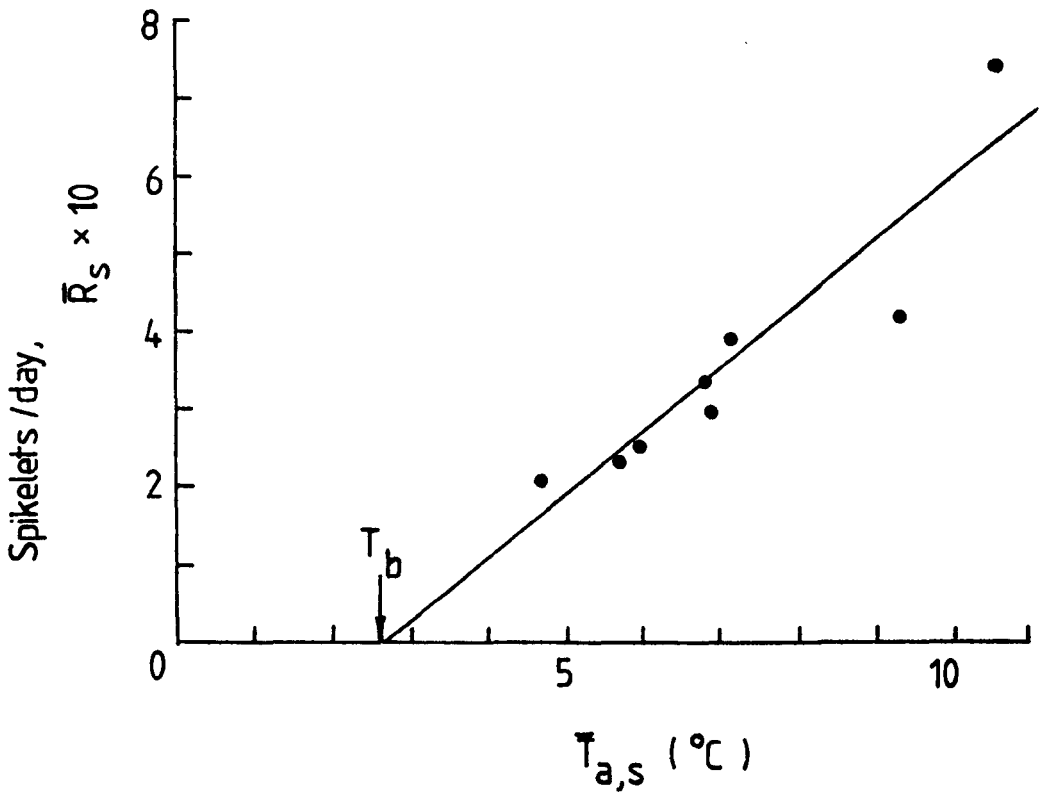
It is already clear that temperature accounted for much of the variability in mean rates between sowings. If temperature was the only controlling factor, the same amount of thermal time would always be needed to produce a leaf, spikelet or floret, each having its own characteristic thermal time requirement. Initiation rate in thermal time ($\overline{R}$ (°Cd)$^{-1}$) should, therefore, always be the same too: for example, the rate of leaf initiation per degree Centigrade day ($\overline{R}l$ (°Cd)$^{-1}$) would always be the same in any sowing. In fact, rate in thermal time varied considerably for leaves and spikelets, and for florets to a lesser extent (Table 4-2), indicating that initiation

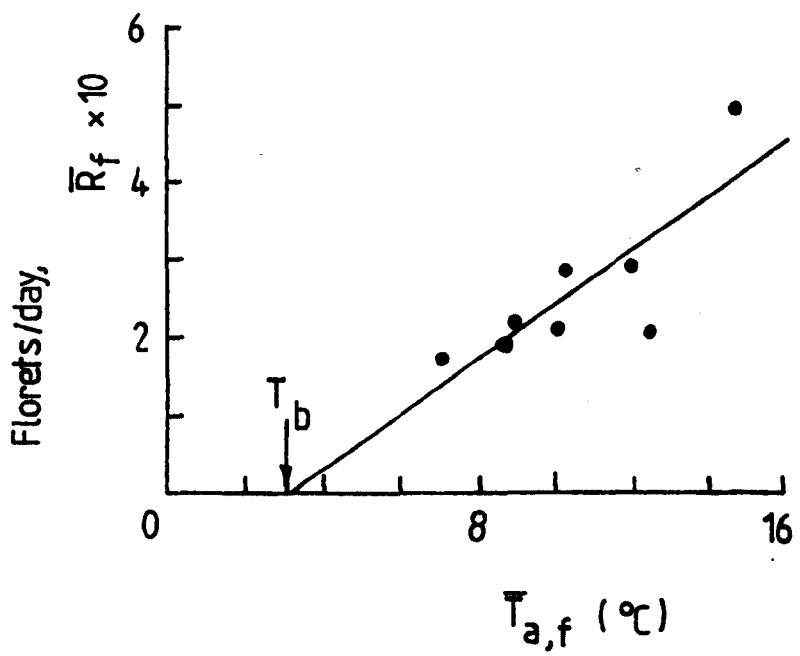
Figure 4-7 The relation of mean daily rate of spikelet initiation after inflexion point ($\overline{R}_s$) to daily mean temperature from then to terminal spikelet formation ($\overline{T}_{a,s}$). T_b is 2.7 $\pm$ 0.74°C. The equation of the fitted line ($p < 0.01$) is:

$$y = -0.222 (\pm 0.097) + 0.082 (\pm 0.013)x$$

Figure 4-8 The relation of mean daily rate of floret initiation ($\overline{R}_f$) to daily mean temperature of the floret initiation phase ($\overline{T}_{a,f}$). T_b is 3.1 $\pm$ 2.1°C. The equation of the fitted line ($p < 0.05$) is :

$$y = -0.110 (\pm 0.129) + 0.035 (\pm 0.012)x$$


8
6
4
2
0
5
10
$\bar{R}_s \times 10$
Spikelets/day,
T_b
$\bar{T}_{a,s}$ (°C)


6
4
2
0
8
16
$\bar{R}_f \times 10$
Florets/day,
T_b
$\bar{T}_{a,f}$ (°C)

is affected by factors other than temperature. The two main possibilities were nutritional differences between sowings, and other weather variables such as insolation and daylength.

Sowing Date	Leaves $\overline{R}_l(^oCd)^{-1}$	Spikelets $\overline{R}_s(^oCd)^{-1}$	Florets $\overline{R}_f(^oCd)^{-1}$
16.11.73	0.0149	0.0449	0.0202
30.10.74	0.0142	0.0418	0.0235
4.10.75	0.0178	0.0451	0.0218
31.10.76	0.0156	0.0554	0.0277
11.10.77	0.0180	0.0431	0.0236
2.12.77	0.0173	0.0587	0.0287
6. 3.78	0.0237	0.0759	0.0353

Table 4-2 Variation of initiation rate in thermal time for leaves, spikelets and florets. The rate is expressed as the mean per degree Centigrade day of thermal time accumulated ($T_b = 0^oC$)

(a) Nutritional differences

Primordium initiation is undoubtedly affected by soil nutrient levels (Aspinall & Paleg, 1963; Langer & Liew, 1973). Large differences in nitrogen apparently had no effect on leaf initiation but markedly affected both $\overline{R}_s$ and D_s (Holmes,1973). Restrictions are imposed by assimilate shortages: Ong & Marshall (1979) found that leaf initiation rate in ryegrass was slowed by severe shading. Kirby & Faris (1970) showed that with increased planting density in barley, D_s was shorter but $\overline{R}_s$ was not affected, and suggested that D_s was curtailed with increasing density because the increase in competition for nutrients was earlier, causing the apical meristem to die earlier.

Reductions in $\bar{R}_s$ for wheat by partial defoliation were reported by Rahman and Wilson (1977).

In the present study, no effect of fertiliser nitrogen on rates or durations could be detected even in a trial where the N applied was much less than the usual farm dressings. (Chapter 6). Variation of plant density between sowings was small compared with that in the work by Kirby and Faris.

(b) Weather variables other than temperature

Because variability of $\bar{R}$ in thermal time was not likely to have been caused by nutritional differences, weather variables appeared to be responsible. Water stress has been shown to affect initiation but is not likely to have been limiting under the field conditions experienced in the present crops. Mean temperature and mean solar radiation are so highly correlated in the field (r^2 = ca. 0.9) that their relative effects on $\bar{R}$ could not be determined. Daylength is left as the most likely modifier of rates in thermal time.

Early work in the field (e.g. Forster et al., 1932; McKinney & Sando, 1935) indicated that wheat development was affected by daylength; more recently, the effect of daylength on development has been investigated by work in controlled environments (Rawson, 1971; Lucas, 1972; Allison & Daynard, 1976; Rahman & Wilson, 1977), and all of it showed that at a given temperature the rate of spikelet initiation was increased by longer days. None of the workers discusses the shape of response of development rate to daylength, but in the present study this was of interest and so polynomials were fitted to the reported data. Though the response was curvilinear over the full range of experimental photoperiods, over the range corresponding to the natural daylengths for spikelet initiation the response was linear.

(v) Daylength Effects on Primordium Initiation

(a) Daylength and plant development

Crops often experience spells of warm or cold weather that are anomalous for the time of the year, but daylength (ϕ) changes regularly and predictably throughout. If the plant has a means of perceiving daylength its development is more reliably linked to the seasons of the year. Many plant species are able to detect daylength changes (see Chapter 5) and wheat is no exception.

The length of the light period must be calculated from the correct end-points. Work by Cooper (1952) and Gott (1961) showed that civil twilight periods (time taken for the sun to sink 6^{o} below the horizon) should be added to the sunrise-sunset time each day to give the true photoperiodically-effective daylength, and this procedure was used here.

(b) Leaf initiation

A crop cannot perceive daylength until it emerges. By analogy with $\overline{T}_{a,l}$ the relation between the mean of current daylength from emergence to the end of leaf initiation ($\overline{\phi}_l$) and rate in thermal time ($\overline{R}_l(^{o}Cd)^{-1}$) was investigated first. The relationship was linear ($p < 0.01$): see Figure 4-9. It was possible that $\overline{R}_l(^{o}Cd)^{-1}$ might have been set by the instantaneous daylength when the crop emerged (ϕ_e) but this correlation was much weaker ($p < 0.5$). It appears that $\overline{\phi}_l$ and not ϕ_e modulated the response of $\overline{R}_l$ to temperature.

(c) Spikelet and floret initiation

It is possible that the influence of $\overline{\phi}_l$ may extend to the initiation rate in thermal time of spikelets ($\overline{R}_s(^{o}Cd)^{-1}$) and of florets ($\overline{R}_f(^{o}Cd)^{-1}$). It is more likely, however, that these rates were modified by ϕ_{inf}, the instantaneous daylength at the time of inflexion, or $\overline{\phi}_s$, the mean of current daylength from inflexion to Ns_{max}.

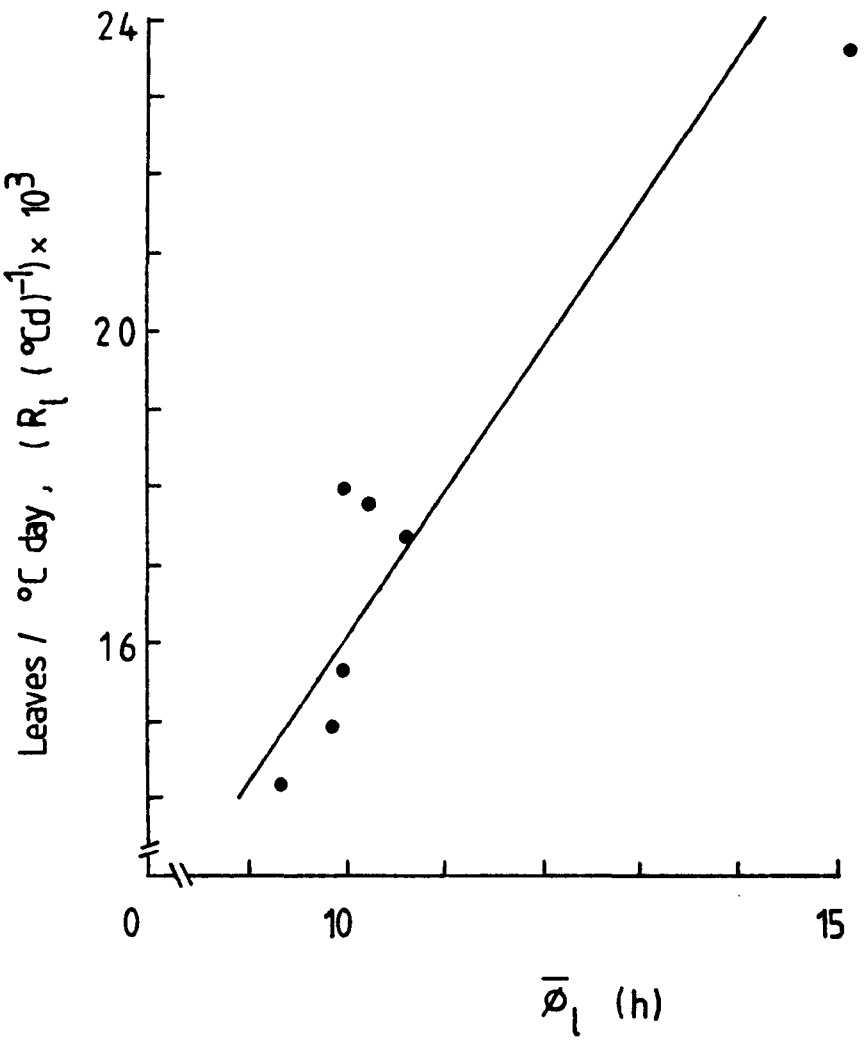


Figure 4-9 The relation of leaf initiation rate in thermal time ($\bar{R}_1$ $(^{o}Cd)^{-1}$) to the mean daylength during the initiation phase ($\bar{\phi}_1$). The relationship is described by a straight line ($p < 0.01$):

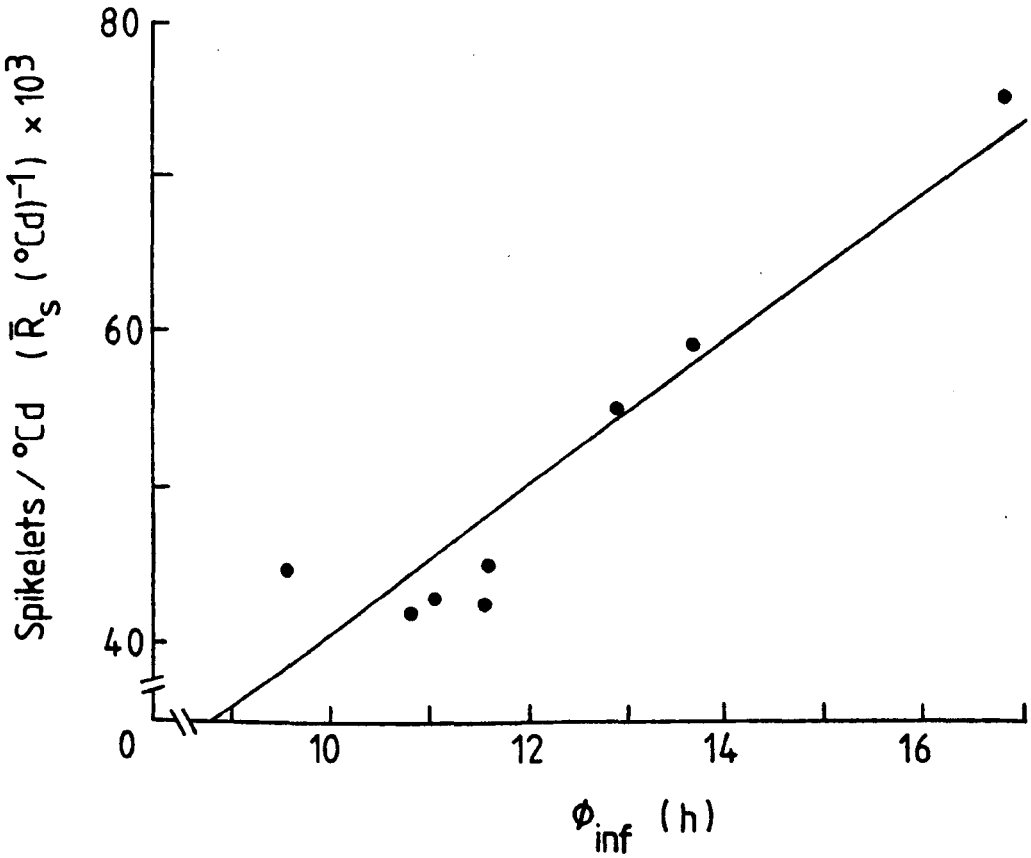
$$y = 1.45(\pm 2.78) + 1.49(\pm 0.26)x$$

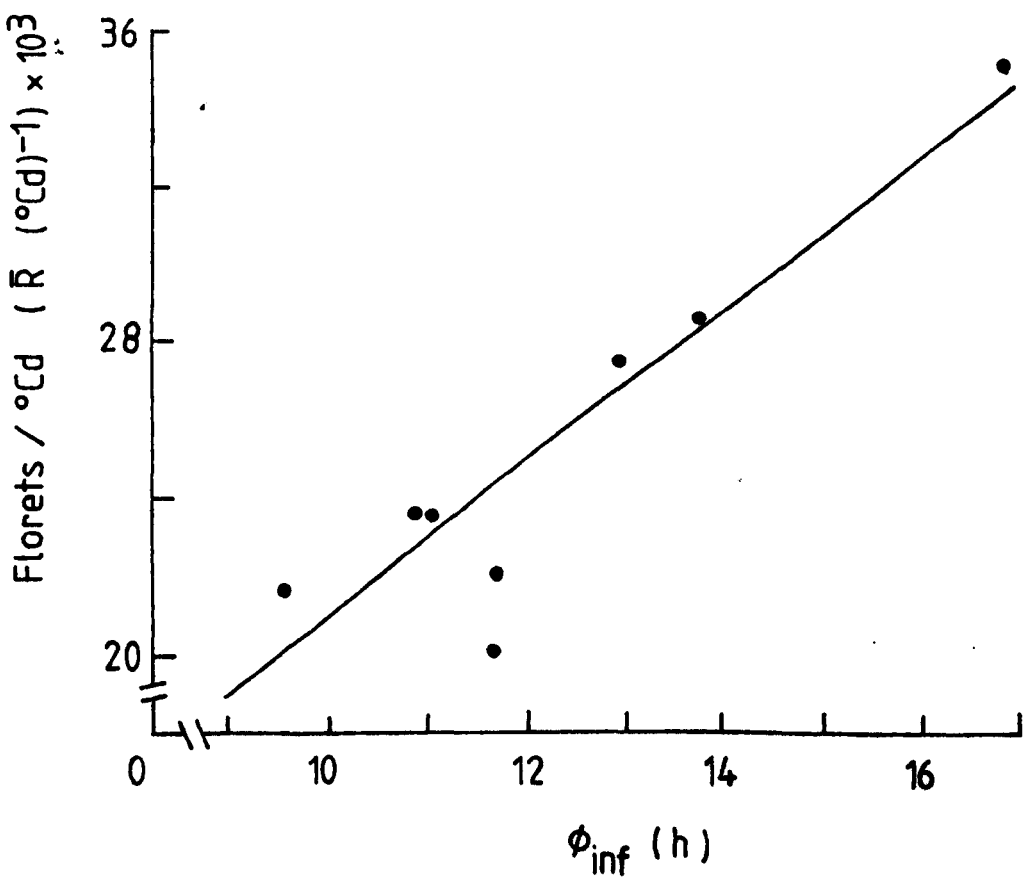
Figure 4-10a The relation of spikelet initiation rate in thermal time ($\overline{R}_f(^{o}Cd)^{-1}$) with the instantaneous day-length at inflexion point (ϕ_{inf}) is described by a straight line ($p < 0.001$).

$$y = -8.07(\pm 8.39) + 4.88(\pm 0.67)x$$

Figure 4-10b The relation of floret initation rate in thermal time ($\overline{R}_f(^{o}Cd)^{-1}$) with the instantaneous day-length at inflexion point is described by a straight line ($p < 0.01$):

$$y = 1.34(\pm 4.43) + 1.99(\pm 0.35)x$$


80
60
40
0
10
12
14
16
Spikelets / °Cd ($\bar{R}_s$ (°Cd)$^{-1}$) x 10^3
ϕ_{inf} (h)


36
28
20
0
10
12
14
16
Florets / °Cd ($\bar{R}$ (°Cd)$^{-1}$) x 10^3
ϕ_{inf} (h)

For spikelets, the correlation with ϕ_{inf} was stronger ($p<0.001$) than with $\overline{\phi}_s$ ($p<0.05$). For florets also, the correlation was stronger with ϕ_{inf} ($p<0.01$) than with $\overline{\phi}_s$ ($p = 0.1$). Though the more significant correlation was therefore with ϕ_{inf} in each case (Figure 4-10), the highly significant correlation of rate with $\overline{\phi}_s$ cannot be ignored. From the statistical evidence, it appears that it was the instantaneous daylength at the time of inflexion that modulated the initiation rate in thermal time of all the primordia subsequently formed, but an effect of current daylength cannot be ruled out.

(d) Daylength and indicated T_b values

In the first estimate of T_b (Figures 4-5, 7, 8) $\overline{R}$ was assumed to depend on $\overline{T}_a$ only, but since the rate (in thermal time) at which organs are initiated is related to daylength (Table 4-2), this factor must also be taken into account.

Experimental evidence in the present work shows that $\overline{R}$ is a linear function of mean temperature $\overline{T}^{\circ}C$, i.e. :

$$\overline{R} = a\,(\overline{T} - T_b) \qquad (1)$$

where a is a constant for a given daylength.

Growth-room work (see (iii)(b)) suggests that at constant temperature the rate of primordium initiation, at least for spikelets, is a linear function of daylength. Assuming a base value ϕ_b (h) for daylength (Robertson, 1973), the relationship can be written as :

$$\overline{R} = c\,(\phi - \phi_b) \qquad (2)$$

where c is a constant for a given temperature.

Because the rate in thermal time is modulated by daylength, a must be proportional to $(\phi - \phi_b)$ or :

$$a = d\,(\phi - \phi_b) \qquad (3)$$

where d is a third constant independent of temperature and daylength.

It follows that :

$$R = d\ (\overline{T} - T_b)\ (\phi - \phi_b) \qquad (4)$$

$$= d\ [\ (\overline{T}.\phi\ -\ (\overline{T}\phi_b + \phi T_b) + T_b.\phi_b)\ ] \qquad (5)$$

Evidence has already been cited for setting $T_b = 0^oC$ for wheat. Measurements in the present work did not define a value for ϕ_b, but from the growth-room work on several wheat varieties referred to earlier, extrapolation of the response of spikelet initiation rate to daylength gives $\phi_b \simeq 0$. If $T_b = 0^oC$ and $\phi_b = 0$ hours, equation (5) reduces to :

$$\overline{R} = d\ (T.\phi) \qquad (6)$$

Thus, provided that T_b and ϕ_b do not change during development and that $\overline{T}$ and ϕ are the sole factors controlling the process, the response of the process rate $\overline{R}$ to $(\overline{T}.\phi)$ should be linear and should pass through the origin. Because $(\overline{T}.\phi)$ represents temperature corrected for the effect of daylength, it will be called <u>corrected temperature</u>.

Figures 4-11, 12 and 13 are plots of $\overline{R}$ against a scale of corrected temperature, for primordia of leaves, spikelets and florets. For leaves the indicated T_b is not very different from that obtained in Figure 4-5, but for spikelets and florets T_b is considerably different from the earlier estimates and not significantly different from 0^oC (in both cases ($p < 0.01$). This implies that the effect of daylength on rate of initiation of spikelets and florets was stronger than its effect on leaf initiation. It is clear that this effect should always be taken into account as otherwise misleading estimates of T_b will result. If the method of correcting $\overline{T}$ for ϕ is a true estimate of the combined effect of these two variables on development, it is appropriate to put $T_b = 0^oC$ for all phases of primordium initiation in wheat.

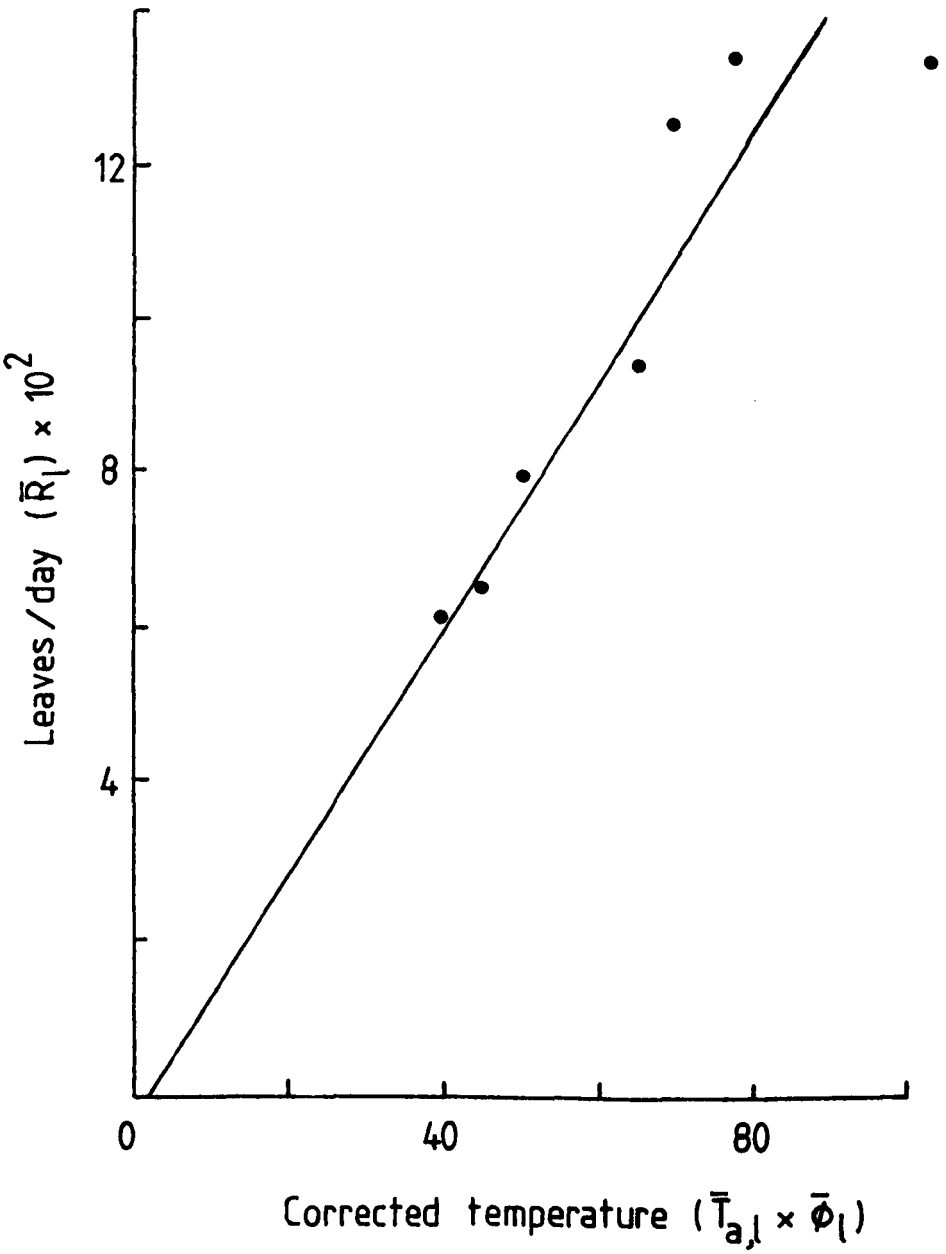


Figure 4-11 The response of mean daily rate of leaf initiation, $\bar{R}_1$, to mean temperature corrected for day-length during the leaf initiation phase ($\bar{T}_{a,1} \times \bar{\phi}_1$). The relationship is described by a straight line (p 0.01).

$T_b = 0.19 \pm 1.85^{\circ}C$.

$y = -0.51 (\pm 1.80) + 0.13 (\pm 0.03)x$

Figure 4-12 Response of the mean daily rate of spikelet initiation $\overline{R}_s$ (after inflexion point) to mean temperature during the spikelet initiation period corrected for instantaneous daylength at inflexion. The linear relationship ($p < 0.001$) has the equation:

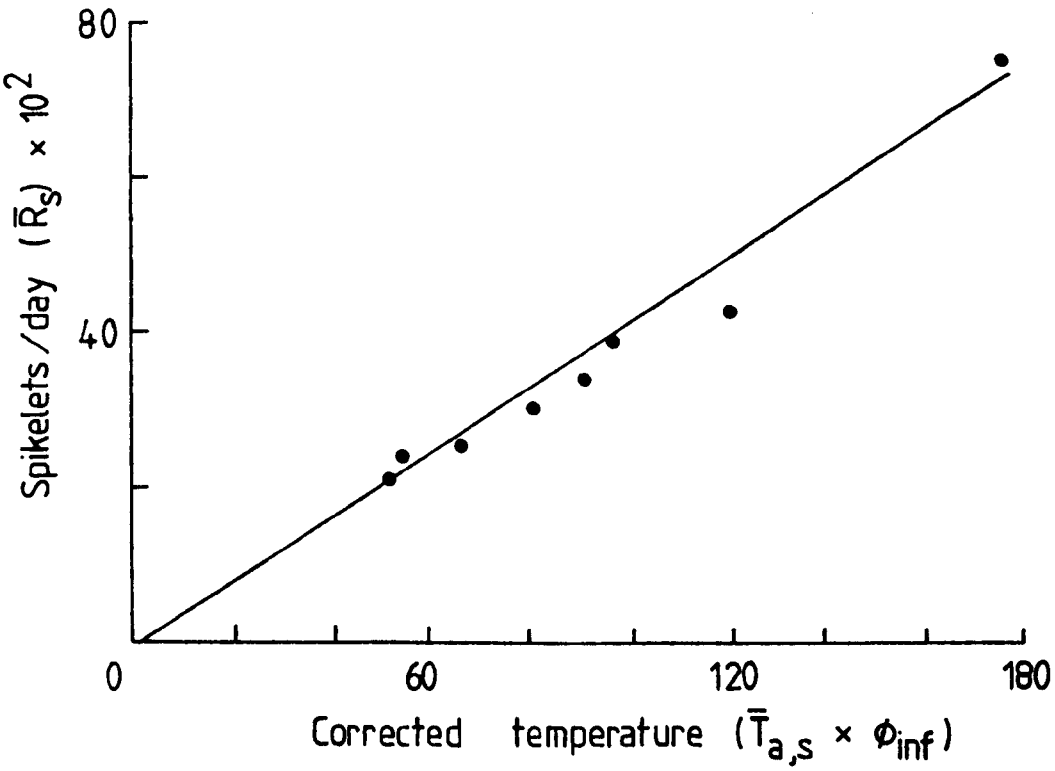
$$y = -0.0012(\pm 0.03) + 0.004(\pm 0.0003)x$$

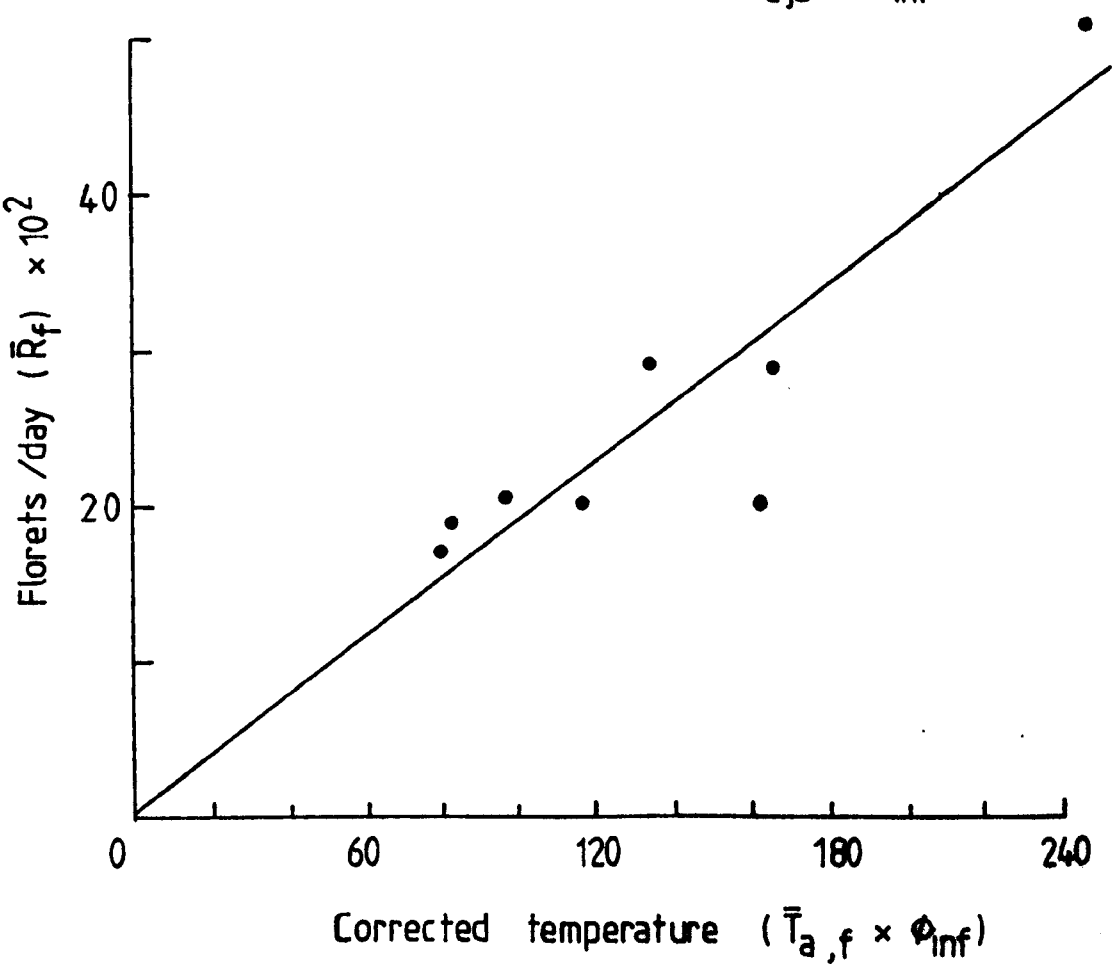
T_b is $0.22^\circ \pm 0.57^\circ C$

Figure 4-13 Response of mean daily rate of floret inititation ($\overline{R}_f$) to the mean temperature during the floret initiation period corrected for instantaneous daylength at inflexion. The linear relationship ($p < 0.01$) has the equation:

$$y = 0.011(\pm 0.05) + 0.0018(\pm 0.0004)x$$

T_b is $0.35^\circ \pm 1.25^\circ C$


80
40
0
60
120
180
Spikelets/day ($\bar{R}_s$) x 10^2
Corrected temperature ($\bar{T}_{a,s} \times \Phi_{inf}$)


40
20
0
60
120
180
240
Florets/day ($\bar{R}_f$) x 10^2
Corrected temperature ($\bar{T}_{a,f} \times \Phi_{inf}$)

(vi) Variation in Time of the Inflexion Point

(a) Inflexion in relation to temperature and daylength

It has been mentioned that though the timing of the inflexion point was usually close to the time of $N1_{max}$ it was sometimes later, and in this case as many as the first four spikelets were formed at the thermal time rate characteristic of leaves (Figure 4-6). Because the variation in timing of inflexion was in both chronological and thermal time it was reasonable to suppose that daylength was involved in determining when the event happened. Calculation of the accumulated corrected temperature was therefore needed. Similar calculations have been made in the "biometeorological time scales" of Robertson (1973) and others; following their terminology, accumulated corrected temperature in the present work is called photothermal time.

Photothermal time was calculated for the period from emergence to inflexion in each sowing. The c.v. for the sum between seasons was found, and compared with the c.v. of thermal time sums from emergence to inflexion. Thermal time had a c.v. of 21% ($\bar{x}$ = 503; range 360-610); photothermal time reduced the c.v. to 15% ($\bar{x}$ = 5161; range 4009-6274). Photothermal time therefore appeared to account the more fully for the observed variation in inflexion point timing. However, evidence from experiments done in controlled environments (Cooper, 1956; Rawson, 1970) suggested strongly that vernalisation might be implicated in determining the timing of inflexion.

(b) Vernalisation response

Ideally the occurrence of delayed inflexion should be sought in comparable published data from field experiments on winter cereals, but none exist. The necessary frequent counts of total primordia have, however, been made in the work of Halse and Weir (1974) and Rawson (1970), both in controlled environments. Rawson presented data for some cultivars

showing a delay of inflexion point beyond Nl_{max}. All the cultivars in which this happened had a vernalisation response, but even at the lowest temperature ($10^{o}C$) used in the growth-room none apparently experienced much vernalisation. The same occurred in Halse and Weir's experiment. 'Maris Huntsman' has a vernalisation response; the delay of inflexion in certain sowings could be explained if it depended upon accumulation of cold experience and in those cases the requisite total of vernalisation was not reached until after Nl_{max}.

In the present study, delayed inflexion was found in two sowings, both made in early October when $\overline{T}_a$ was relatively high. Both initiated leaves quickly at first, and reached Nl_{max} without experiencing as much cold as later sowings, in which, on the vernalisation hypothesis, the requisite vernalisation must have been reached at about the same time as Nl_{max}. In the early-sown crops additional primordia that became spikelet sites would be initiated during the further time needed to complete the cold experience.

Temperatures from -4^{o} to $+12^{o}C$ have been shown to cause vernalisation in cereals but between 1^{o} and 7^{o} appears to be the most effective (Purvis, 1961). The effectiveness of different temperatures has mostly been investigated in controlled environments; from this work two shapes of vernalisation response have been proposed.

1. Shape of response

Hansel (1953 , cited by Purvis, 1961) found that for winter rye there was a broad optimum range of vernalising temperature at 1^{o} - $7^{o}C$, at the ends of which effectiveness fell rather sharply with change of temperature. This may be termed the plateau response.

In contrast, from an experiment in which winter wheat was vernalised on a precise temperature gradient, Trione and Metzger

(1970) concluded that there was a sharp optimal temperature of 7°C. This peak response appears to be implied from the work of Chujo (1966), who found that for wheat the largest effect of vernalisation was at 4°-8°C or 8°-11°C, depending on cultivar.

Although little is known about the efficiency of temperatures for vernalising plants in the field, an analysis to estimate the amount of vernalisation experienced by each sowing in the present work was attempted.

2. Vernalisation analysis

A major difficulty is that, as compared with controlled environments, it is unclear how fast or at what temperatures vernalisation is completed under field conditions: Cooper (1956) found that winter wheat was completely vernalised after 6 weeks of refrigeration at 0-5°C, yet Ishihara (1960) showed that vernalisation could be completed in as little as 6 weeks in the field even if the daily maximum temperature rose as high as 15°C.

The literature showed that in growth-room work temperatures from 0°C to 10°C had been used in cold treatments, so this was selected as the range for investigation. The total time (from sowing to inflexion) spent in ranges differing by 1° steps was calculated using hourly temperatures indicated by the TEMPSUM programme. The range most effective for vernalisation was assumed to be the one minimising the c.v. between sowings for vernalising time to inflexion. If the plateau response was the more appropriate, c.v. would vary little no matter what the temperature range chosen. If the peak response was appropriate instead, c.v. would be minimised by a narrow temperature range.

The outcome was that the 6-7°C range minimised the c.v. (=14.3%) and that an average of 240 hours (range, 185-301) would be needed in it before inflexion occurred. An almost equally good fit was given by the 5-7°C range (c.v. = 15.3%), with 480 hours (range, 338-559) before inflexion. These temperature ranges agree well with those found to be optimal by Chujo and by Trione and Metzger, supporting the idea of a peak response.

The 15% c.v. for both photothermal time and vernalising hours to inflexion implies that neither one alone could adequately explain the variation in its timing, possibly because vernalisation was influenced by daylength as some reports suggest.

(c) Vernalisation and daylength

A connection between vernalisation and daylength was emphasised by Purvis and Gregory (1937), who found that if plants were protected from chilling and given short days they behaved like ones which had been chilled: short days replaced cold experience. Plants in the field experience cold temperatures and short days simultaneously, but Cooper's work (1960) on Lolium and wheat showed that heading was no earlier when these conditions were given together than when either was given separately. Evans (1959) demonstrated for Lolium that in longer days the effective temperature range for vernalisation appeared to be higher with increasing daylength; this finding implies that appreciable vernalisation may occur in grains on the maturing ear (cf. Gregory and Purvis, 1938).

In the present work, the period between crop emergence and the time of inflexion point was usually one during which daylength decreased to a minimum of 9 hours and then increased again. During the same

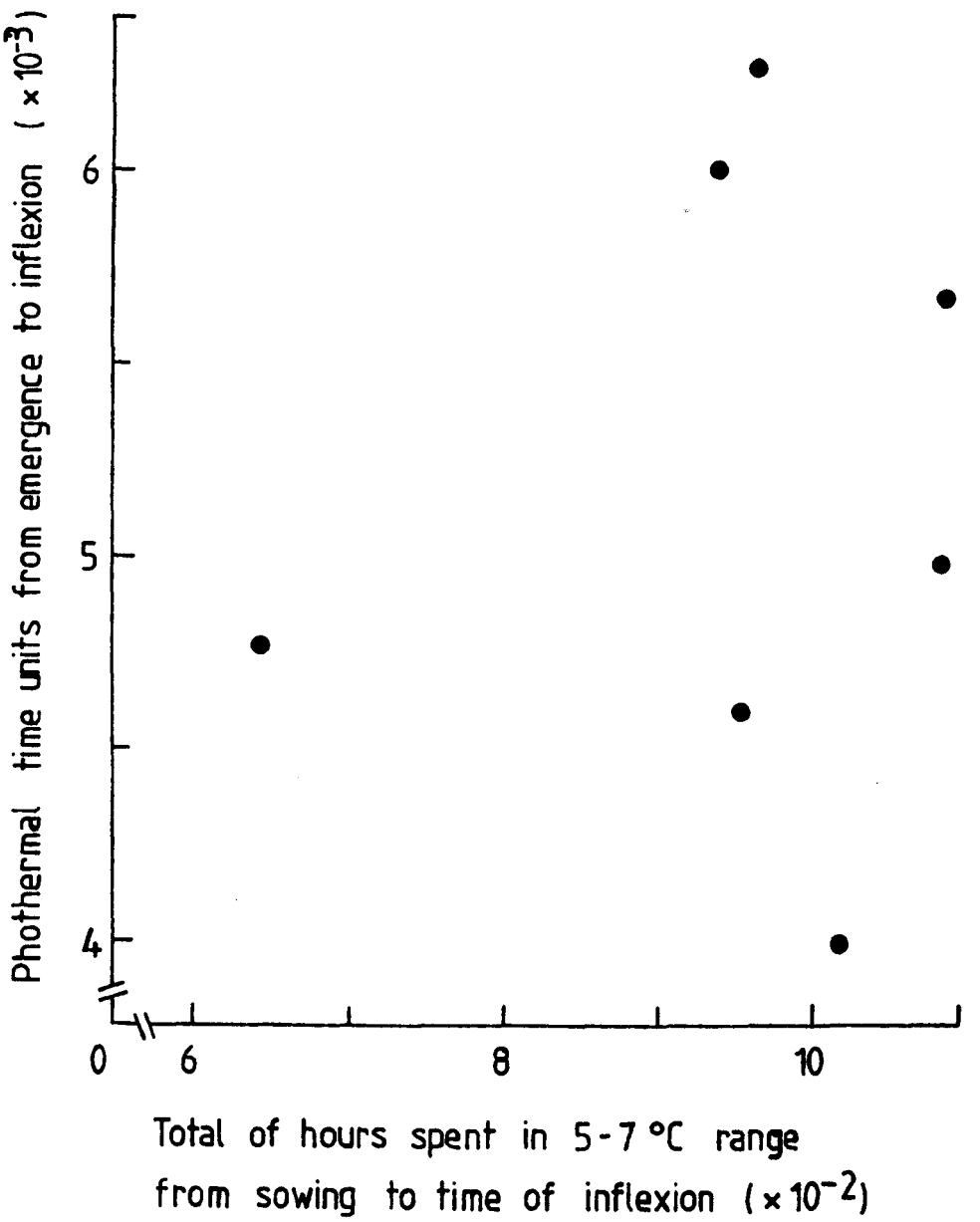


Figure 4-14 The relationship between the amount of time since sowing spent in the vernalising temperature range 5-7°C and the amount of photothermal time $\lfloor (\bar{T}_a \times \phi) \rfloor$ from emergence taken to reach the inflexion point.

period, temperatures were continually fluctuating. Under such conditions the relationship between daylength and the progress of vernalisation is likely to be very complex. The reason for the similarity of c.v. to time of inflexion given by calculations of photothermal time and vernalising hours is unclear: when the total of vernalising hours at 5-7°C was plotted against the corresponding photothermal time, there was no consistent relationship between them (Figure 4-14).

Both Evans (1959) and Japanese work on winter wheat bring out an important aspect of the relation between daylength and vernalisation: it appears to be night temperature which is effective in promoting vernalisation. In the cultivars used in the Japanese work, vernalisation resulted when the night temperature was 10°C or less, and was not reversed by a day temperature even as high as 30°C (Chujo, 1966; Ishihara, 1963) yet Purvis and Gregory (1952) found that in rye vernalisation was reversed by temperatures above 25°C. Sub-zero temperatures were not investigated and the plateau response mentioned earlier suggests that they are relatively ineffective. However, in the crops studied in the present work sub-zero minimum temperatures were not frequent and in any case the minimum temperature is often attained for only a short time during the 24-hour period, so that even on a night with a sub-zero minimum some vernalisation may be assumed to have occurred. The relationship of photothermal time to inflexion with number of vernalising nights since sowing was therefore investigated, but there was not a strong correlation.

Because it appears that daylength influences the low-temperature effect, it is very likely that vernalisation in the total darkness that the plant experiences before it emerges will differ in effectiveness from vernalisation it receives in the regular sequence

of night and day after emergence. Hashimoto and Hirano (1961) concluded that vernalisation was most effective in young plants but did not discuss the possibility of a difference in pre- and post-emergence vernalisation. A working hypothesis was used in the present case, namely that the number of vernalising nights experienced before emergence in some way determined the plant's response to photothermal time after emergence. A complex response may be involved: if after emergence the plant continues to be vernalised, its response to photothermal time may change continuously as a result. To see if the hypothesis appeared tenable the number of nights with minimum temperature $\leqslant 10^{\circ}C$ before emergence was plotted against the photothermal time sum from emergence to inflexion. There was in fact a strong correlation ($p < 0.01$): see Figure 4-15. The hypothesis was further tested on the more extensive range in number of vernalising nights given in Rawson (1970), where times of inflexion were also known. Rawson appears to have used a day/night regime at constant temperature, but the details that he gives do not make this clear, and vernalisation may in fact have been in continuous light or continuous darkness; his results should be interpreted with caution. His data revealed a curvilinear relationship between number of vernalising periods and photothermal time to inflexion (Figure 4-16). The Sutton Bonington points (Figure 4-15) were close to the same curve.

It therefore seems that the number of vernalising nights that the crop experiences before emergence exerts a profound influence on its response to photothermal time afterwards. However, it is still not possible to say more than that vernalisation and photothermal time are both apparently important in causing the observed change in primordium initiation rate. Extensive further work is needed to elucidate the underlying interaction that is implied.

Figure 4-16 The same relationship as in Figure 4-15, for data from controlled environment work of Rawson (1970) and Halse and Weir (1974). A curvilinear function describes the relationship. The points from Sutton Bonington field data (Fig. 4-15) lie close to the same line: the line was fitted by eye.

○ Data of Rawson

□ " " Halse & Weir

● Sutton Bonington field data

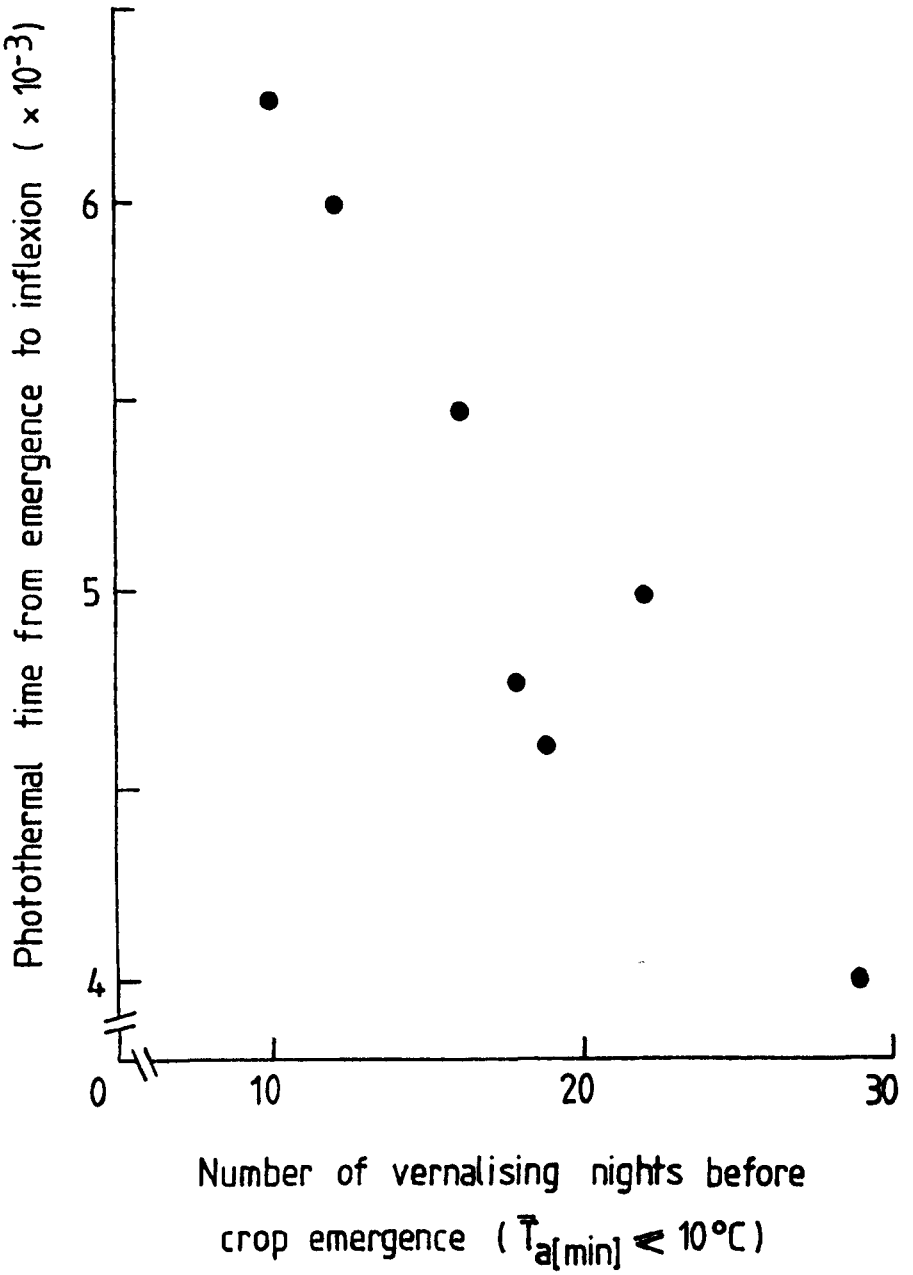
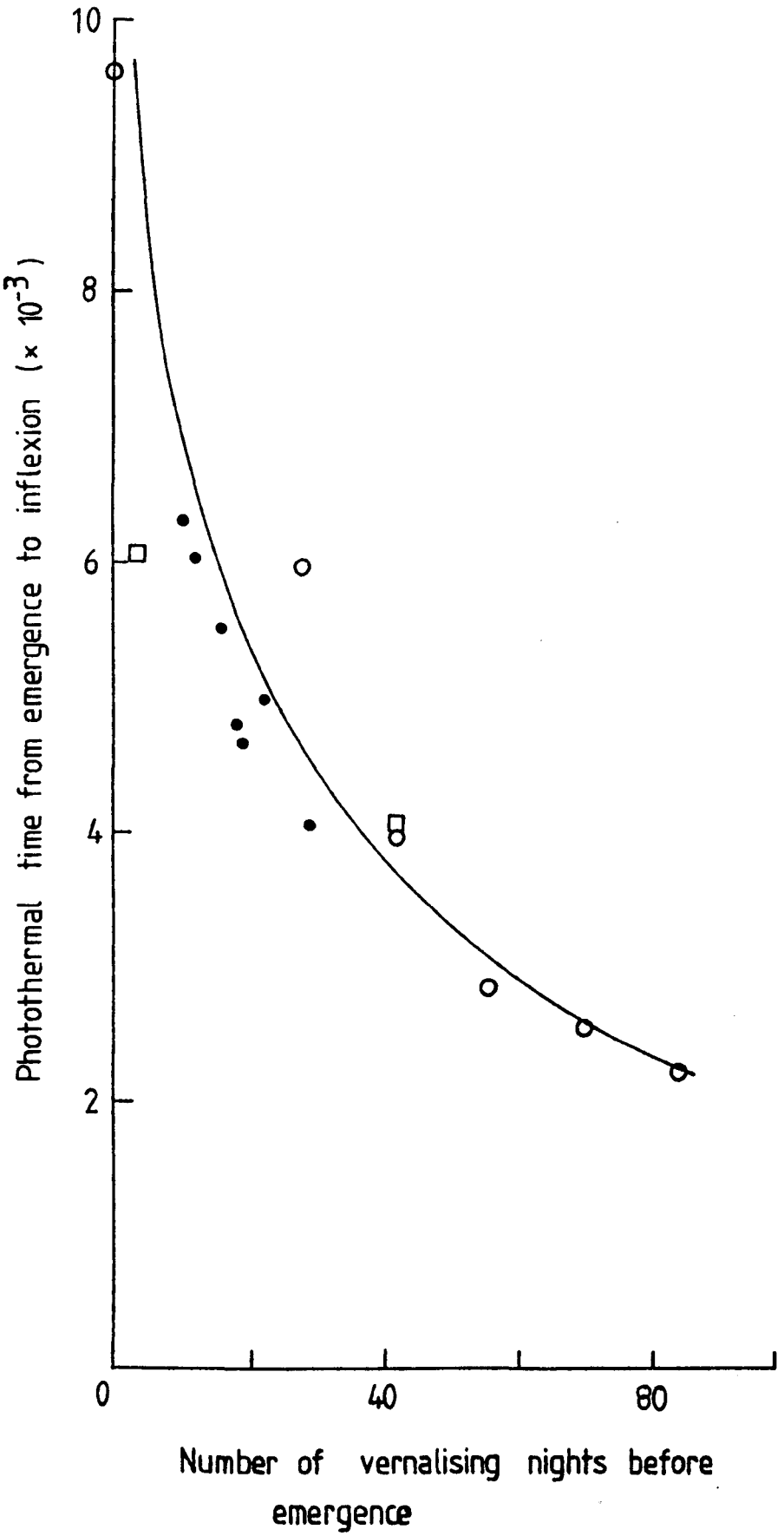


Figure 4-15 The number of vernalising nights before crop emergence in relation to the amount of photothermal time after emergence taken to reach inflexion point. The relationship is highly significant ($p < 0.01$).


10
8
6
4
2
0
40
80
Photothermal time from emergence to inflexion (× 10⁻³)
Number of vernalising nights before emergence

(vii) Control of Maximum Numbers

Earlier mention has been made of the genetic element determining organ numbers. In different sowings in the present work, maximum leaf and spikelet numbers varied rather little (Table 4-3). This was probably because genotype determined the plant's response to combinations of temperature and daylength in such a way as to ensure completion of the life-cycle at the appropriate time of the year no matter what the time of sowing.

Crop & Month of Sowing	Leaves	Spikelets
73 N	11	20.4
74 O	12	20.2
75 O	12	19.5
76 O	11	17.5
77 O	12	19.6
77 D	10	17.6
78 M	11	16.7

Table 4-3 Comparison of final numbers of leaves and spikelets in crops of 'Maris Huntsman' grown at Sutton Bonington.

From the foregoing analysis in terms of $\overline{T}_a$ and ϕ, it is not surprising that photothermal time sum to a given stage of development was more consistent than thermal time alone (Table 4-4), and if photothermal time could be corrected for the effect of vernalisation, the consistency should be even better. Maximum organ numbers were thus apparently controlled by temperature and daylength operating against the genetic background of the cultivar.

Index and Starting-Point		Developmental Stage Taken as End-Point					
		Nl_{max}	Inflexion	DR	Ns_{max}	Nf_{max}	Anthesis
Chronological time (d)	$\bar{x}$	90	109	140	164	173	214
(from sowing)	% c.v.	27.4	27.0	21.7	22.7	27.5	18.9
Thermal time (^{o}Cd)	$\bar{x}$	520	623	785	961	1213	1476
(from sowing)	% c.v.	15.0	17.5	17.0	18.0	16.2	14.0
Photothermal time units	$\bar{x}$	4237	5161	7482	10092	14121	19156
(from emergence)	% c.v.	10.1	15.3	10.1	12.4	12.9	4.7

Table 4-4 A comparison of methods for specifying the time taken to reach key stages in development. The mean, $\bar{x}$, is for the seven sowings shown in Table 4-2 and % c.v. is its coefficient of variation

Maximum floret number per spikelet and maximum leaf number varied very little no matter when the crop was sown. Because there was a considerable range of $\overline{R}$, this implies that a given rate was uniquely related to a corresponding duration, and that both $\overline{R}$ and D (or more appropriately, 1/D) had similar responses to corrected temperature. That this was the case for leaves and florets is shown in Figures 4-17 and 4-18: both $\overline{R}$ and 1/D were linearly related to corrected temperature. The indicated T_b for 1/D was in each case apparently lower than that for $\overline{R}$, but the difference was not significant ($p = 0.05$).

Variation in Ns_{max} between sowings was proportionately larger than that for either leaves or florets, and this appeared to be because $\overline{R}_s$ and $1/D_s$ had different responses to corrected temperature (Figure 4-19). The linear relation of $\overline{R}_s$ to corrected temperature has already been established. A straight line also accounted for most of the variation ($p = 0.001$) in the relationship of $1/D_s$ to corrected temperature, but there was a significant quadratic component as well ($p = 0.05$), so that at higher corrected temperatures duration would be reduced proportionately more than $\overline{R}_s$, and Ns_{max} would therefore be correspondingly smaller. Thus, in 1976/7 and in the December and March 1977/8 sowings, spikelet initiation began late, when $\overline{T}_a$ was high and ϕ_{inf} large, and Ns_{max} in these cases was smaller than in the sowings where spikelets began to be initiated earlier.

Determination of Ns_{max} cannot be described adequately by a single rate and duration in crops where inflexion was delayed; the slower rate and the faster one and their corresponding durations must be taken into account separately: this has been done in Appendix II.

(viii) Tiller Bud Initiation

Tiller bud primordia merit separate consideration because

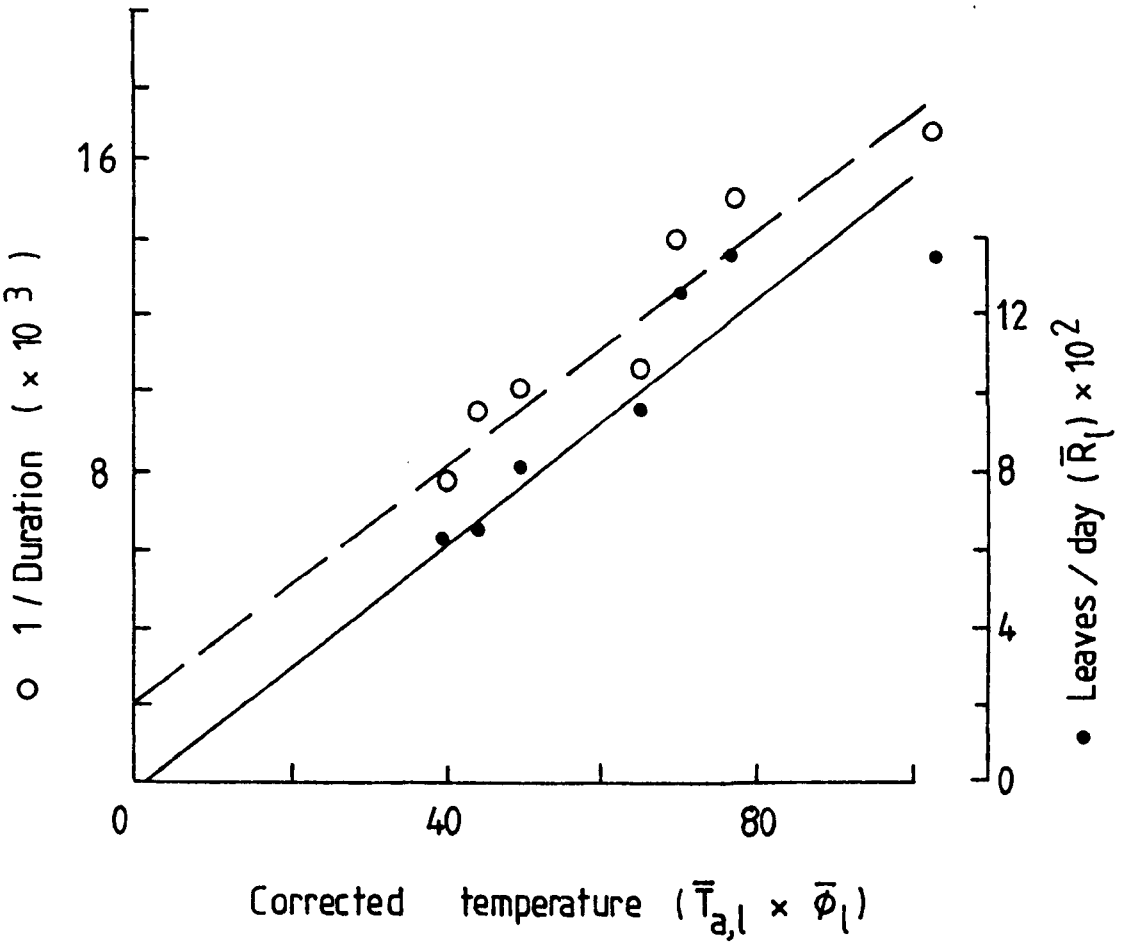


Figure 4-17 Comparison of response of mean daily rate of leaf initiation (as in Fig. 4-11), and of inverse of the phase duration ($1/D_1$), to corrected temperature during the leaf initiation phase. The values for T_b indicated by the two lines are not significantly different ($p = 0.05$). The equation of the line for $1/D_1$ vs. corrected temperature (p 0.01) is:

$$y = 0.22(\pm 0.142) + 0.014(\pm 0.002)x$$

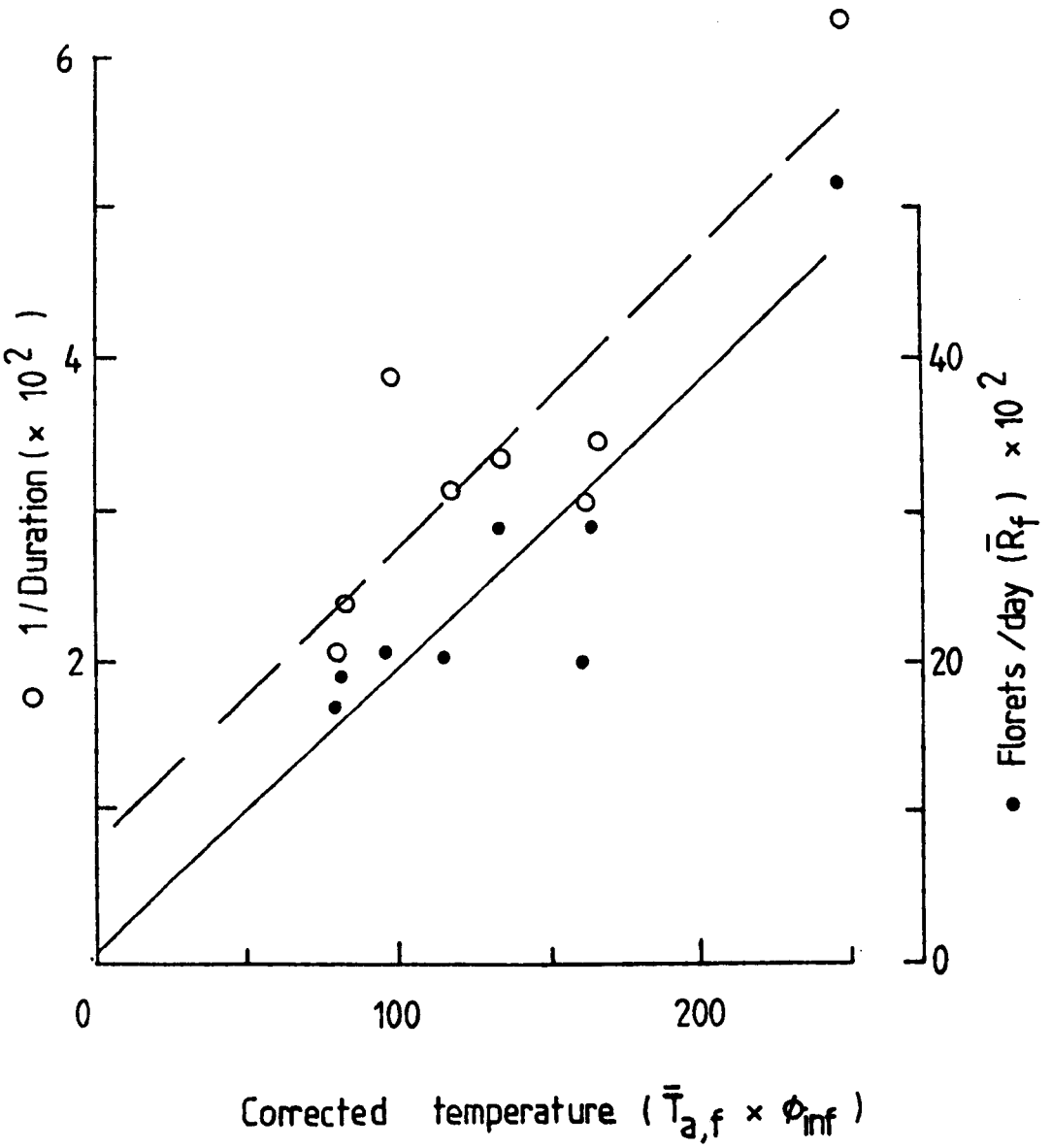


Figure 4-18 Comparison of the response of mean daily rate of floret initiation (as in Fig. 4-13), and of inverse of the phase duration ($1/D_f$), to corrected temperature during the floret initiation phase. The values for T_b indicated by the two lines are not significantly different ($p = 0.05$). The equation of the line relating $1/D_f$ to corrected temperature (p 0.01) is:

$$y = 0.009(\pm 0.053) + 0.002(\pm 0.003)x$$

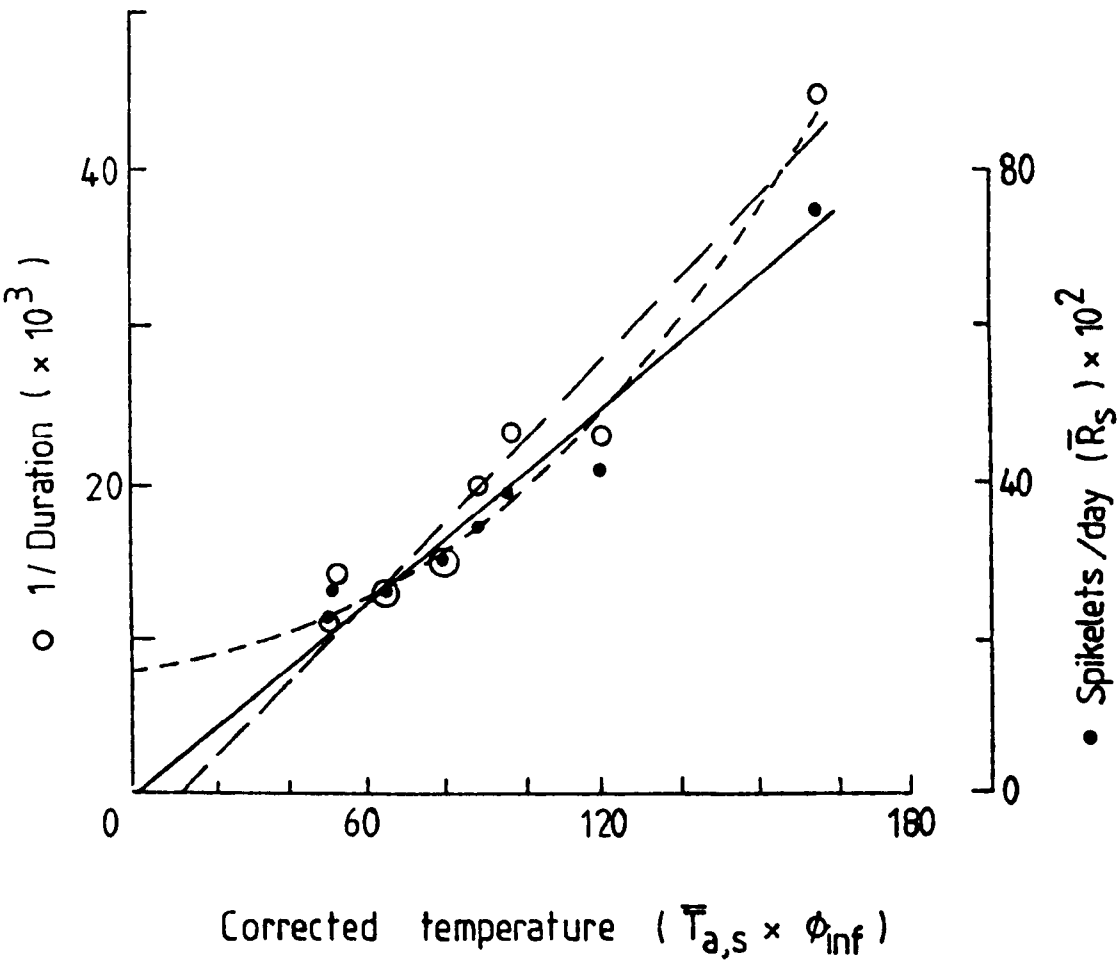


Figure 4-19 Comparison of the response of mean daily rate (as in Fig. 4-12; solid line) and of inverse of the phase duration ($1/D_s$) of spikelet initiation to corrected temperature during the initiation phase. A straight line ($y = -3.17(\pm 2.44) + 0.25(\pm 0.024x)$) accounts for most of the variation in $1/D_s$ vs. corrected temperature ($p = 0.001$) but there is a significant quadratic component ($p = 0.05$). The quadratic equation is: $y = 8.24 + 0.013x + 0.001x^2$. The base temperatures indicated by the two straight lines are not significantly different ($p = 0.05$).

Figure 4-20 The initiation of tiller buds in thermal time, and its relation to the initiation of apical primordia as in Fig. 4-4. Nti and Nt_{max} are the tiller bud number present in the grain and at the end of bud primordium initiation respectively.

Cumulative total primordium number
0
10
20
0
500
1000
Total tiller primordium nº
0
4
8
Leaves
Spikelets
Co
Nt_i
Nl_i
Nt_max
Nl_max
Ns_max

although axillary structures they are originally vegative and therefore unlike spikelets and florets (Chapter 3). Figure 4-20 shows the initiation of tiller primordia on the MS in thermal time, with apical primordium initiation for comparison. The rate at which they were initiated in thermal time ($\overline{R}_t(^{o}Cd)^{-1}$) was slower than for leaves and $\overline{R}_t$ was evidently strongly related to $\overline{T}_{a,t}$. This slower rate of bud initiation has been reported by Fletcher and Dale (1974): in barley the plastochron for initiation of tiller buds was always longer than that for leaves, and the entire bud initiation process appeared the more sensitive to nutritional deficiencies. In the present work tiller bud initiation stopped when the MS began reproductive development. This correlation suggests that bud initiation stopped when it did because assimilate was diverted to the apical region, probably as the result of increased apical dominance brought about by enhanced hormone production at the apex (cf. Nicholls, 1974). The ending of tiller bud initiation could not have been caused by a diversion of assimilate in response to demands imposed by stem extension, because this had not begun at the time in question.

V THE SUCCESSION AND GROWTH OF LEAVES

(i) Introduction

The significance for dry matter production of light interception by a crop canopy has stimulated many attempts to elucidate the physiology of leaf growth. The effects of environmental factors have been studied in controlled environments (e.g. Friend, Helson & Fisher, 1962; Auld, Dennett & Elston, 1978) and sometimes in the field as well (Watts, 1972; Syme, 1974). Because of the inherent uncertainty of extrapolating growth room results to the field (Chapter 1), field observations of leaf growth are preferable (e.g. Gallagher, 1976: Peacock, 1975; Williams & Biddiscombe, 1965), and were made in the present work.

Study of leaf growth requires consideration of leaf succession, and this topic will now be dealt with briefly.

(ii) Leaf Succession

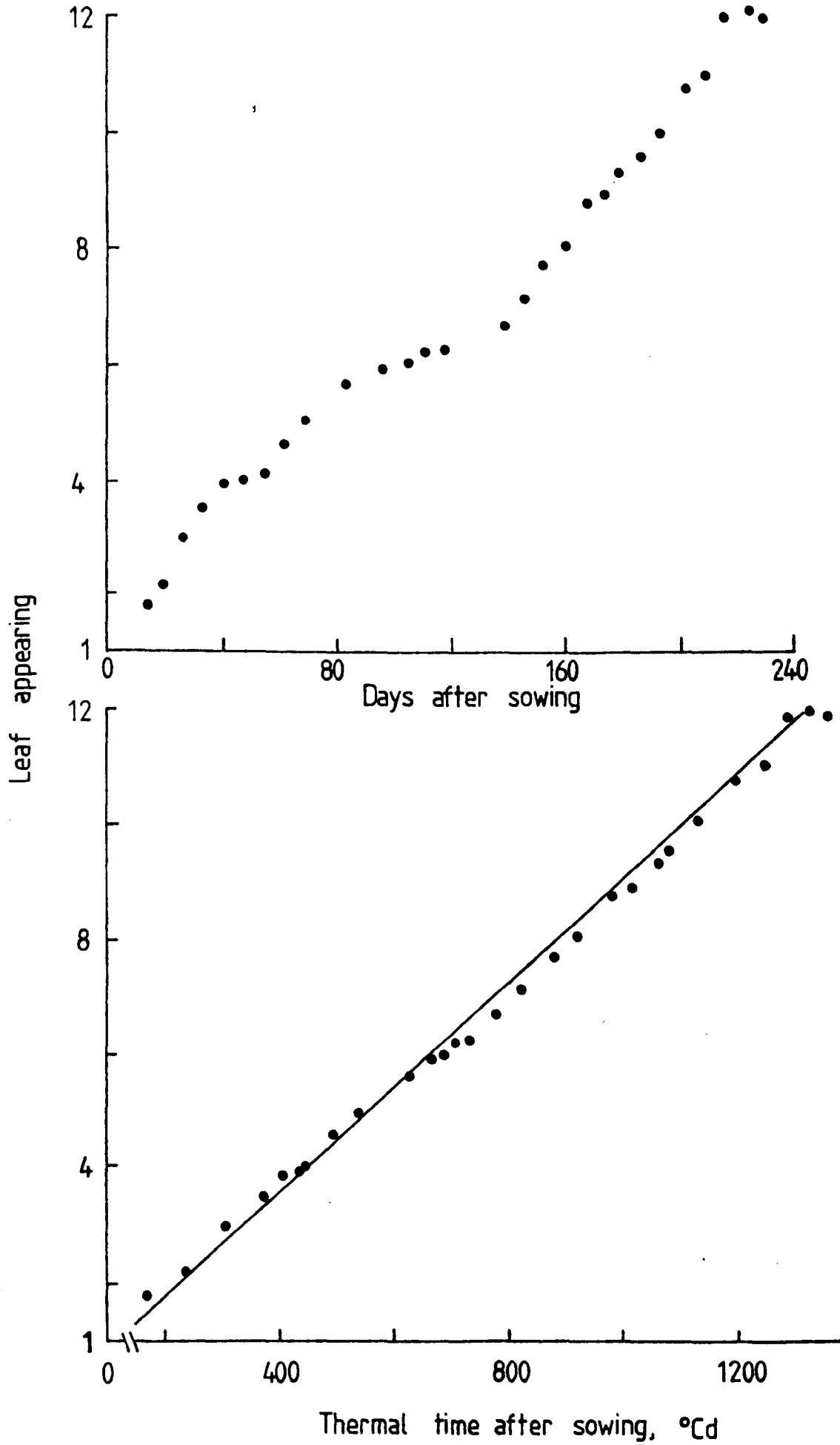
(a) General considerations

Leaf succession in grasses has a distinctive pattern. Owing to the arrangement and manner of growth of the leaves, each one is at first completely enclosed by the surrounding sheaths of older leaves. Consequently the next leaf due to appear has to grow before the tip of its lamina reaches the top of the sheaths and emerges into full light. The time at which this happens is generally called the time of appearance of that leaf. Later, the ligule of the leaf emerges into full light as laminar extension is completed and this was called leaf unfolding in the present study. An additional variable, here called leaf appearance stage (L.A.S.), was derived from combination of the two just described. Thus, if

Figure 5-1 Leaf appearance in chronological time (days after sowing, D.A.S.) of the crop sown in October 1977

Figure 5-2 Leaf appearance data of Fig. 5-1 plotted aginst thermal time after sowing (^{o}Cd) calculated above 0^{o}C. The equation of the straight line ($p < 0.001$) is:

$$y = 0.43 + 0.0082x$$


12
8
4
1
0
80
160
240
Days after sowing
Leaf appearing
12
8
4
1
0
400
800
1200
Thermal time after sowing, °Cd

there were four unfolded leaves and the next two had appeared but not yet unfolded, this was equivalent to a L.A.S. of 4 + 2 and to a L.A. of 6.

Studies of cereals and grasses show that leaf appearance rate (R_a) is strongly dependent upon temperature (Anslow, 1966; Thomas & Norris, 1977). In the field this is manifest as an increased rate in chronological time when temperatures increase in spring and early summer (Figure 5-1). It has been shown for some temperate cereals that R_a is a linear function of thermal time accumulated above $0^{\circ}C$, and that this is expected from the results of work in controlled environments, in which R_a is constant at constant temperature (Gallagher, 1976).

(b) Field observations

From the samples taken, leaf appearance could be estimated to a standard error of 10% of the mean or less in all sowings. Because sampling was frequent an accurate knowledge of leaf appearance, unfolding and L.A.S. was obtained throughout the life of the crop.

As already noted, a plot of leaf appearance in chronological time curves sharply upwards with the onset of warmer weather, but when plotted against thermal time above $0.0^{\circ}C$ (Figure 5-2) the relationship is linear ($p < 0.001$) and the slope of the line is the mean rate of leaf appearance in thermal time ($R_a(^{\circ}Cd)^{-1}$). When the crop emerges from the soil, the tip of the coleoptile and of leaf 1 reach the surface at the same time: it is meaningless to designate a leaf appearance of 0 and for this reason the y-axes of the graphs in Figs. 5-1 and 5-2 start at 1.0. For all crops, thermal time from sowing to coleoptile emergence was $120^{\circ}Cd$ above a base of $0.0^{\circ}C$ (cf. Bierhuizen, 1973)

From the data for all sowings, it was evident that with later sowing the leaf appearance per unit of thermal time tended to be greater. Because thermal time differences in primordium initiation rate had been ascribed to differences of daylength (Chapter 4), correlations of $R_a(^oCd)^{-1}$ with daylength were sought. There is some evidence from Figure 5-2 that $R_a(^oCd)^{-1}$ is a function of daylength: the deviation about the fitted line appears to be systematic and the trend of the deviation approximately coincides with the change of daylength through the season. The possibility that current daylength modified the rate in thermal time was supported by the significant relationship of this rate with the mean of current daylength during the time from crop emergence to flag leaf appearance ($p < 0.01$). However, other evidence suggested that the effect of daylength upon R_a in thermal time was not so simple.

A small trial sown on 8th June experienced much longer days than any of the other sowings during the time that its first few leaves were appearing, and might therefore have been expected to display the fastest rate of appearance for the whole series. Instead, the rate for this sowing was very close to that for a sowing that emerged in mid-December. The only similarity of environment for these two sowings is that for both the rate of change of daylength was very small at the time that the crop emerged. This result strongly suggested that it was not simply daylength but the magnitude of its rate of change at emergence ($d\phi / dt$), and possibly its sign, which modified the rate of leaf appearance in thermal time thereafter. To test this hypothesis against the relationship for current daylength, $d\phi / dt$ at crop

For p.78

atum

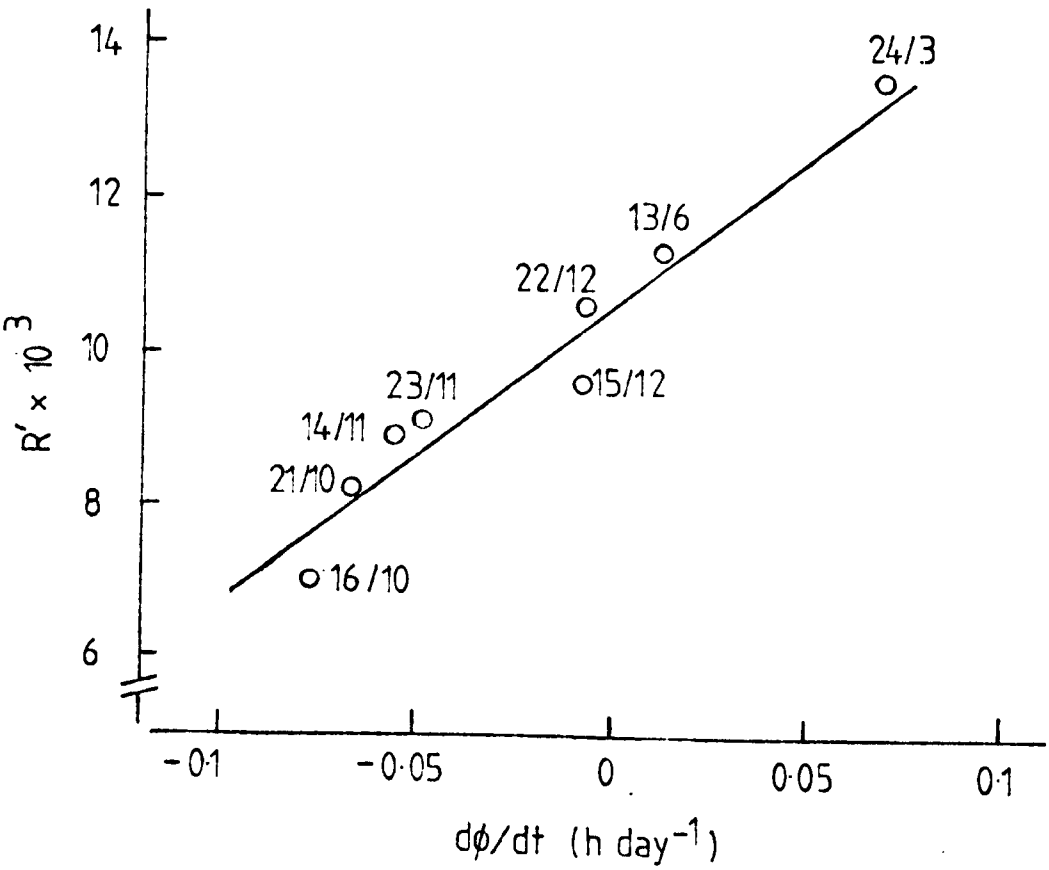


Figure 5-3 In the equation: $a = (10{\cdot}6 \pm 0{\cdot}2) \times 10^{-3}$, $b = (0{\cdot}04 \pm 0{\cdot}004)$ $\Big\}$ $(^{\circ}C\ day)^{-1}$

Figure 5-3 Mean rate of leaf appearance in thermal time ($\bar{R}_a(^{\circ}Cd)^{-1}$) plotted against rate of daylength change at crop emergence ($d\phi/dt$). The date beside each point is that when the crop it represents emerged. The equation of the fitted line ($p < 0.001$) is:

$$y = 10.42(\pm 0.18) + 0.026(\pm 0.002)x$$

emergence was calculated for each sowing, and when the calculated values were plotted against the corresponding R_a ($^oCd)^{-1}$ values, a stronger correlation was evident ($p < 0.001$): Figure 5-3. It therefore appears that R_a in thermal time is set mainly by $d\phi/dt$ at the time of emergence, although there may be some secondary effect of current daylength (see (iv)(c-3)).

Although a difference in $d\phi/dt$ is a subtle change to detect, it is the only unambiguous key to the time of year and may be of great importance to an annual plant, such as wheat. Evidence from elsewhere is hard to find. However, when Ipomaea, also an annual, was sown at different dates and grown in glasshouses at controlled temperature under natural daylength, its rate of leaf appearance in thermal time appeared to depend upon the time of sowing (Ashby & Wangermann, 1950). As Vince-Prue (1975) comments, ". . . the possibility that shortening daylengths are seen differently from lengthening ones has hardly been examined in plants, although this type of response is known in animals". Such a possibility seems likely because it is now known that many plant species are able to measure small differences in daylength: reviewing the evidence for time-measurement systems, Vince-Prue concluded that they are probably based upon an endogenous circadian rhythm of phases with different sensitivity to light, and that phytochrome is responsible for the phasing of the rhythm.

(iii) Leaf Growth

(a) Growth of the individual leaf

An understanding of leaf growth requires some knowledge of what happens to the cells during its progress, so this process will be dealt with before reporting leaf growth in the field in relation to environmental variables.

Passing directly into further development and growth after its inception (Chapter 3), the graminaceous leaf primordium at first has distinct apical and marginal meristems and an adaxial or ventral meristem which generates the laiminar midrib (Yamazaki, 1963a). Apical and marginal meristems are distinct only briefly: activity soon becomes confined to an intercalary meristem at the base of the young leaf. This region becomes divided into distal and proximal portions by the formation of a band of parenchyma cells: at this time the ligule forms. Sharman (1942) found that these events in maize coincided with emergence of the tip of the developing leaf from within the lower ones ensheathing it.

Sharman showed that laminar growth progresses by a wave of cell elongation and maturation passing from the tip to the base. As the lamina grows into full light, cell extension in the emerged portion stops abruptly, probably because of the change in light environment (Begg & Wright, 1962). In the tissues formed by the intercalary meristem below the ligule, events result in growth of the leaf sheath. Growth of the lamina is completed when the ligule appears into full light, but there are several reports that the sheath continue to grow for a time afterwards (iv c.3).

(b) The relation of cell division and extension to leaf growth

Leaf growth may be interpreted in terms of two fundamental processes, cell division and cell extension. Ashby & Wangermann (1950b) claimed that in Ipomaea the two were consecutive, a view which appears to be shared by Langer (1972): he states that cell division in the lamina of a grass ceases when the ligule is differentiated. In the present work, dissections showed that the

ligule was differentiated when the leaf was only about 10 mm long, so if Langer's statement is correct most of laminar growth resulted from the extension of cells formed very early in the life of the leaf.

Sunderland (1960) pointed out that Ashby and Wangermann's conclusion was based on study of epidermal cells, in which division stops earliest. He domonstrated that in lupin and sunflower, division and extension were concurrent in other leaf tissues until one-half to three-quarters of final leaf size, depending on the species, so that the two-phase view of leaf growth was clearly untenable. Sunderland's findings are supported by Maksymowych (1963) from work with Xanthium. More relevantly for the present work, they are also supported by data of Williams & Rijven (1965) for wheat leaf growth. These workers obtained good estimates of cell number per leaf. Figure 5-4 shows that cell division went on almost until the leaf reached its final size. When the leaf was the length at which ligule differentiation occurred in the present study, only 7.5% of the final cell number was present. Even at leaf appearance less than 40% of the final number of cells had been differentiated. However, because these workers used wheat grown in a controlled environment with a high proportion of fluorescent light, their data may not be applicable to plants grown in the field.

Production of new cells clearly continues while those already formed are extending. It seems essential that this should happen, for normally division and extension are different phases in a continuous process: if treatments are given that halt division, growth soon stops because there are no more new cells to extend.

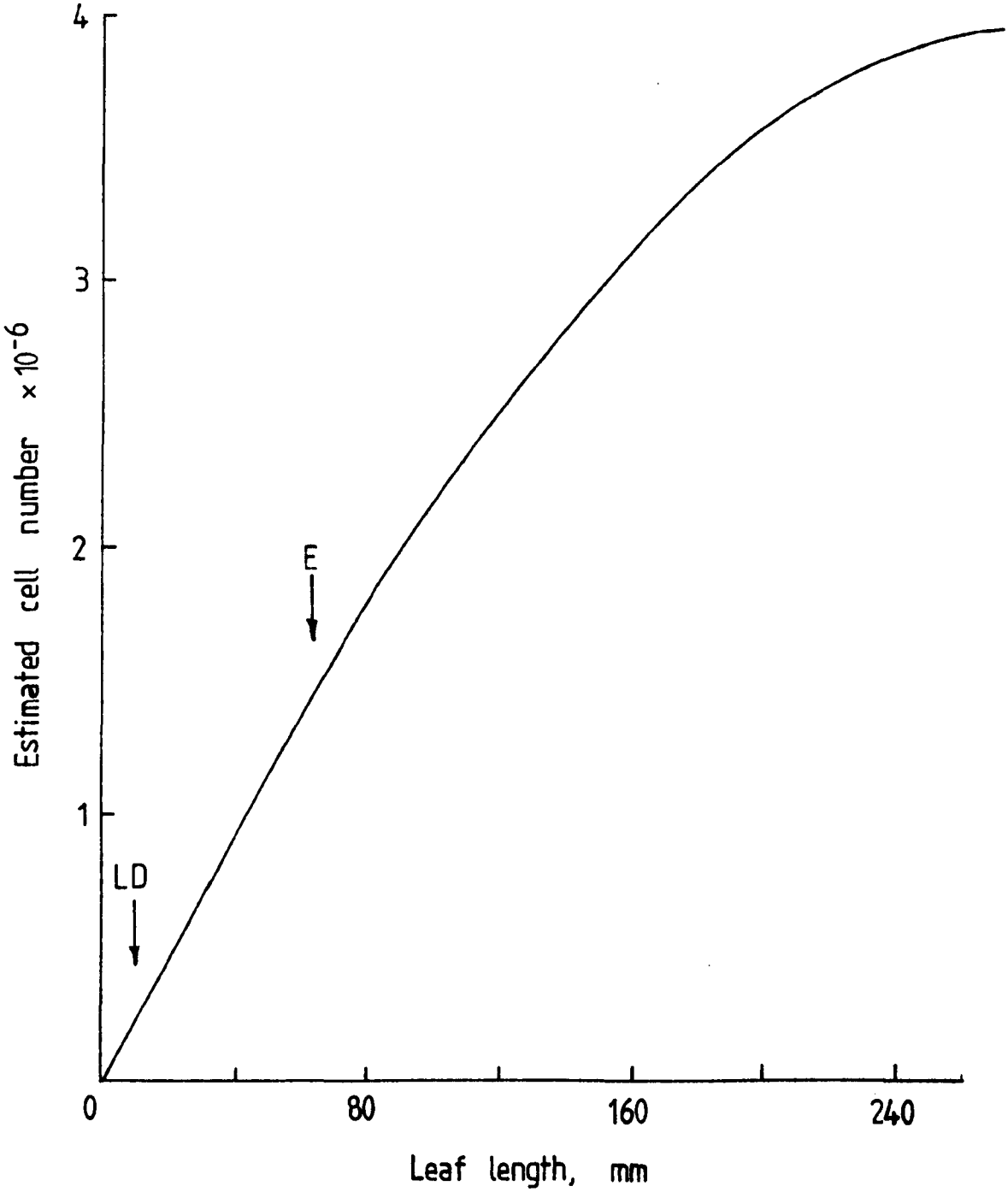


Figure 5-4 The increase of cell number during extension growth of the fourth leaf (= lamina + sheath) in wheat. Plot made from data of Williams & Rijven, 1965.

LD = length at which ligule differentiated (in present study)

E = time of appearance of leaf tip (Williams & Rijven)

There is a close correlation between cell number and leaf enlargement: Brown (1976) suggests that this implies that rate of division is a rate-limiting step for the rate of enlargement of the organ.

The relative importance of the division and extension of cells in determining leaf growth rate and final size was quite clear to at least one of the older authorities: ". . . the formation of cells is a phenomenon subordinate to, and independent of, growth." (Sachs, 1887, quoted in Brown, 1976). Though this dogmatic view is no longer acceptable in the light of experimental evidence, it is still not entirely certain how much division and extension each contribute to leaf growth (Auld, Dennett & Elston, 1978). Some workers (Wilson & Ludlow, 1968) have considered that the two processes should not be regarded as determinants of leaf growth because extension of cells may be limited by nutrient supply. Increase in cell number during early growth of the leaf is more or less exponential (Williams, 1960; Dale, 1976) but there is at first little concurrent cell extension: at this time the cells are of the order of 15 μm long, and there is a high relative rate of leaf extension (R'_e) although the leaf is still less than 1 mm long (Williams & Rijven, 1965; Gallagher, 1976). When such cells extend their increase in length is often up to 200 μm (Brown, 1976). This implies that, although division and extension are concurrent throughout most of the growth of the leaf, it is cell extension that contributes most to the increase in leaf size.

(c) Ontogenetic factors in leaf growth

A systematic difference in the size of the laminae of successive leaves has been reported from several species of the Gramineae. The laminae were progressively longer at higher leaf

positions, reaching a maximum at a position several nodes before the flag-leaf in rye-grass (Borrill 1959; Edwards, 1967) or at the penultimate leaf in barley (Kirby, 1973). For wheat, Borrill found that the node number at which the longest leaf occurred varied according to low temperature and daylength treatment, but Gallagher (1976) found that in field crops the penultimate leaf was longest.

In the present work, it was found that the first four or five leaves were of similar length and of similar width, but thereafter the length and width both increased at successively higher positions up the stem: the same finding was reported by Gallagher (1976). This change is associated with the increases in size of the apical dome when successive leaves are initiated (Abbe, Randolph & Einset, 1941; Yamazaki, 1963b), and from Figure 4-1 the flag leaf would be expected to be the longest and widest of all. This is apparent when the sizes of the leaves that developed from the primordia represented in Figure 4-1 are examined (Figure 5-5). The width of both lamina and sheath increased with higher leaf position, as did the length of the whole leaf (= lamina + sheath) and of the sheath alone. However, it was not the flag leaf (11 or 12 according to season) that had the longest lamina; this was also the case in the other seasons for which there are leaf measurements (Figure 5-6). Because photosynthesis by the flag leaf lamina accounts for about 65% of the assimilate required for ear growth and grain filling (Marshall, 1978), its size is of especial importance.

Results obtained in 1975/6 (Figure 5-6b) show clearly that ontogenetic differences in leaf size are expressed even in

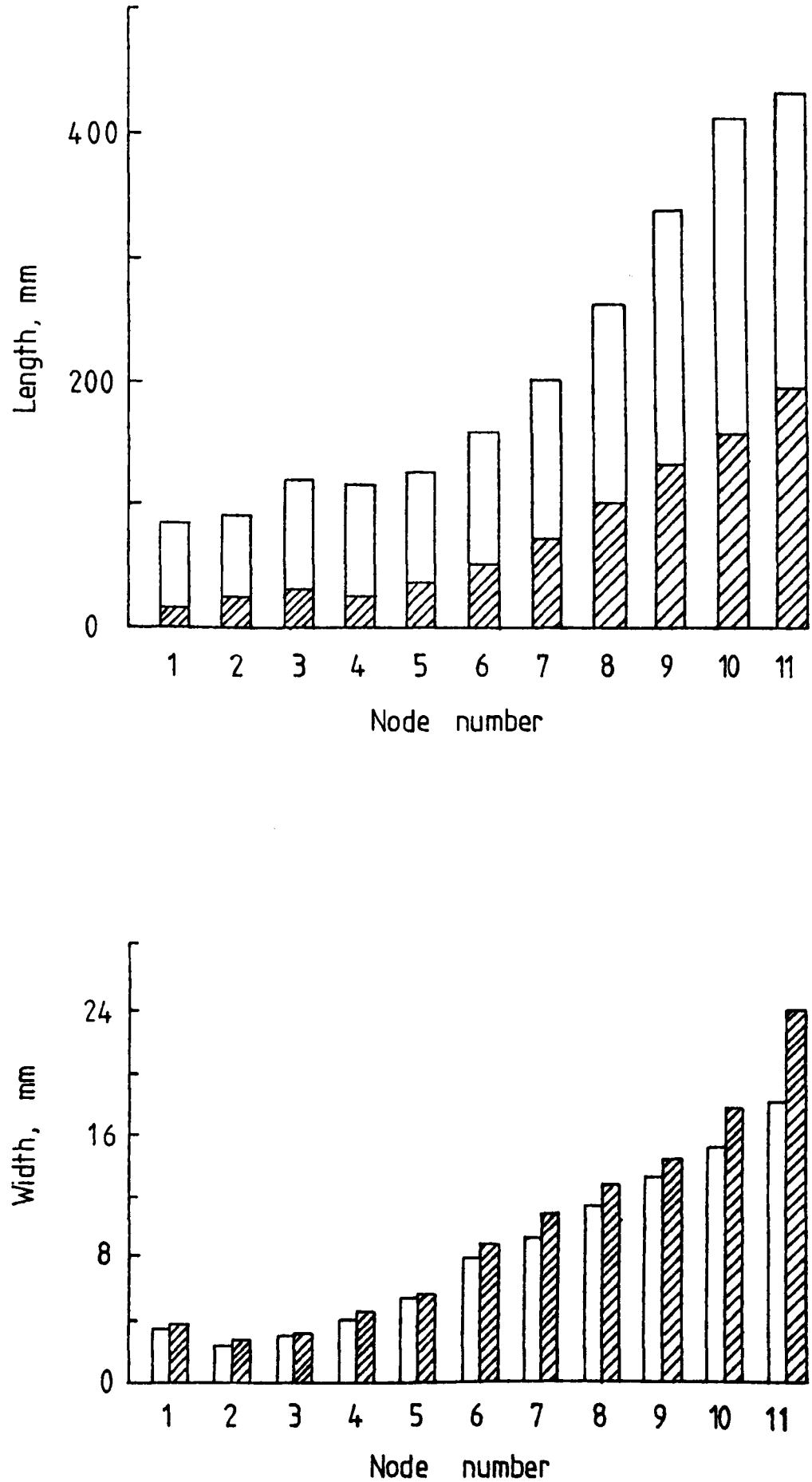


Figure 5-5 Final length and width of lamina (□) and sheath (▨) in the control plot, 1976/7 crop

Figure 5-6 The pattern of final lengths of laminae in different seasons.

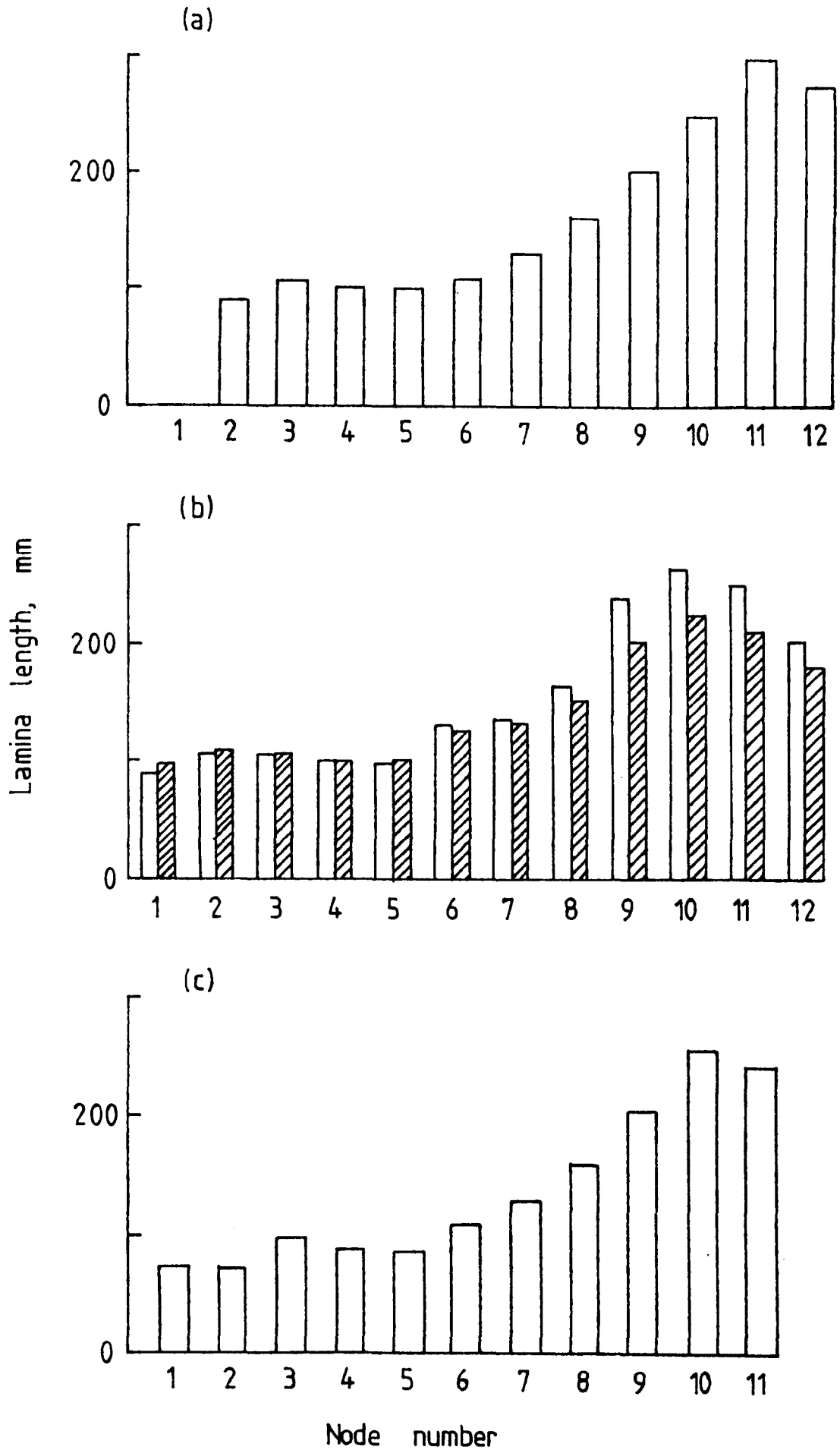
(a) 1974/5 (Data of Gallagher, 1976)

(b) 1975/6 □ +N treatment

▨ ON treatment

Note the similar pattern of leaf lengths in the two treatments

(c) 1976/7. Data from control plants


(a)
200
0
1 2 3 4 5 6 7 8 9 10 11 12
(b)
Lamina length, mm
200
0
1 2 3 4 5 6 7 8 9 10 11 12
(c)
200
0
1 2 3 4 5 6 7 8 9 10 11
Node number

nitrogen-deficient plants, so in analysing leaf growth it is essential to remember that final leaf size is influenced by a combination of ontogenetic and environmental factors.

(iv) Analysis of leaf growth

(a) Leaf growth in relation to time and weather

Gallagher (1976) made an extensive review of the literature and an experimental study of the effects of weather on leaf growth. In the present context it is appropriate to deal with weather effects briefly here, and then to concentrate mainly on results from crops in different seasons (iv c).

Figure 5-7a shows a typical set of measurements from 1 mm to final size for the time course of laminar length growth. Distortions are introduced by the daily temperature variations but by plotting against thermal time instead they are removed, because leaf growth is strongly influenced by temperature (Anslow, 1966; Thomas & Norris, 1977), particularly that of the stem apex (Peacock, 1975; Watts, 1972). In 1977, soil warming was applied and hourly extension rates were measured by LVDT auxanometers (Chapter 2). During the time that the stem apex was in the soil, leaf extension rate (R_e) of both warmed and control plants was strongly correlated ($p < 0.001$) with soil temperature at 1 cm, $T_{s0.01}$. Later, when the apex had risen above the soil surface, R_e was strongly correlated ($p < 0.001$) with air temperature at 0.5 m ($T_{a0.5}$). The dependence of R_e upon temperature was linear in each case (Figure 5-8), and held for both day and night temperatures. Similar results were reported by Gallagher from his more detailed investigations.

Temperature is not, of course, the only significant weather variable. Leaf growth may be strongly affected over short periods and in the longer term by high levels of solar radiation

Figure 5-7 Extension growth of the laina of leaf 8 (1975/6, +N)

(a) Growth in chronological time (D.A.S.)

(b) Growth in thermal time (^{o}Cd) above a base of 0.0^{o}C. The bars on each side of the points are two standard errors apart. The line fitted to the points representing 90% of extension growth has the equation $y = -526 + 0.68x$ ($p < 0.001$)

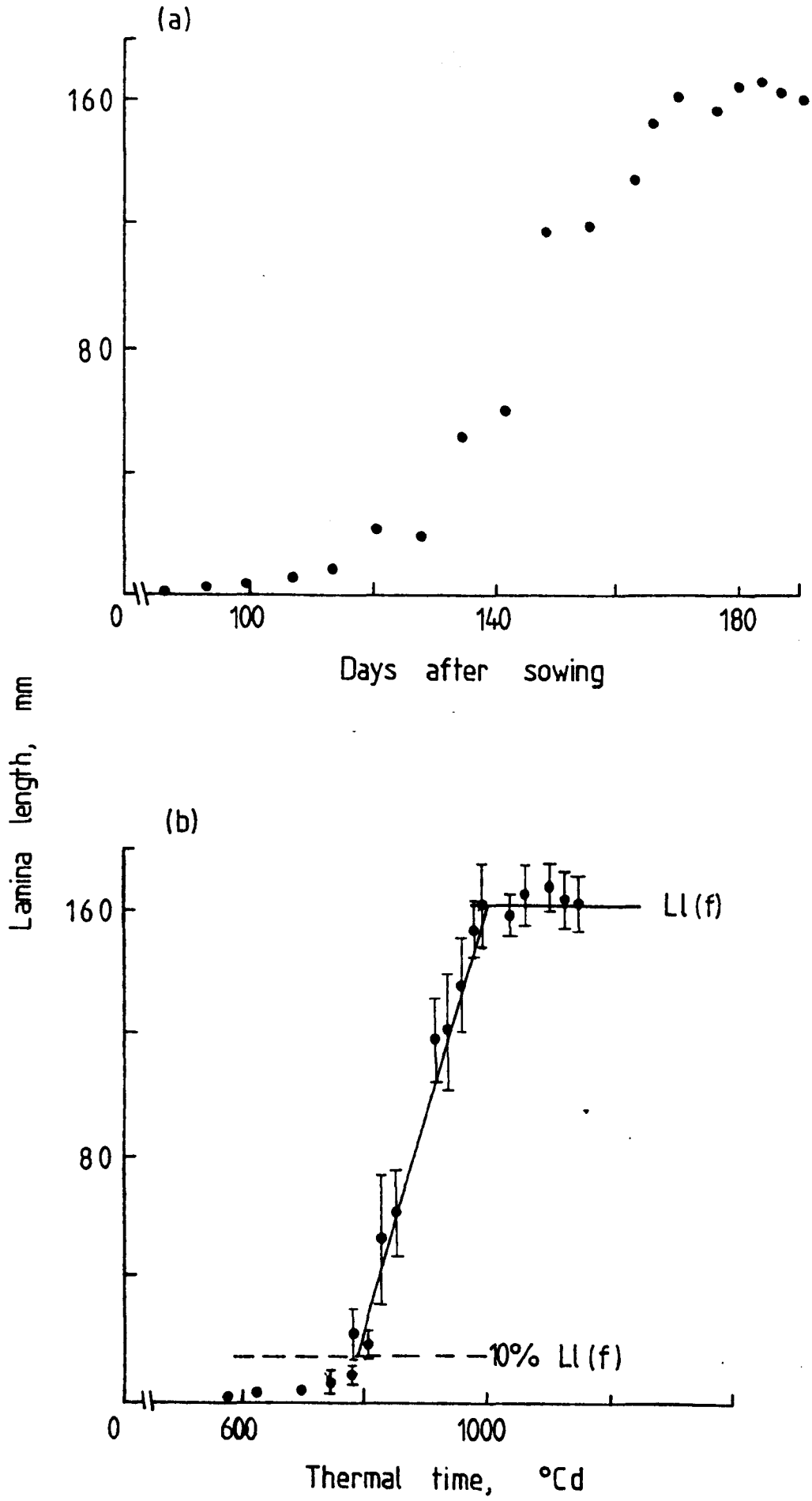

(a)
160
80
0
100
140
180
Days after sowing
Lamina length, mm
(b)
160
80
0
600
1000
Ll(f)
10% Ll(f)
Thermal time, °Cd

Figure 5-8 Auxanometer measurements of hourly rates of leaf extension as a function of temperature, (a) at 1 cm in the soil ($T_{s\ 0.01}$) and (b) at 0.5 m in the air ($T_{a\ 0.5}$). Open circles, daytime measurements; full circles, night

(a.1) Leaf 9, 9/10 May 1977 (Control)

$$y = -0.81(\pm 0.19) + 0.14(\pm 0.015)x \quad (p < 0.001)$$

(a.2) Leaf 10, 9/10 May 1977 (Warmed)

$$y = -0.90(\pm 0.19) + 0.15(\pm 0.011)x \quad (p < 0.001)$$

(b) Leaf 11, 1/2 June 1977 (Control)

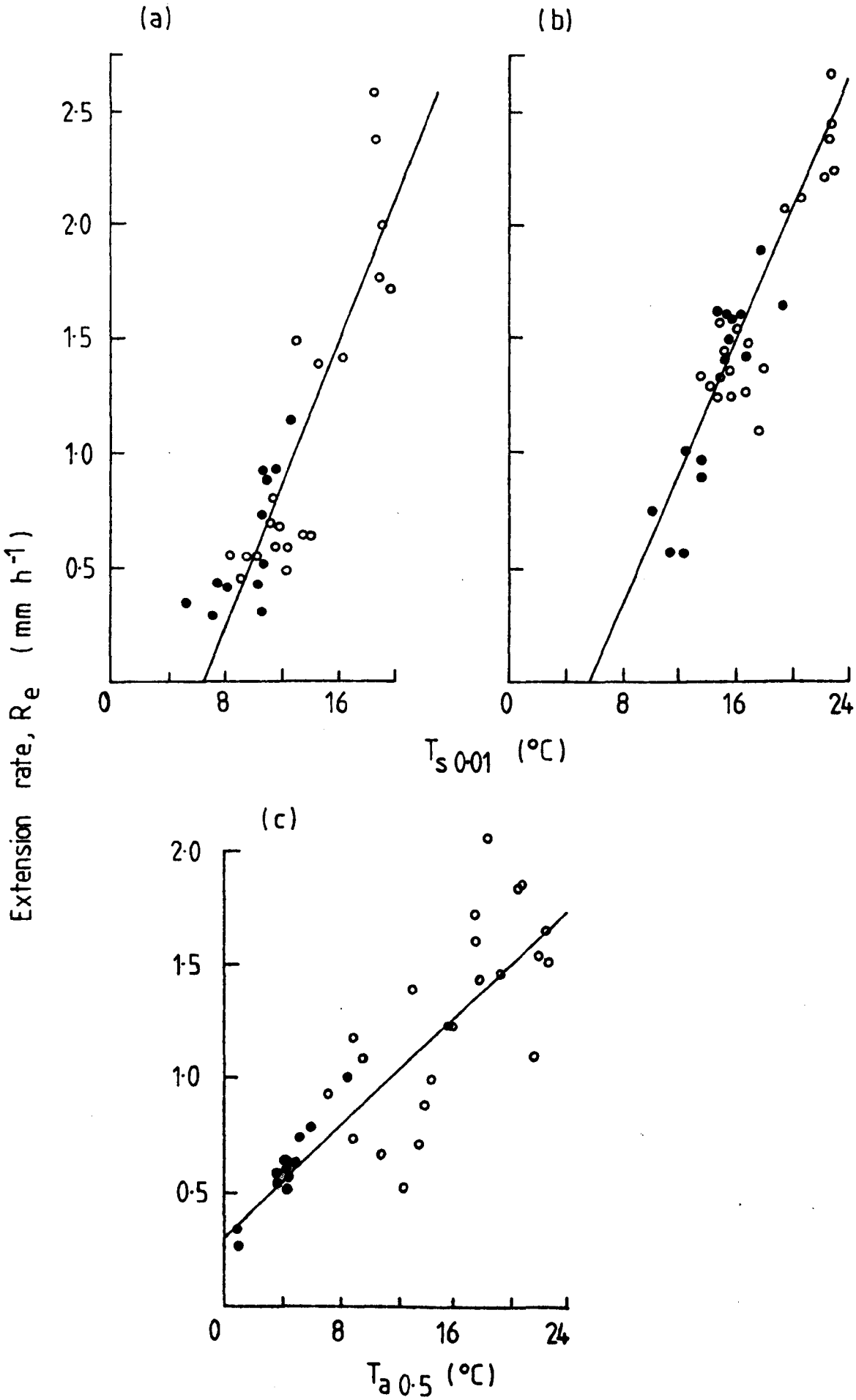
$$y = 0.35(\pm 0.11) + 0.058(\pm 0.008)x \quad (p < 0.001)$$

Values of T_b are: (a.1) $6.4 \pm 7.8^{\circ}C$

(a.2) $5.9 \pm 8.1^{\circ}C$

(b) $-5.8 \pm 11.3^{\circ}C$

The three estimates are not significantly different ($p = 0.05$)


(a)
(b)
(c)
Extension rate, R_e (mm h^{-1})
2·5
2·0
1·5
1·0
0·5
0
8
16
24
$T_{s\,0\cdot01}$ (°C)
$T_{a\,0\cdot5}$ (°C)

causing temporary or prolonged water stress. Rainfall is important in three ways which can affect leaf growth. First, the amount of rainfall influences plant water status; second, with inadequate rainfall, applied fertilisers are not properly washed into the soil; and third, excessive rainfall during winter tends to remove nutrients by leaching.

(b) Quantitative description of leaf growth

The relative rate of leaf extension, R'_e, begins to decline after about the first 10% of total laminar extension (Williams & Rijven, 1965). Gallagher showed that for the remaining 90% of extension a linear function well described the length growth of any lamina in thermal time calculated above a base of 0.0°C. This linear relation held also for laminar width growth, and the length and width growth of the sheath or of the whole leaf. The present study amply confirms Gallagher's findings: a typical example of laminar growth in thermal time is given in Figure 5-7b. All measurements greater than 10% of final organ length (L_f) and up to the last point less than L_f were used in calculating the regression line: these criteria were adopted in the present analysis. Because a continuous temperature record was available it was easy to convert points in thermal time to the corresponding chronological times.

A linear description allows growth to be considered in terms of a mean rate ($\bar{R}_e$) and a duration (D_e) of linear growth, in the same way as for the analysis of primordium initiation in Chapter 4. A similar description of leaf growth has been used for grasses (Edwards, 1967) and for beans (Dennett, Auld & Elston, 1978). It is particularly useful as a means of comparing growth in different seasons and for taking account of the ontogenetic differences in leaf size already outlined.

(c) Leaf growth in different seasons

1. Pattern of growth of successive leaves

Only a few detailed studies of leaf growth in cereals have been published (Kirby, 1973; Williams, 1960; Gallagher, 1976). From all of them it appears that as leaf position increases there is a longer period of increasing R_e, before it declines as linear growth begins, and that this as well as the difference in leaf primordium size at initiation may contribute to the ontogenetic differences in final leaf size.

Ontogenetic size differences begin at about leaf 5: using results obtained from 'Maris Huntsman' in 1974/5, Gallagher (1976) showed that each leaf had a different rate of extension per unit of thermal time ($\bar{R}_e(^oCd)^{-1}$) during the linear growth phase. There was a linear relation between the rate in thermal time and final leaf length, and he found that the reciprocal of duration of linear growth, $1/D_e$, was linearly related to $\bar{T}$, the mean temperature during linear growth. He concluded from these findings that the difference in final size between leaves of different ontogenetic rank was the result of their differences in $\bar{R}_e$ $(^oCd)^{-1}$ and was not a temperature effect. When mean daily rate of linear extension, $\bar{R}_e$, is plotted against $\bar{T}$ the effect of the inherent differences in $\bar{R}_e(^oCd)^{-1}$ is clearly seen (Figure 5-9). Gallagher's data are not well fitted by a straight line ($p < 0.01$) owing to the considerable scatter. For data from the present work the fit is more nearly linear ($p < 0.001$) but because there is a highly significant quadratic component ($p < 0.05$) the relationship is curvilinear. The same curve is a good approximation to Gallagher's data.

A confusing picture results, therefore, if data from several different leaves are used together in determining the

Figure 5-9 Mean daily rate of laminar extension ($\overline{R}_e$) in relation to mean temperature ($\overline{T}$) during the linear phase of growth.

(a) Data of Gallagher (1976)

(b) Data of 1976/7, control plants

The equations of the best fitting lines are :

(a) $y = -9.61(\pm 4.22) + 0.23(\pm 0.54)x$ ($p < 0.01$)

(b) $y = 0.95 - 0.48x + 0.164x^2$ ($p < 0.05$: see text)

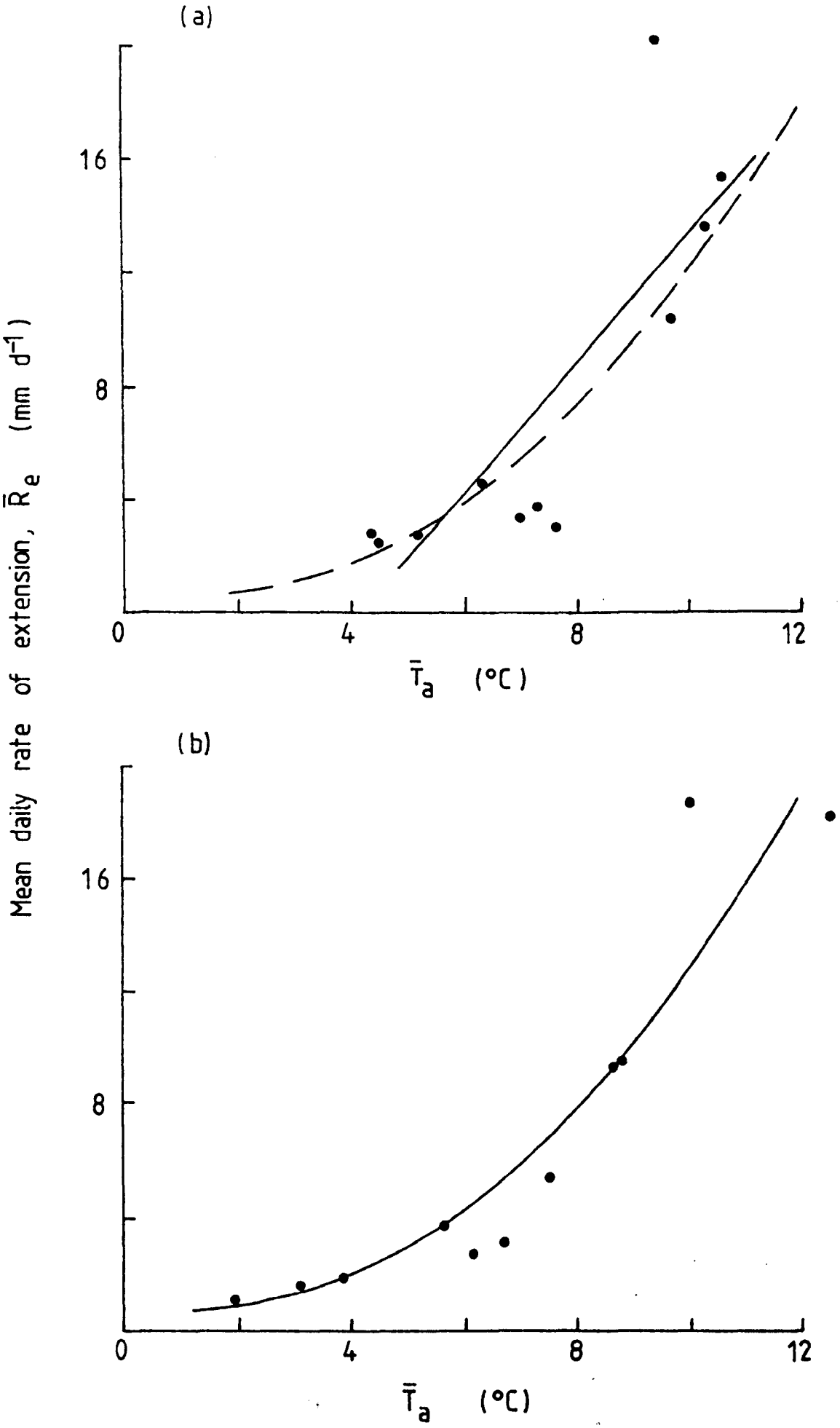

(a)
16
8
0
4
8
12
$\bar{T}_a$ (°C)
Mean daily rate of extension, $\bar{R}_e$ (mm d^{-1})
(b)
16
8
0
4
8
12
$\bar{T}_a$ (°C)

Table 5-1

Analysis of the linear growth phase of laminae, 1975/6

Leaf No.	Ll(f) (mm ± s.e.)	$\overline{Re}$ (mm d^{-1})	$\overline{Re}(^{o}Cd)^{-1}$ ($mm(^{o}Cd)^{-1}$)	De (d)	$\overline{Ta}$ (^{o}C)
+N 5	100 ± 2.0	2.38	0.49	38	4.8
6	130 ± 3.7	2.82	0.45	42	6.3
7	136 ± 3.1	2.47	0.57	46	4.3
8	164 ± 2.7	3.32	0.71	58	4.7
9	241 ± 3.1	4.26	0.72	51	5.9
10	264 ± 4.7	7.72	0.95	31	8.1
11	248 ± 4.6	8.60	0.89	26	9.7
12	202 ± 3.9	11.70	1.07	16	10.9
ON 5	102 ± 2.2	2.35	0.49	39	4.8
6	124 ± 5.1	3.45	0.46	32	7.5
7	132 ± 3.2	2.39	0.53	49	4.5
8	153 ± 3.4	3.21	0.68	58	4.7
9	199 ± 4.1	3.64	0.62	49	5.9
10	211 ± 3.0	6.91	0.82	27	8.4
11	212 ± 5.5	7.03	0.74	27	9.5
12	179 ± 5.3	11.2	0.96	14	11.7

temperature response of $\bar{R}_e$. This is probably why Peacock (1975) concluded that in ryegrass the response was exponential. Yet for the same species, others using data from several leaves found that a linear description was appropriate (Keatinge, Stewart & Garrett, 1979), possibly because they took much larger samples and presented the sample means of $\bar{R}_e$, which would conceal differences in $\bar{R}_e(^oCd)^{-1}$.

In 1975/6 and 1976/7 treatments were imposed that affected leaf growth, and the results from these can now be examined.

2. Leaf growth in 1975/6

In this season a treatment with full nitrogen fertilisation, +N, (Table 2-1) was compared with one that received N only in the seedbed (ON): Table 5-1 shows the analysis of laminar growth in each.

Statistical analysis showed that for leaf 8 and up to the flag leaf (12) there was a significant difference ($p = 0.05$) in final lamina length, $L_{l\ f}$, of the same leaf in the two treatments. The duration of linear growth, D_e, and also its timing, was similar for the same leaf in each treatment: this would be expected if D_e is controlled by temperature, which would have been the same in both treatments. The response of D_e to temperature showed no difference between treatments and was linear ($p < 0.001$): Fig. 5-10. The relationship $1/D_e$ vs. temperature was also well fitted by a straight line ($p < 0.001$) but owing to an equally significant quadratic component a curvilinear function was an even better fit. Because there was no treatment difference for D_e vs. temperature, the differences in $L_l(f)$ must therefore have resulted from differences of $\bar{R}_e(^oCd)^{-1}$ in corresponding leaves, and the analysis shows that

Figure 5-10 (a) Duration of the linear phase of lamina extension (D_e), and (b) reciprocal of phase duration ($1/D_e$), in relation to mean temperature during the extension phase ($\overline{T}_a$). Data of 1975/6: open circles, +N plants; full circles, ON plants. The equations of the lines are :

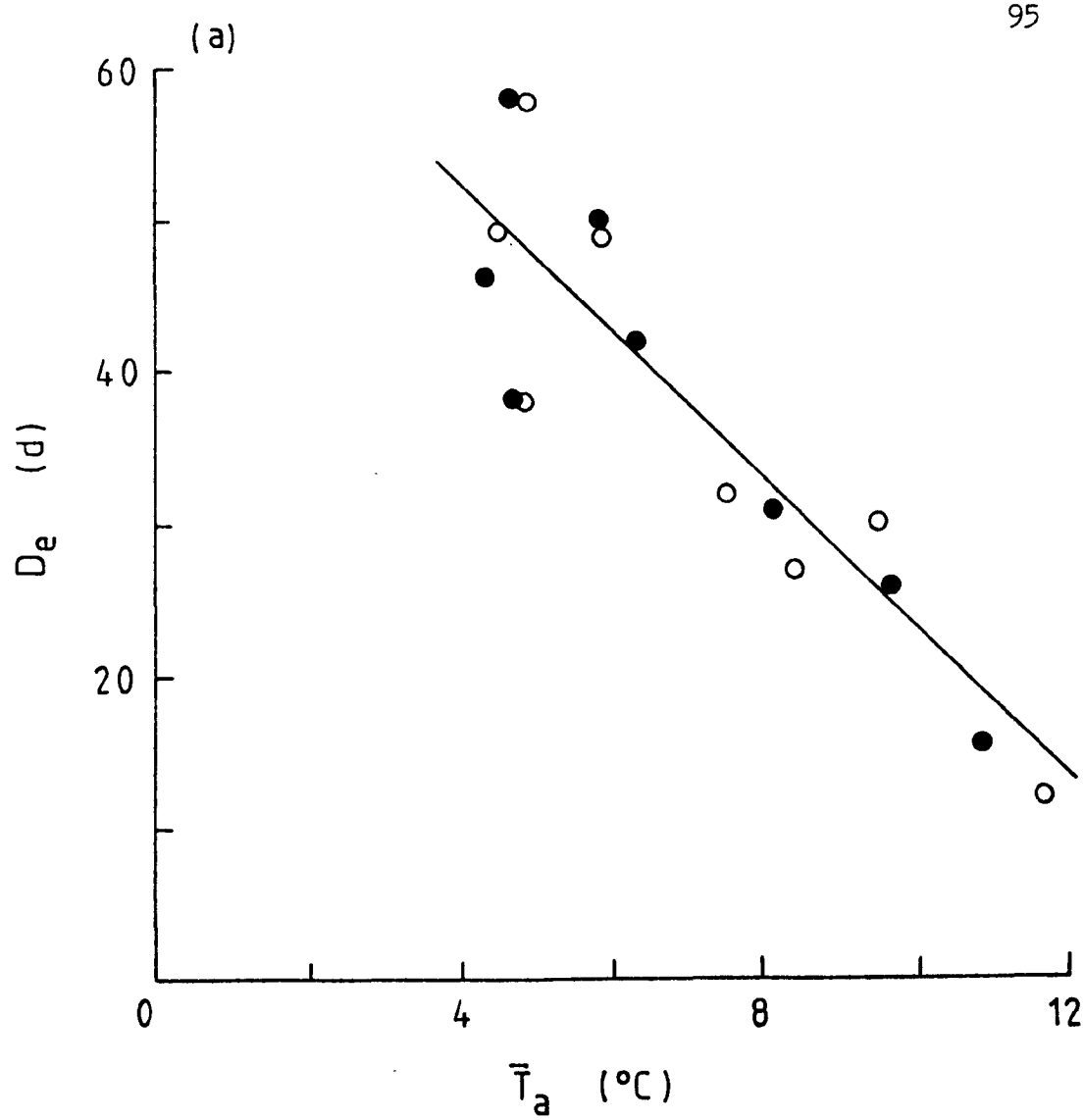
(a) $y = 72.77(\pm 4.73) - 5.03(\pm 0.64)x \quad (p < 0.001)$

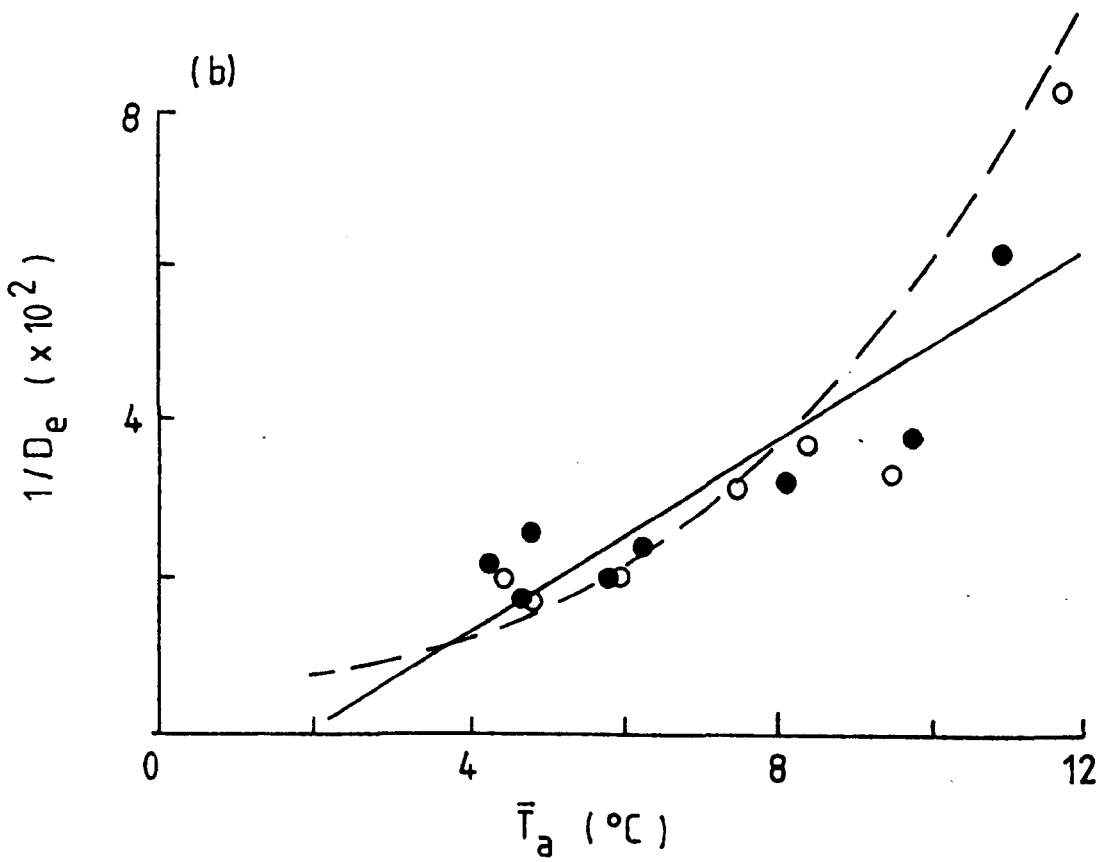
straight line:

(b) $y = -1.18(\pm 0.70) + 0.63(\pm 0.09)x \quad (p < 0.001)$

quadratic:

$y = 0.69 - 0.17x + 0.074x^2 \quad (p < 0.001)$


(a)
60
40
20
D_e (d)
0
4
8
12
$\bar{T}_a$ (°C)


(b)
8
4
$1/D_e$ ($\times 10^2$)
0
4
8
12
$\bar{T}_a$ (°C)

this was so. However, the differences were just less than significant at the 5% level.

Between treatments, no leaf showed a significant difference in laminar width growth per unit of thermal time, and there was no significant difference in final lamina width ($p = 0.05$).

High, compared with low, nitrogen levels increase both the mean size and total number of leaf epidermal cells (Njuko, 1957). In sugar-beet Morton & Watson (1948) found a consistent and increasing effect of N on the epidermal cell size of mature leaves from the fifth to the twentieth. Unfortunately, epidermal cell size is not the most reliable of guides to leaf growth and appropriate studies of the effects of N differences on cell size and number in cereals appear to be lacking. The mean overall effect of N deficiency is to decrease protein synthesis, which affects cell division even more than cell extension (Hewitt, 1963).

Evidently leaf growth in the ON plants was not manifestly affected by N deficiency until leaf 8 expanded. In this and subsequent leaves, presumably $\bar{R}_e(^{\circ}Cd)^{-1}$ was smaller because either division and extension of the cells, or both, were less than in the +N treatment. The growth of these leaves may well have been affected by water stress as well, for rainfall was much lower than average both before and during the time they were extending. Even the +N plants probably had unfavourable growing conditions during this time: as in ON leaf 10 had the largest lamina, and not the penultimate leaf (11) as would be expected from the data of Gallagher (1976) and of other seasons. Though the +N plants received dressings on 4th March and 6th May, there was little rain to carry the nitrogen down into the soil. That the unusual

Table 5-2

Analysis of the linear growth of laminae 1976/7

Leaf No.		Ll(f) (mm ± s.e.)	$\bar{R}e$ (mm d^{-1})	$\bar{R}e(^{o}Cd)^{-1}$ ($mm(^{o}Cd)^{-1}$)	De (d)	$*\bar{T}$ (^{o}C)
Control	1	78 ± 3.8	1.16	0.57	27	2.0
	2	72 ± 9.0	1.50	0.47	52	3.2
	3	98 ± 4.9	1.93	0.49	44	3.9
	4	89 ± 4.5	2.72	0.44	29	6.2
	5	88 ± 5.3	3.15	0.46	26	6.8
	6	110 ± 3.1	3.67	0.64	27	5.7
	7	129 ± 3.7	5.45	0.72	21	7.6
	8	157 ± 5.7	9.46	1.09	15	8.7
	9	203 ± 4.7	9.52	1.08	19	8.8
	10	257 ± 7.8	18.70	1.85	12	10.1
	11	241 ±13.7	18.20	1.44	12	12.6
Warmed	6	108 ± 3.5	4.06	0.56	24	7.2
	7	134 ± 4.1	6.51	0.69	18	9.5
	8	169 ± 4.6	12.91	1.17	12	11.0
	9	197 ± 8.9	9.16	0.73	19	12.6
	10	265 ±15.1	14.95	1.12	16	13.3
	11	258 ±13.4	19.68	1.67	12	11.8

* For warmed plants soil temperature at 1 cm during the period of warming was taken into account when calculating $\bar{T}$.

pattern of final leaf length differences appeared even in these plants may reflect a combination of partial N deficiency and water stress during growth of the later leaves.

The leaf growth data for this season should be interpreted with caution because they may not be typical. Fertiliser was not applied until 4th March, when six leaves had already unfolded (L.A.S. = 6+1), and by this time the growth of the leaves in both treatments may have been affected by shortage of nitrogen. A different pattern of leaf size differences may have been expressed if fertiliser had been applied earlier (cf. Borrill, 1959)

3. Leaf growth in 1976/7

During this season the soil temperature in part of the crop was increased by up to 3-4^{o} above ambient by means of soil warming cables (Chapter 2). When warming began on 21st March 1977 the fifth leaf was appearing and the modal L.A.S. was 4+1. when it was ended on 15th May the warmed plants had mean leaf appearance of 10.3 (L.A.S. 9+1), compared to 9.2 (L.A.S. 8+1) in the remainder of the crop. While soil warming was in progress the entire linear phase of laminar extension took place in leaves 7, 8, 9 and 10, its latter part in leaf 6, and its earlier part in the flag leaf, 11.

Whether the lamina, sheath, or whole leaf is considered, the chief effect of warming was to increase the daily rate of length and width growth. This effect was expected, because the stem apex was in the soil at the time and apical temperature is known to control leaf expansion (iv.a). Because warming caused no change in the dimensions of any leaf, a rise in $\overline{R}_e$ was accompanied by a fall in D_e. (Table 5-2). However, this general conclusion

must be qualified because the analysis suggests that leaves 9 and 10 of the warmed plants had an anomalous temperature response. From the mean temperature at which they grew, both would be expected to have had a higher $\overline{R}_e$. In both, $\overline{R}_e(^oCd)^{-1}$ was significantly less than for the same leaves in the control plants. As would be expected from the $d\phi/dt$ hypothesis proposed in (ii(b)), the rate of leaf appearance in thermal time ($R_a(^oCd)^{-1}$) over the whole season was the same in both treatments. Despite this long-term uniformity of R_a in thermal time, both leaves 9 and 10 took nearly 60% more thermal time to unfolding than the rest. This would not be expected if the rate was controlled by $d\phi/dt$ alone. Because soil warming accelerated R_a in chronological time, leaf 7 and those succeeding it emerged into full light at daylengths shorter than they would have experienced otherwise. Thus, when leaf 9 appeared in the warmed treatment, daylength was 16.3h, but was 17h when it appeared in the control; for leaf 10, the respective daylengths were 17.3h and 17.7h. The implication is that current daylength can influence R_a in thermal time, and that the anomalous temperature response of $\overline{R}_e$ in leaves 9 and 10 was a consequence of this. An appeal to relevant sampling errors as the source of the anomaly seems unjustified for they were of similar size in both sets of plants.

Being more complete than those of 1975/6, the 1976/7 data may be used to test Gallagher's (1976) conclusions that L_f is a function of $\overline{R}_e(^oCd)^{-1}$, that $1/D_e$ is a function of $\overline{T}$, and that in both cases the relationship is linear (iv c.1). As Figure 5-11 shows, these relationships are clearly apparent in the 1976/7 data even though the anomalous points described above are included. Though the data from warmed and control plants were described by

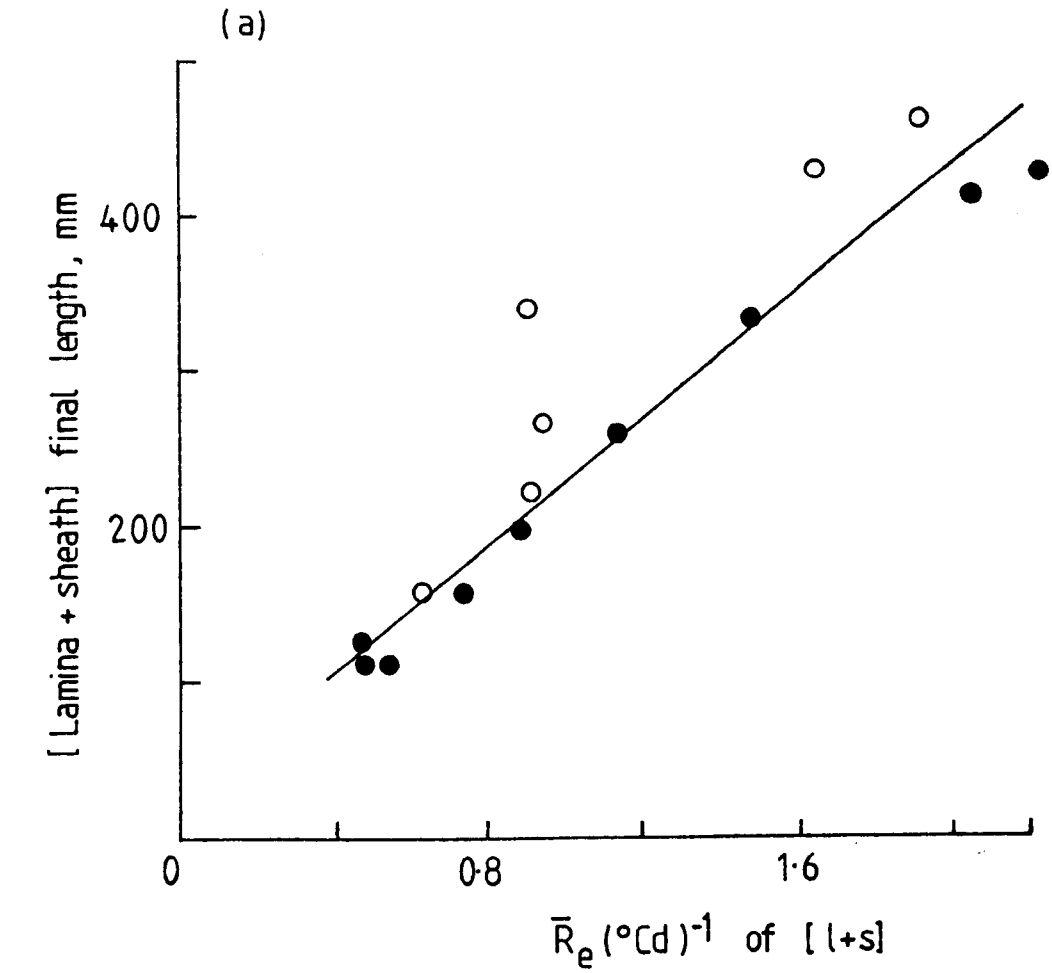
Figure 5-11 (a) Relation of final length of (lamina + sheath) to mean rate of extension in thermal time ($\overline{R}_e(^{\circ}Cd)^{-1}$). The fitted line has the equation:

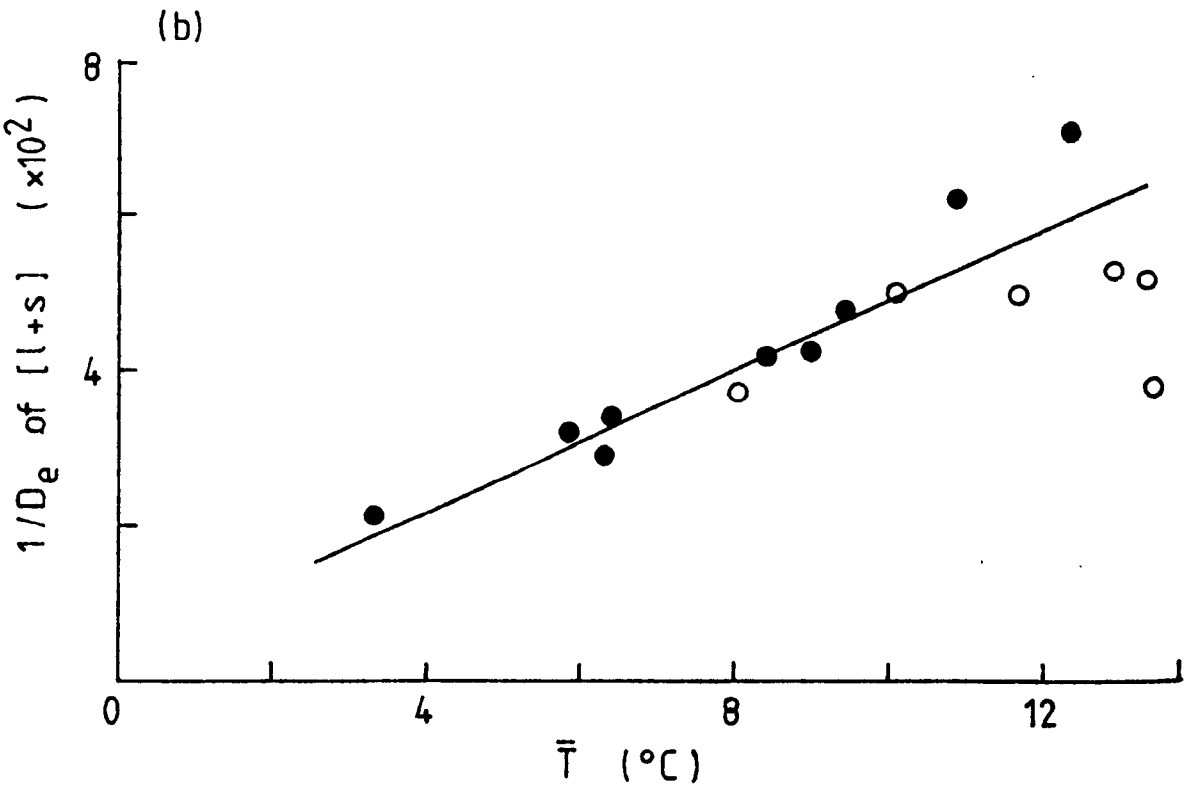
$y = 47.54(\pm 31.12) + 194.88(\pm 23.83)x \quad (p < 0.001)$

(b) Relation of reciprocal of duration of extension of (lamina + sheath), $1/D_e$, to mean temperature during extension, $\overline{T}$. The fitted line has the equation:

$y = 0.34 + 0.46x \quad (p < 0.01)$

Data of 1976/7. Open circles, warmed plants; full circles, control. For the warmed plants, soil temperature at 1 cm during the period of warming was taken into account when calculating $\overline{T}$.


(a)
[Lamina + sheath] final length, mm
400
200
0
0·8
1·6
$\bar{R}_e$ (°Cd)$^{-1}$ of [l+s]


(b)
$1/D_e$ of [l+s] (×10^2)
8
4
0
4
8
12
$\bar{T}$ (°C)

the same function, the distribution of the points for $1/D_e$ strongly suggests that the relationship was different in the two treatments, and this reinforces the possibility that leaf appearance was affected by current daylength. There was no significant difference between the base temperatures indicated by the lines for $1/D_e$ vs. $\overline{T}$ in Figures 5-10b and 5-11b ($p = 0.05$).

Correlation of the ending of lamina growth with ligule emergence has been frequently reported but the timing of sheath growth less so (iii a). Comparison of the timing of growth in these two components of the leaf (Figure 5-12) confirms reports that the sheath grows for a time after the lamina has stopped.

Shortly after the start of soil warming, the increase in $\overline{R}_e$ that took place on the main stem, and on at least the biggest tiller, resulted in a correspondingly fast increase of green area per plant (G.A.) compared with the control. The rate of increase of G.A. was particularly fast as the temperature rose quickly during the first fortnight of warming. After this a steady state was reached; with soil temperature held 3-4^{o} above ambient there was no further rise in the rate at which G.A. increased (Figure 5-13). Even with warming, because of late sowing and the decidedly cold winter it was late April before the crop reached G.A. of 1 m^2 m^{2-1}, achieved before the end of February in 1975/6. (Chapter 7).

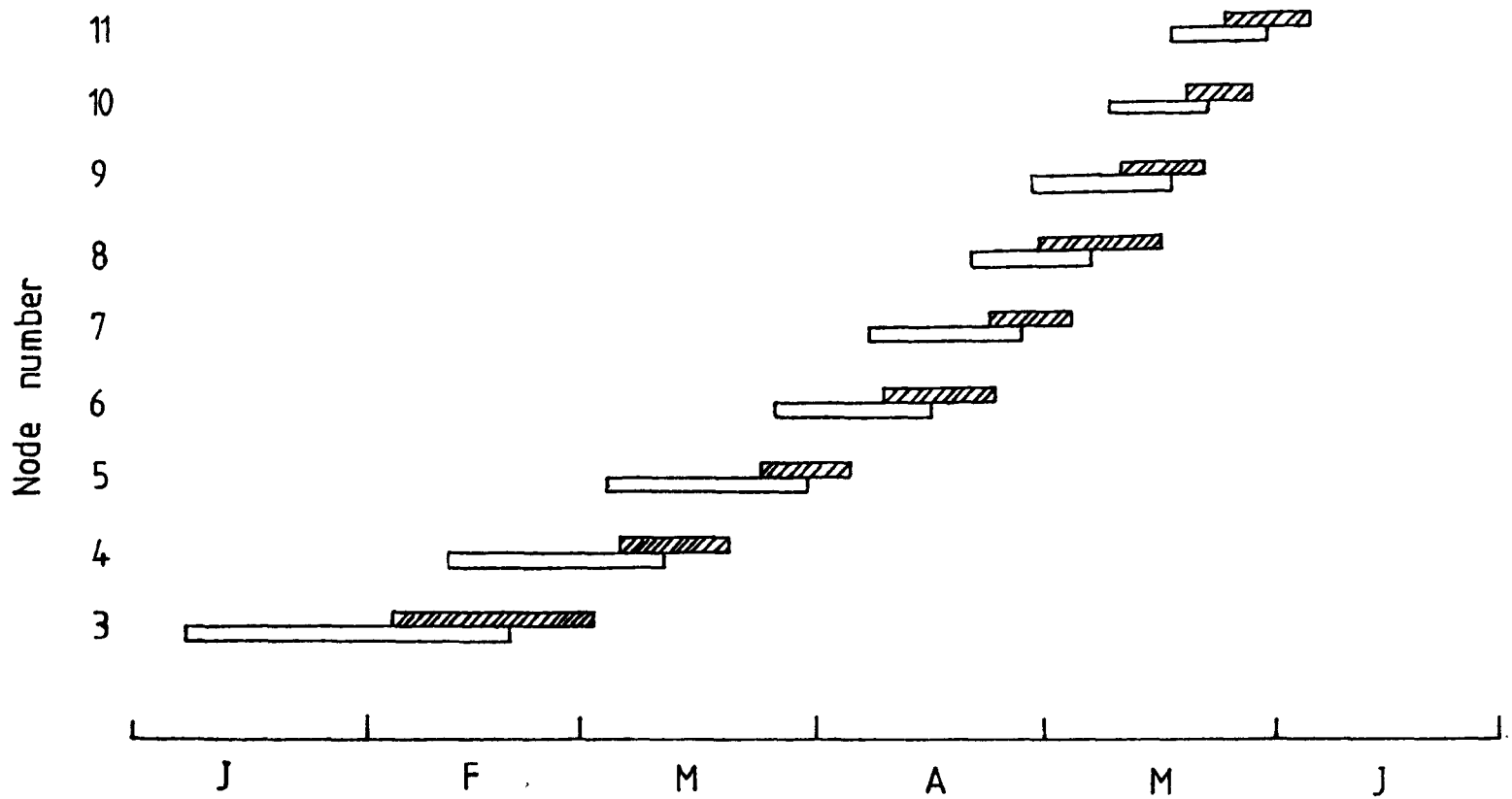


Figure 5-12 The duration and timing of extension growth of the lamina (□) in relation to that of the sheath (▨). Data from control plants, January-June 1977

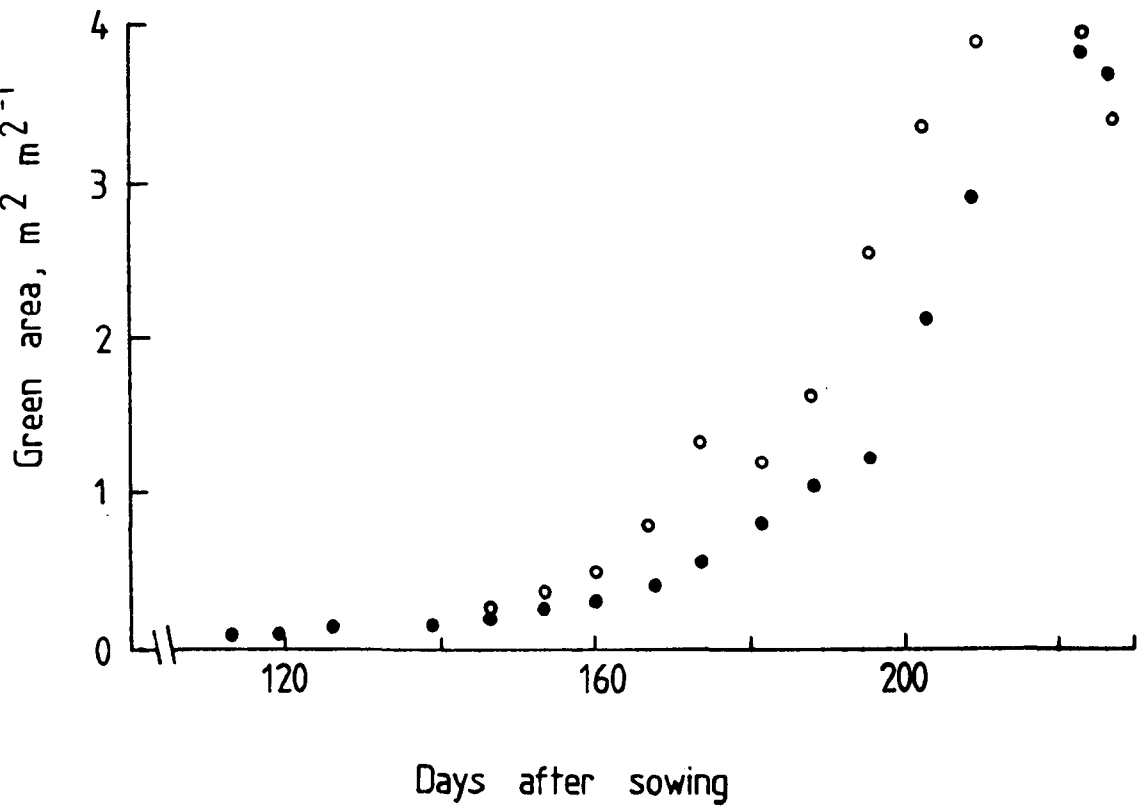


Figure 5-13 Increase of crop green area in control and warmed plots, 1976/7. Open circles, warmed; full circles, control

VI FURTHER DEVELOPMENT OF THE EAR

(i) Introduction

With the end of floret initiation in the developing ear, maximum floret number is attained. Because each grain grows from a fertilised floret, it might appear that each floret present at this time should be a potential grain site. In fact, potential grain number is not established until anthesis (see (iii)).

Survival of florets depends upon factors such as nitrogen and assimilate availability; crop yield is closely linked to the number of florets that develop far enough to bear a grain. The later processes in ear development will now be considered.

(ii) Maximum Floret Number

(a) Formal expression

The maximum floret number per ear (Nfe_{max}) has two factors: maximum spikelet number per ear (Ns_{max}: Chapter 4); and maximum floret number per spikelet (Nf_{max}). Because Nf_{max} is biggest in spikelets of the mid-ear region and is smaller in those towards the base and tip, the mean value per spikelet, $\overline{Nf}_{max}$, should be used. In these terms, maximum floret number per ear is given by:

$$Nfe_{max} = Ns_{max} \times \overline{Nf}_{max}$$

(cf. Gallagher et al., 1975; 1976). Because the ear population of the crop includes both tillers and main stems, the overall mean maximum spikelet number per ear, $\overline{Ns}_{max}$, is more appropriate. In the results that follow, however, only main stems are considered because no tiller data were available for some sowings.

(b) Variation in maximum floret numbers

Table 6-1 shows the variation of Nfe_{max} with sowing date and treatment. Because there were different treatments each will be dealt with separately.

Table 6-1 Components of maximum floret number per ear (Nfe_{max}). The standard error of the mean is shown. See text for explanation of symbols.

Crop & Treatment	Ns_{max}	$\overline{Nf}_{max}$	Nfe_{max}
1973/4	20.1 ±0.2	7.4	149
1974/5 +N	20.3 ±0.2	6.2 ±0.2	126
" ON	20.3 ±0.3	6.0 ±0.4	122
1975/6 +N	19.2 ±0.1	6.6 ±0.03	125 ±1.5
" ON	18.5 ±0.05	6.3 ±0.07	117 ±1.9
1976/7 Control	17.3 ±0.2	7.4 ±0.07	128
" Warmed	18.4 ±0.4	7.5 ±0.12	138
1977/7 October	19.6 ±0.3	7.3 ±0.15	143 ±2.4
" December	17.6 ±0.6	7.1 ±0.4	125 ±4.6
" March	16.7 ±0.2	6.7 ±0.4	112 ±3.4

1. Nitrogen fertiliser

In the 1974/5 experiment done by Gallagher (unpublished), the fully fertilised plot (+N) received 96 kg ha^{-1} nitrogen on 1st May, 1975, and the minimally fertilised plot was given P and K only. Between these treatments there was no significant difference in Nfe_{max} (L.S.D. = 43.6).

In 1975/6 the difference in the amount of nitrogen in the +N and ON plots was bigger than in 1974/5 (Table 2-1). Routine sampling revealed no significant difference between the treatments in either Ns_{max} or $\overline{Nf}_{max}$, but a difference was established from a

very large sample of ears (180) taken at the time of maximum floret number. The figures in Table 6-1 show that in the ON plants both Ns_{max} and $\bar{N}f_{max}$ were significantly smaller ($p = 0.05$) than in the +N ones. During initiation no difference of either $\bar{R}_s$ or D_s was found in the two plots presumably because the routine samples, though satisfactory for estimating most characteristics, were not big enough to detect such small differences. It must be assumed that the nitrogen shortage in the ON treatment slightly decreased either $\bar{R}_s$ or D_s, or both, (cf. Langer & Liew, 1973) but from the data available there is no way of knowing which happened. Whatever its cause, the outcome was that Nfe_{max} for the +N ears was smaller than for the ON ears.

2. Soil warming

The soil warming treatment of 1976/7 had a small effect on spikelet number: Ns_{max} of plants in the warmed plot was significantly bigger than in the control ($p = 0.05$). There was no difference in $\bar{N}f_{max}$ but the difference in Ns_{max} resulted in Nfe_{max} being smaller in the control plot.

3. Sowing dates in 1977/8

The sowing made in October was comparable with crops sown at similar times in other seasons, but Ns_{max} in the December sowing was markedly lower ($p = 0.05$). Ns_{max} of the March sowing was smaller than for December but the difference was not significant. Throughout, the tendency was for Ns_{max} to fall with delay in sowing (Table 6-1): Sargent (1976) found the same trend for sowings of the same cultivar made at Sutton Bonington over the same range of sowing dates. The reasons for Ns_{max} declining in later sowings have been discussed in Chapter 4. Sowing later resulted in smaller $\bar{N}f_{max}$, though its decrease with lateness of sowing was comparatively

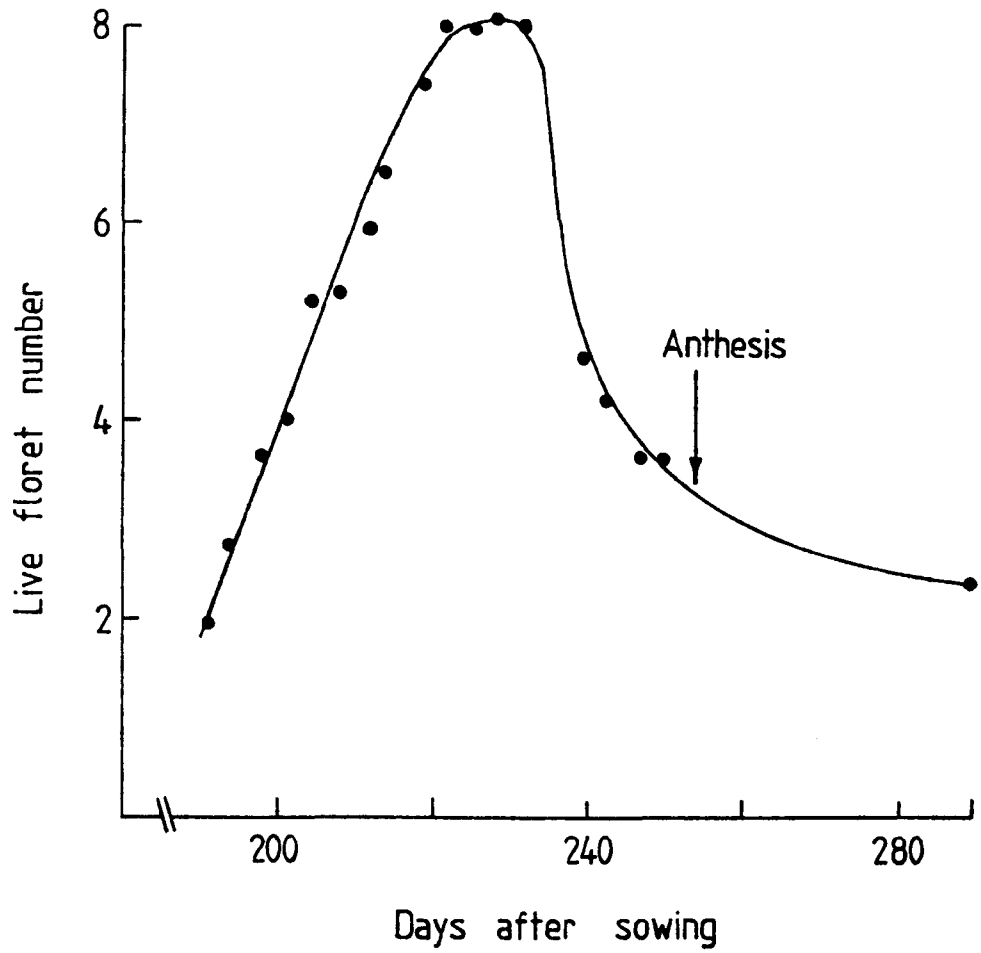


Figure 6-1 The time course of live floret number in the 9th spikelet; MS ear of 1976 + N treatment. Soon after reaching a maximum the number fell because distal florets stopped developing and died. Though final number was more or less determined at the time of anthesis there were some deaths afterwards.

less than that in Ns_{max}. The combined decreases caused Nfe_{max} to be progressively smaller with later sowing.

(iii) Floret Survival

Maximum floret number refers to live florets, defined as those with turgescent tissues and apparently capable of continued differentiation. Shortly after $\overline{Nf}_{max}$ is reached it is maintained for a brief period (Figure 6-1). The more distal florets in each spikelet then begin to lose turgescence: they stop developing and die when differentiation of their floral parts is still rudimentary (Langer & Hanif, 1973). As Figure 6-1 shows, the number of florets continuing differentiation drops sharply until about the time of anthesis, and the same finding has been reported by many other workers (e.g. Evans, Bingham & Roskams, 1972). In the present study $\overline{Nf}_{max}$ was typically about 7 and a mean of 2.4 florets per spikelet survived to anthesis. At anthesis, each surviving floret had green anthers and fully developed stigmata and was therefore a potential grain site, but frequently there are further floret deaths after anthesis.

Gallagher (pers. comm.) has suggested that floret death can be thought of as having a vertical dimension of deaths up the ear and a horizontal one of deaths up the spikelet. The vertical dimension is represented by the death in some spikelets of all the florets: the spikelets so affected are usually basal ones, and sometimes those at the tip of the ear as well. The horizontal component is the death of the more distal florets in each spikelet. The approach may be useful so long as it is realised that the two dimensions probably do not reflect a physiological separation within the ear.

Table 6-2 Components of fertile floret number and final yield. The standard error of the mean is shown. Numbers enclosed by brackets are assumed values. See text for explanation of symbols.

Crop & Treatment	Ns_f	S_f	$\bar{N}f_f$	F_f	F_g	Nfe_f	$\bar{N}g_e$	$\bar{W}g$ (mg)	Grains m^{-2}	Yield $t\ ha^{-1}$
1973/4	-	-	2.0	0.27	-	-	27.9±1.4	51.1±0.8	9680	4.95±0.33
1974/5 +N	15.5±0.2	0.76	2.4±0.1	0.39	0.82	37.2	30.5±0.8	50.8±0.5	10065	5.12±0.17
" 0N	-	-	-	-	-	-	27.0±2.0	48.3±0.8	7695	3.67±0.31
1975/6 +N	15.3±0.1	0.80	2.6±0.04	0.40	0.66	39.7	26.5±1.1	36.7±0.4	9380	3.41±0.15
" 0N	12.6±0.2	0.68	2.0±0.04	0.32	1.0	25.4	25.4±1.2	36.1±2.3	6833	2.50±0.30
1976/7 Control	-	-	-	-	-	-	26.5	45.5±0.6	10944	5.03±0.21
" Warmed	-	-	-	-	-	-	25.7	49.6±1.0	9380	4.62±0.36
1977/8 October	15.4±0.1	0.78	(2.9)	(0.4)	(0.82)	(46.0)	37.8±0.4	46.5	18285	(8.51)
" December	14.3±0.2	0.82	(2.8)	(0.4)	(0.82)	(42.8)	35.1±0.8	45.8	14820	(6.79)
" March	13.8+0.1	0.82	(2.7)	(0.4)	(0.82)	(42.3)	34.7±0.6	42.4	11830	(5.01)

Data on floret survival in the different sowings studied is given in Table 6-2 and will be dealt with in the same categories as maximum floret number.

1. Nitrogen fertiliser

No information was available about any possible difference in floret survival between the 1974/5 +N and ON plots. Though mean grain number per ear, $\overline{Ng}_e$, was larger in the +N treatment (= 30.5) than in the ON (= 27.0), this difference was not significant ($p = 0.05$, L.S.D. = 5.3).

In the 1975/6 season, a sample of 220 ears taken just before anthesis showed that the number of florets surviving, Nfe_f, was significantly larger ($p = 0.05$) in the +N than in the ON treatment, and this would be expected from the corresponding differences in Nf_{max} (Table 6-1). The number of spikelets with fertile florets (Ns_f) and number of florets per fertile spikelet (Nf_f) were both significantly ($p = 0.05$) greater in the +N plants. In terms of Gallagher's analysis, therefore, the difference in Nfe_f arose from differences in both the vertical and horizontal dimensions of floret death. The figures make the point that even in the +N plants all the florets died in the basal spikelets; in 14% of the ON plants all the florets died in the two or three most distal ones as well.

2. Soil warming

It had been expected that soil warming would result in plants bearing either more grains per ear or more ears per plant, or both, because the warmed plants had a large leaf area index (L.A.I.) earlier in the season and intercepted more radiation than the control plants around the time when tiller deaths were beginning.

However, despite the slightly greater spikelet number of the warmed plants, their $\bar{N}g_e$ at harvest was not significantly different from the control; also, they had fewer ears per plant. Soil warming therefore failed to increase the survival of florets, or of tillers, and the yield data (Table 6-2) show that the grain weight per unit ground area did not differ significantly between the two plots.

From the measurements taken it is impossible to be sure why soil warming did not have the effects expected. Van Dobben (1962) pointed out that under long days or higher temperatures, or both, development of a crop is speeded up but its growth is not increased proportionately, so that the amount of growth per unit of developmental time is smaller. The present results could be explained if there was less growth per unit of developmental time in the warmed plants than in the controls: in this context developmental time is equivalent to thermal time. Dry weight data showed, however, that during and after warming, the absolute growth-rate of the MS per unit of thermal time was greater in the warmed plants (2.53 mg $(^{o}Cd)^{-1}$) than in the control (2.22 mg $(^{o}Cd)^{-1}$). An alternative explanation is that maintenance respiration was increased by higher temperature (McCree, 1974). Since warming was given when the nights were comparatively long, and the heating had to be left on all night, assimilate produced during the day, which might ultimately have increased floret survival at a lower night temperature, could have been used instead for faster maintenance respiration.

3. Sowing dates in 1977/8

The fertile fraction of Ns_{max} was similar in each sowing; Ns_f in the October sowing was significantly greater than in the December one ($p = 0.05$), but the difference in Ns_f between the

December and March sowings was not significant. $\bar{N}f_f$ did not vary significantly between them (Table 6-2). Though Ng_e declinedwith later sowing, even in the March sowing it was considerably larger than in the usual October-sown farm crops available for comparison. Since Ns_f and $\bar{N}f_f$ for the MS ears were no bigger than in crops of the other seasons, this suggests that $\bar{N}g_e$ was bigger because floret survival was greater in ear-bearing tillers. In turn, this suggests that nitrogen fertiliser requirements were correctly estimated, vindicating the use of detailed developmental observations as a guide to application timing. Even so, in all three sowings all the florets died in the two or three basal spikelets.

(iv) Possible Causes of Floret Death

Despite extensive work it is still not clear why some florets die, but there is indirect evidence that it may be because there is competition for assimilates in which the more distal florets fare the worse. When Kirby and Jones (1977) removed tillers from barley plants, the MS was heavier and its grain yield greater than in control plants; this yield increase was partly due to more florets per ear surviving. In wheat, the highest numbers of grains were borne by those spikelets which had the greatest pre-anthesis dry weight (Scott, Docherty and Langer, 1975) and results of Fischer and Laing (1976) suggested that grain number per spikelet was particularly sensitive to a reduction in light and assimilate levels in the crop. Gallagher (unpublished) examined data of Bremner and Davidson (1978) and showed that in the semi dwarf wheats which they used, greater floret survival and more grains per ear were associated with a faster MS growth rate per floret before anthesis.

Competition for assimilates appears to be an important factor, but not the only one that is involved. The first three florets of the spikelet have direct connection to the main vascular supply in the rachis of the ear; those more distal have a less direct supply via sub-vascular elements (Hanif & Langer, 1972). Development of these vascular connections does not appear to have been studied in wheat. However, Kirby and Rymer (1974) found that vascular connection from the rachis in barley were not established until the awn initial stage. Development is approximately parallel in the two species so this stage corresponds to the time when floret initiation in the wheat spikelet is ending, suggesting that the differences in floret vascular supply may take effect as soon as the connections are made. The weights of the grains set in the first three florets are not equal: Kirby (1974) found that their weight order was grain 2 > grain 1 > grain 3. If the vascular supply to each of these florets is equally efficient, this implies a difference between them in capacity to accept assimilate: Rawson and Evans (1970) found that grain 2 had the highest relative growth rate and Kirby (1974) showed that in spring wheat the differences in weight were related to time of ovary initiation.

Whatever the mechanisms, the basal florets of the spikelet appear to be the better placed in competing for assimilate, yet even those florets died in the basal spikelets. The reason could well be that the priorities for assimilate distribution between spikelets are strongly established early in development. Kirby (1977) showed the primordia of mid-ear spikelets to be the largest of all when they are initiated, and it is the mid-ear region where double ridges and floret development begin earliest. If the biggest primordia have the highest priority in the

distribution of available assimilates, the spikelets in that region would receive the most assimilates from the beginning. From their relative sizes at initation, spikelets at the extremities of the ear would be expected to be at a competitive disadvantage. In fact, some grains set in distal spikelets, commonly right up to the terminal spikelet itself, and so the basal spikelets appear to be at the greater disadvantage. Langer and Hanif (1973) attribute the failure of floret survival in basal spikelets to their generally slower rate of floret development.

(v) The Determination of Grains per Fertile Spikelet

Data for floret survival and yield (Table 6-2) were from at least 6 samples each of 1m of two adjacent rows, but in 1977/8 were derived from fewer and smaller samples and should be accepted with caution.

In the 1973/4 and 1974/5 wheat crops studied by Gallagher, about 20% of the florets fertile at anthesis died afterwards, and floret deaths occurred after anthesis in every season studied in the present work (Table 6-2). Evans and Rawson (1970) made a detailed study of the phenomenon and found that when the basal florets in the central spikelets of wheat were sterilised 2 days before anthesis, grain was set in the normally empty distal florets. They concluded that the development of grains in the earliest pollinated florets inhibited grain set in the more distal florets. This conclusion was supported by the work of Evans, Bingham and Roskams (1972), who further concluded that it was not a shortage of assimilates that caused the inhibition but a hormonal correlative mechanism.

In the 1975/6 ON treatment, no florets died after anthesis. ON anthesis was at the same time as in the +N treatment, in which

floret deaths occurred after anthesis. It is hard to see how a hormonal mechanism of the kind postulated by Evans et al. could be different in two sets of plants at an identical stage of development. A nutritional explanation seems more likely. At about the time of anthesis, soluble carbohydrates are most abundant in the plant (Yoshida, 1972); also, nitrogen-deficient plants tend to be rich in soluble carbohydrates because the shortage of nitrogen restricts protein synthesis (Hewitt, 1963). In the ON plants, therefore, it is likely that more assimilate per fertile floret was available at anthesis than in the +N plants, so that their floret survival was proportionately greater.

Drought during and immediately after anthesis causes a reduction in grain set and reduces yield (Wardlaw, 1970). In 1976, a very dry winter was followed by an exceptionally dry spring and it was very hot and dry around the time that anthesis occurred on 6-7 June. Figures for ON floret survival suggest that water stress did not affect the number of grains set, a conclusion supported by the fact that $\bar{N}g_e$ in the 1975/6 crop was comparable with that of 1976/7, a crop which grew in a cool, damp summer. The effect of drought on the 1975/6 crop was apparent in its comparatively low yield, associated with a curtailed duration of grain growth (Gallagher, Biscoe & Hunter, 1976).

(vi) Crop Yield: Formal Expression

Formal expressions for yield were derived by Gallagher et al. (1975; 1976) and their format is used in the present context: the formulae are essentially an expansion of those of Engledow (1925): see Chapter 1. The components of yield will now be considered, using the terms of the foregoing sections.

From the notation used in Chapters 3 & 4 maximum spikelet number per ear can be expressed as:

$$Ns_{max} = \bar{R}s \times Ds \qquad (1)$$

with the proviso that sometimes two rates and durations should be considered. A similar form of expression is used for maximum floret number per spikelet:

$$Nf_{max} = \bar{R}f \times Df \qquad (2)$$

If $\bar{N}s_{max}$ is the mean spikelet number of the entire ear population of the crop and $\bar{N}f_{max}$ is the mean floret number per spikelet, the mean maximum floret number per ear, $\bar{N}fe_{max}$, is:

$$\bar{N}fe_{max} = \bar{N}s_{max} \times \bar{N}f_{max} \qquad (3)$$

As development continues distal florets fail to differentiate further, and die. By the time of anthesis all the florets are dead in a few of the spikelets: the remaining number of fertile spikelets is then given by:

$$\bar{N}s_{max} \times Sf \qquad (4)$$

Where Sf is the fraction of spikelets with live florets. Even in those spikelets the distal florets die, and if Ff is the proportion of florets surviving, the mean fertile floret number per spikelet at anthesis will be:

$$Nf_{max} \times Ff \qquad (5)$$

Because some of the florets fertile at anthesis later die, an additional term, Fg, is needed to describe the fraction of fertile florets bearing a grain at harvest and (5) becomes:

$$\bar{N}f_{max} \times Ff \times Fg \qquad (6)$$

Thus the mean grain number per ear, $\bar{N}g_e$, is given by:

$$\bar{N}g_e = (\bar{N}s_{max} \times Sf) \cdot (\bar{N}f_{max} \times Ff \times Fg) \qquad (7)$$

Figure 6-2 The relationship between grain yield and number of grains per unit ground area in crops of 'Maris Huntsman'

■ Data of Pearman, Thomas and Thorne, 1978

o Data of Sergeant, 1976

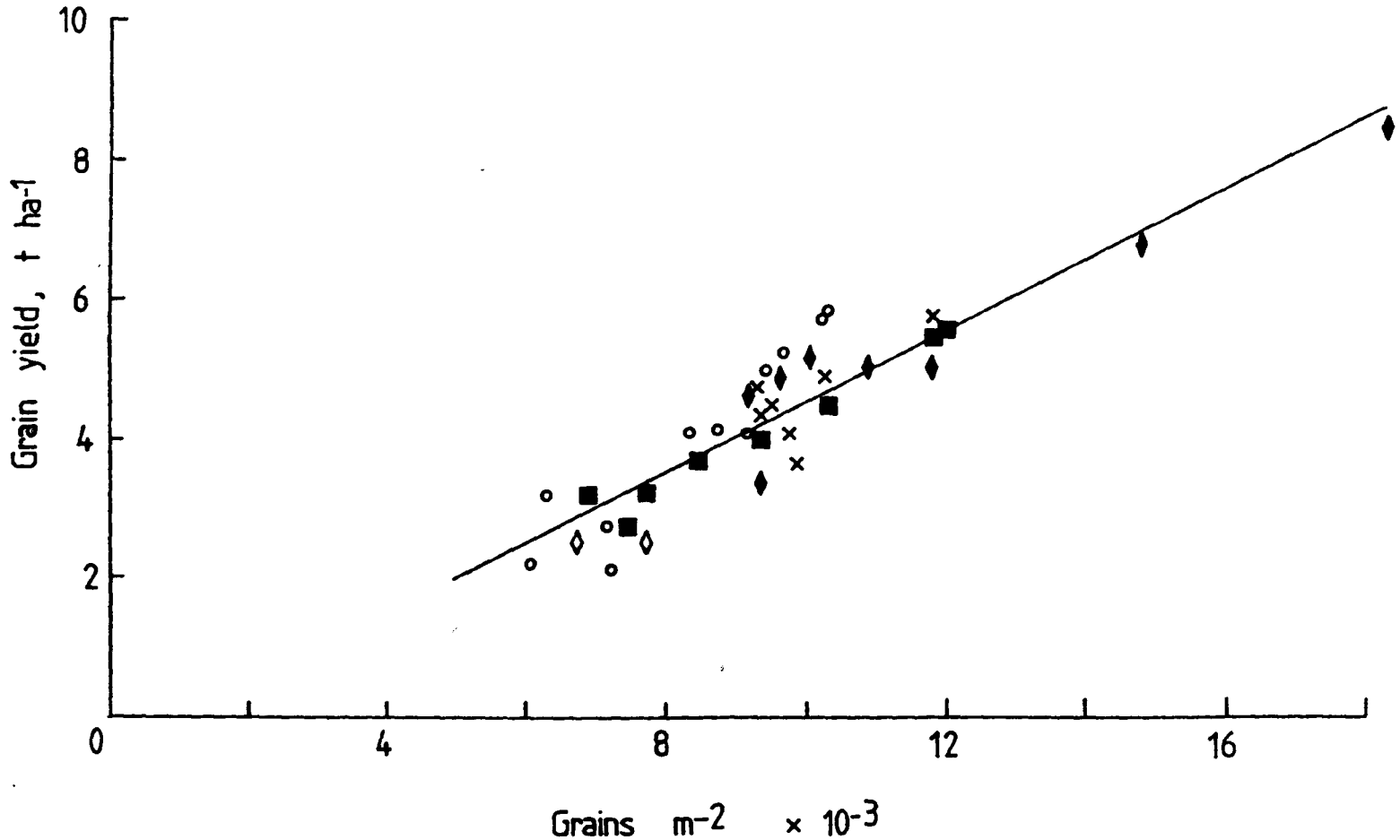
Other points, from Sutton Bonington crops treated as follows:

♦ Full nitrogen fertilisation

◊ Minimal nitrogen fertilisation

× Various treatments (e.g. warmed; irrigated; partially defoliated, etc.)

$$y = -0.56(\pm 0.39) + 0.52(\pm 0.04)x$$


Grain yield, t ha-1
10
8
6
4
2
0
4
8
12
16
Grains m-2 × 10-3

Representing mean weight per grain as $\bar{W}g$ and the mean ear number per unit area as $\bar{N}e$, the final yield, Y, per unit area of crop is therefore:

$$Y = \bar{N}g_e \times \bar{W}g \times \bar{N}e \qquad (8)$$

As equation (8) implies, once final grain number is fixed (i.e. after anthesis and the fertilisation of the ovary) crop yield will depend upon the amount of dry matter accumulated in the grain during the period of grain filling. However, in the present work $\bar{W}_g$ did not vary much between seasons ($\bar{x}$ = 44.6 mg; c.v. = 11.8%), and in studies on the same variety by Sergeant (1976) and Pearman, Thomas and Thorne (1978), $\bar{W}_g$ was similarly stable for a considerable range in yield. Yield must therefore have been strongly dependent upon grain number per unit area of crop, and the strong relationship between these two variables (p 0.001) is evident in Figure 6-2, in which results obtained by the other workers as well as those from the present study are shown.

Because yield is strongly dependent upon grain number, the understanding of the relationship between weather and the processes which determine this number is of paramount importance. Some aspects of the relationship are considered in the final chapter.

VII WEATHER, DEVELOPMENT AND CROP YIELD

(i) Study of Development in the Field

Most work on the response of cereal development to environmental variables has been confined to growth-rooms, in which the response to individual components of the environment can be tested.. However, unless growth-room measurements are complemented by suitable field studies there is always doubt as to whether the observed responses correspond to those of field-grown plants. Hitherto, in the attempt to understand how weather influences crop development in the field the usual approach has been to make statistical correlations between weather variables and the timing of "growth stages". This term is inaccurate; the stages really reflect progress in development. Because they are ill-defined with respect to events at the shoot apex and are widely spaced in developmental time, they cannot provide more than a rough indication of how development is affected by weather. Field studies in greater detail are needed to reveal how weather affects the several components of yield, for there is a strong relationship between yield and grain number: see Chapter 6. Probably the main reason why field studies of development have seldom been made is the apparent difficulty of relating development to the rapid and continuous variation of weather factors.

The present work has shown that this difficulty can be overcome: if detailed measurements are made and appropriately analysed, the development of winter wheat in the field can in fact be successfully correlated with weather variables far more precisely than the "growth stage" approach has permitted. Development is strongly correlated with two variables, namely temperature and daylength,

and these also influence leaf appearance; the correlations will now be summarised.

(ii) Temperature and Daylength Effects

(a) Apical development

The rate of formation of apical primordia in chronological time showed considerable fluctuations. These were diminished when temperature was taken into account, emphasising its importance as a controlling factor in the processes that result in primordium initiation. Initiation was linearly related to temperature: the base temperature, T_b, was estimated for leaf initiation and was found to be $0^{\circ}C$ (Table 4-1), a value similar to the few other estimates reported for wheat.

There was good agreement between accumulated air temperature measured at 2m and accumulated soil temperature measured at 1 cm depth. This was both physiologically important and analytically convenient: the plant apex was in the soil for much of the time that apical primordia were being initiated; and the temperature of the apex could be estimated accurately from screen temperatures. When the total number of primordia produced since sowing was plotted against temperature accumulated above $0^{\circ}C$, the rates of initiation in thermal time of leaves and of spikelets were both linear; spikelets were initiated about three times faster than leaves. The change in rate occurred at a distinct point of inflexion which usually coincided with the start of initiation of primordia destined to become spikelets but was sometimes later (Fig. 4-6).

Observations from several seasons showed that the daily rate of leaf initiation was linearly related to the mean air temperature during the initiation phase. A similar relationship described the rates of initiation of spikelets and of florets with

the mean air temperature during their respective initiation phases. Estimated values of base temperature rose in the later developmental phases. The estimate for spikelet initiation was $2.7 \pm 0.7^{\circ}C$ and for florets it was $3.2 \pm 2.1^{\circ}C$; these values are not significantly different ($p = 0.05$). Examination of the possible reasons for this shift suggested that it was likely to be related to changes in daylength. Linear relations between daylength and the rate of initiation in thermal time were established for leaves, spikelets and florets. The effective daylength for the initiation of leaves appeared to be the mean of current daylength during leaf initiation. For spikelets and florets it appeared that it was the instantaneous daylength at inflexion point which was effective but an effect of current daylength during the initiation phase is not ruled out.

It therefore appeared that initiation rate was controlled both by mean temperature and by daylength. When mean daily initiation rates of leaves, spikelets and florets were each plotted against a scale representing the combined effects of daylength and temperature, linear relationships were apparent and T_b was $\simeq 0^{\circ}C$ for the initiation of all three kinds of primordia. It is therefore appropriate to set $T_b = 0^{\circ}C$ throughout.

The linear relationships of initiation rate with temperature (T) and with daylength (ϕ) that were found contrast with the picture given by controlled environment work. Usually, such work has shown that initation rate is a quadratic function of T at constant ϕ and of ϕ at constant T. Linear relationships do emerge from some of this work, however, within the range of temperatures and daylengths at which primordia are normally initiated in the field in this country. The temperatures and daylengths used

in growth-rooms often extend above this range for T and both above and below for ϕ. The only quadratic relationship for an initiation process that was established in this study was for the inverse of the phase duration for the initiation of spikelets with corrected temperature, and even then the curve was of opposite sign to most of those describing growth-room results.

The timing of the inflexion point of the primordium initiation rate in thermal time was explicable in terms of either daylength or of vernalising hours spent in the 5-7°C range. The fact that there was a linear relation between the number of vernalising nights before emergence and the amount of photothermal time after emergence taken to reach inflexion suggested that inflexion timing might depend upon an interaction of the two. Controlled environment work on vernalisation offers little guidance as to how vernalisation might proceed in the fluctuating temperatures of the field; even the monumental researches of Gregory and Purvis are not very helpful. The Japanese field work (Ch.4) on vernalisation was not combined with plant dissections and mostly conflicted with growth-room work on the question of what temperatures promote vernalisation.

(b) Leaf appearance

Leaf appearance was found to depend strongly on temperature. Leaf appearance rate was linear in thermal time calculated above 0°C, a base temperature already established for the process by other workers. Variation in leaf appearance rate in thermal time was traced to the influence of daylength, but its effect was more subtle than that on primordium initiation. It appeared that the direction and magnitude of ϕ at crop emergence ($d\phi/dt$) determined the rate of leaf appearance in thermal time during the rest of the season. Evidence from the trends in some of the leaf appearance graphs

and from leaf extension in the soil-warming treatment of 1976/7 implied that current daylength might have a secondary effect.

(iii) The Relationship of Weather and Development to Yield

When all the seasons studied are considered, a striking feature is that, despite wide differences in sowing date and weather conditions, the maximum numbers of organs produced on the main stem of winter wheat tend to be stable (Table 4-3). This stability of number reflects the compensatory relationship between initiation rate (R) and development rate (1/D) : when R is fast, phase duration (D) is correspondingly short. Although the tendency is to compensation, in longer and warmer days the development rate for spikelets increases faster than the initiation rate (Fig. 4-19). Thus, with later sowing spikelet number tends to decline, because at the time that spikelet initiation begins days are long and comparatively warm and the developmental phase is hurried through. Even so, spikelet number is not drastically reduced: see Table 4-3.

Lower yield is associated with later sowing, but the effects of weather upon development are probably not the only cause. The association of high yield with early sowing appears to be the result of a complex link between growth, development and weather. For a wide range in sowing date (5 months in the present work) the range in time of anthesis is fairly small (mid-June to mid-July). Because of the similarity of organ numbers, therefore, plants of early and late sowings have to pass through nearly the same amount of developmental time but have different amounts of chronological time in which to do so. Early-sown plants make much more growth per unit of developmental time than late-sown ones; by the time of anthesis, there is a considerable difference in size between plants from an early sowing and those from a

late one. A large amount of growth per unit of developmental time is associated with high survival of florets, and in the early-sown plants more assimilate is available per floret, resulting in high survival and thus more grains per ear. A large amount of growth per unit of developmental time also favours the survival of ear-bearing tillers, which make a substantial contribution to high yield (cf. Table 6-2). The role of growth in the achieving of high yield underlines the importance of applying adequate amounts of fertiliser at the right stages of plant development.

It therefore appears that the influence of weather on yield is through growth as well as through development. In controlled environments, however, it may well be that conditions are more crucial for development than for growth, and not only because of the difference in light quality. In the field, development appears to respond to $d\phi / dt$, and to an interaction of vernalisation and daylength; in controlled environments it is difficult to simulate such influences satisfactorily.

The present work has shown the need for more extensive and discriminating field experiments to investigate further the relationships between development and environmental factors. Insight into the relation of development to weather could be gained by modifying natural daylength. It would be interesting to know to what extent maturing grains are likely to be vernalised in the ear. Our lack of knowledge about vernalisation under field conditions suggests several lines of inquiry. Little is known about the precise temperature ranges effective for vernalisation ,about the details of its relationship to daylength, nor about the causes of the timing of inflexion and the possible importance of this event for spikelet initiation.

The processes involved in cereal growth and their responses to

environmental factors have already been extensively investigated. By comparison our knowledge of processes involved in cereal development and how they are influenced by environmental factors in the field is meagre. Our knowledge about the inter-relations between growth and development and their importance in the determination of yield is practically non-existent. It is to be hoped that research will be done to correct this imbalance.

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Appendix I. A Comparison of Winter Wheat Development Stages.

L.A.S.	Feekes development stage	Zadoks development stage	Apical development stage	Growing point/ear length (mm)
1 + 1	1 (One shoot)	11	Early vegetative (6 leaves initiated)	ca 0.2
3 + 1	2 (Tillering begins)	13, 21	Late vegetative (Leaf initiation stops)	ca 0.3
5 + 1	5 (Leaf Sheaths strongly erected)	15, 23	Early reproductive (Spikelets being initiated and DR forming)	ca 0.6
8 + 1	6 (First node visible)	18, 23, 31	Reproductive (3 florets in central spikelets)	4-5
9 + 1	7 (Second node visible)	19, 23, 32	Reproductive (floret initiation stops)	15-25
Flag leaf emerged	9-10 (Ligule of last leaf visible)	39-49	Late reproductive (floret death occurring)	50-80
Ear emerged	10.5 (Ears emerged)	59	Fertile floret number determined	80-120

Appendix II. Leaf Initiation in 'Maris Huntsman'

Year and date of sowing	Leaf initiation phase ended: Date	Days after sowing	°Cd after sowing	$\overline{T}_{a,1}$ (°C)	$\overline{R}_1$ (Leaves d^{-1})	D_1 (d)	$N1_{max}$	ϕ_1 (h)
16.11.73	24 Feb	100	525	5.0	0.080	100	11	10.1
30.10.74	2 Feb	95	660	6.9	0.095	95	12	9.5
4.10.75	16 Dec	72	510	6.8	0.125	72	12	10.4
31.10.76	9 March	129	540	4.0	0.062	129	11	9.9
11.10.77	17 Dec	67	525	7.8	0.134	67	12	10.1
2.12.77	18 March	106	480	4.1	0.066	106	10	10.6
6.3.78	5 May	60	405	6.7	0.133	60	11	15.4

Appendix III. Inflexion Point and Double Ridges in 'Maris Huntsman'

Year and date of sowing	Inflexion point timing: Date	Days after sowing	°Cd after sowing	ϕ_{inf} (h)	Double Ridges first seen: Date	Days after sowing	°Cd after sowing	ϕ_{DR} (h)
16.11.73	27 Feb	105	550	11.7	7 April	142	760	14.6
30.10.74	11 Feb	104	683	10.8	8 April	158	920	14.7
4.10.75	16 Jan	104	730	9.5	21 Feb	140	855	11.4
31.10.76 (Control)	16 March	136	600	12.9	15 April	166	770	15.2
11.10.77	14 Feb	136	750	11.0	13 March	153	900	12.8
2.12.77	27 March	115	535	13.7	20 April	139	690	15.5
6.3.78	8 May	67	460	16.8	21 May	76	560	17.7

Appendix IV. Spikelet Initiation in 'Maris Huntsman' (i.e. from completion of collar initiation to terminal spikelet formation)

Year and date of sowing	Spikelet initiation ended: Date	Days after sowing	°Cd after sowing	$\overline{T}_{a,s}$ (°C)	$\overline{\phi}_s$ (h)	$\overline{R}_s$ (spklt. d^{-1}): Pre-inflexion	$\overline{R}_s$ (spklt. d^{-1}): Post-inflexion	D_s (d): Pre-inflexion	D_s (d): Post-inflexion	Ns_{max}
16.11.73	7 May	172	985	6.9	14.4	-	0.30	-	64	20.0
30.10.74	30 April	182	1160	6.0	13.7	-	0.26	-	75	20.3
4.10.75	2 April	180	1075	5.2	11.1	0.14	0.21	21	73	19.3
31.10.76 (Control)	3 May	184	925	6.8	14.7	-	0.34	-	48	17.3
11.10.77	20 April	191	1125	4.6	11.7	0.06	0.24	51	66	19.6
2.12.77	9 May	158	840	7.1	15.7	-	0.39	-	43	17.6
6.3.78	28 May	83	655	10.5	17.5	-	0.75	-	21	16.7