Paper 3
ENVIRONMENTAL INFLUENCES ON THE DEVELOPMENT, GROWTH AND YIELD OF BARLEY

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INTRODUCTION

Both farmers and researchers are aware of the large variations in yield that can be caused by differences of weather and soil type. An example of this was given by Austin (1978) for two series of field experiments on grain yield of wheat, one investigating the influence of nitrogen fertiliser, and the other cultivar differences. Both series were over several years at several locations, and Austin's analysis showed that the influence of site and season was much greater than the effect of the treatments. This problem is not new. It was keenly appreciated by Gregory (1926) who wrote,

"It is, for instance, impossible to interpret the effects of manures on crop yield by an experimental method consisting of repetitions year by year of field trials, unless variations in climate are taken into account in assessing the results of such experiments.... The production also of new varieties suitable for local climatic conditions must always remain a matter of pure empiricism, until the interaction of the climatic complex with the physiological processes of distinct races is understood."

Since that statement was made, there have been many studies of the influence of environmental factors on the growth and yield of cereals; see Thorne (1974) and Evans and Wardlaw (1976) for reviews. Initially, experiments were done in the field and in glasshouses. The influence of environmental factors on yield was usually examined by studying the weight and area of plant organs and the morphological processes determining the number of ears per plant, grains per ear and mass per grain (Engledow and Wadham, 1923; Gregory, 1926; Watson, 1947; Aspinall *et al.,* 1964), but the close correlations between variables such as sunshine, temperature and daylength made it difficult to determine the influence of individual weather elements with confidence. Partly in reponse to these difficulties, much of the more recent work has been done in controlled environments (Aspinall and Paleg, 1963; Cannell, 1969; Chowdhury and Wardlaw, 1978). Together with many others, these researches have provided much information about the influence of temperature, insolation and photoperiod on the physiological processes governing crop growth and yield.

It has, however, often proved difficult to predict the behaviour of crops in the field from the results of experiments done in controlled environments (Evans, 1963; Ritchie, 1981). One reason for this is the difference between the two environments, and the effects that this may have on plant behaviour. For example, light intensities in the field are usually much stronger and change more quickly than in controlled environments. Similarly, the roots of cereals can penetrate to 2 m or more in deep soils, which they cannot do in most pots. Another reason why extrapolation is difficult results from the complex inter-relations between the many physiological processes governing yield. During the last two decades the advent of electronic computers has enabled the development of simulation models which can deal with complex physiological inter-relations (e.g. de Wit *et al.,* 1970). Notionally, one of the main aims of these models is to predict the behaviour of crops in the field from known physical and physiological relationships. Work with such models proceeds, but so far they seem to have emphasised our ignorance rather than our understanding of crop growth, and have had little influence on practical activities, though there are important exceptions to this (e.g. Hackett *et al.,* 1979).

A realisation of the possible inadequacies of experiments done in controlled environments, coupled with the need to test predictions from simulation models, has brought detailed field studies into fashion. In these studies agronomists, physiologists, and physicists have taken their vast armoury of instruments and data-logging devices into the field and examined the growth of crops over hourly or even shorter periods (Biscoe, Scott and Monteith, 1975; Leach, 1980; Day *et al.,* 1981).

Ostensibly, most of these investigations into cereals and their environment have been made to help solve the problem so clearly outlined by Gregory above. But how useful have these investigations been? Sceptics might argue that as most of the activities of farmers and plant breeders are based on the results of empirical field trials — where the influences of site and season are ignored or smothered by the crude practice of averaging — the value of detailed investigations is negligible. Others would argue that the principles governing the response of crops to their environment are slowly beginning to emerge; and further, that a knowledge of these principles is essential to making rational assessments of the limitations to yield imposed by sites, seasons, husbandry practices and cultivars.

This paper aims to show how knowledge of the physiology of barley and the physics of its environment can be used to understand some of the influences of climate, husbandry and genotype on barley yields.

MEASUREMENTS AND ANALYSIS

At the outset, it is important to distinguish between the processes of growth and development. In this paper, *growth* will be used to refer to the change in dry mass or area of a plant or its organs. Growth in dry matter is the resultant of photosynthesis, respiration and translocation; growth in area is associated with the division and expansion of cells, followed by their shrinkage and death. Growth rates are usually expressed as changes in mass or area per unit time.

Development may be simply defined as the progress of a plant towards maturity. Development is conventionally assessed by the time taken for a plant to pass through a series of morphological stages, which are usually defined by the differentiation of various tissues and organs. The interval between two stages is commonly referred to as a phase with a duration of say t_n days where the subscript refers to the phase in question. If the interval between stages is short then development is rapid. It is convenient to define a development rate as the average fraction of the total phase duration completed each day, i.e. $1/t_n$. To understand how environmental factors influence yield, it is essential first to determine how they control the development rate of a crop, for it is the development rate which determines when and for how long the various physiological and morphological processes involved in yield formation occur. Indeed it is arguable that fluctuations in growth should not be considered in relation to chronological time, but rather in relation to developmental time, as alluded to by Cooper (1979). The influence of environmental factors on development will therefore be considered first.

TABLE 1: Stages of barley development.

Stage	Phase	Symbol in Text
Sowing		
	Germination *Kirby and Riggs (1978)*	t_g
Emergence		
	Leaf initiation *This paper*	t_l
Collar initiation		
	Ear initiation	t_i
Terminal spikelet		
	Ear growth	t_e
Anthesis		
	Grain growth	t_k
End of grain growth		

DEVELOPMENT

The following analysis is based mainly on 13 crops of spring barley *(Hordeum distichum* cv 'Proctor'*)* grown at the School of Agriculture, Sutton Bonington. Details about crops, sites and seasons have been described elsewhere (Biscoe, Clark *et al.,* 1975; Scott and Dennis-Jones, 1976; Turner, 1977). Although the results of the analysis will strictly be valid for only one site and cultivar, where possible comparison will be made with other work to try and establish that the analysis is of more general validity.

We distinguish six stages of development defining the beginnings and ends of five phases of development (Table 1). The stage of emergence is rather artificial in terms of organogenesis but is important as it marks the first time when the crop can be influenced by sunlight. The definition of the phases of leaf and ear initiation and ear growth was discussed by Kirby and Riggs (1978). The inflorescence of barley is indeterminate and the expression "terminal spikelet" should be regarded as an abbreviation for "last spikelet initiated" (Table 1). The definition of the ear growth phase adopted here is slightly different from that used by Kirby and Appleyard (1980), who used ear emergence instead of anthesis (Table 1). In practice, this difference will have a negligible effect on the outcome of the analysis. The temperatures during the developmental phases referred to below are the mean of the daily maximum and minimum temperatures recorded in a meteorological screen. Measurements in temperate climates have shown that mean air temperatures correspond closely to the mean tissue temperatures of plants over periods of several days such as this analysis is concerned with (Arnold and Monteith, 1974; Baker, 1979). Photoperiod was defined as the duration of day length including civil twilight in the morning and evening.

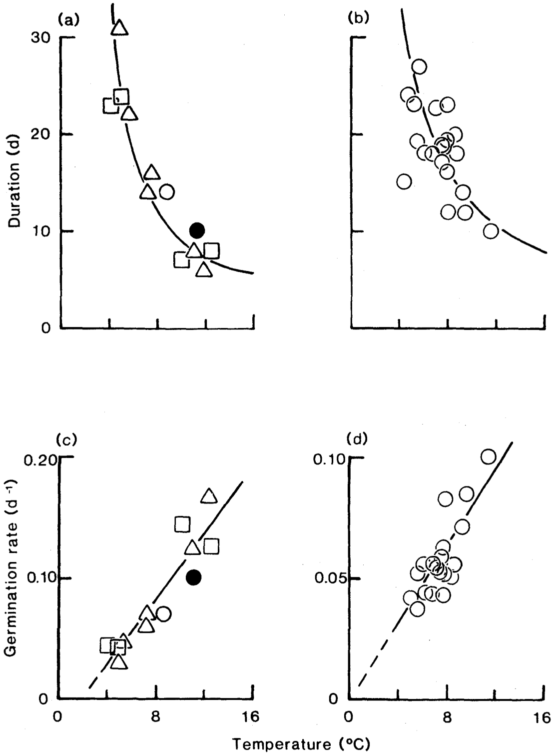

Figure 1: The relation between the duration from sowing to emergence (t_g) and temperature for crops of barley grown at (a) Sutton Bonington in: (o) 1972; (△) 1974; (□) 1975; and (●) 1976; and (b) several locations (Irwin, 1931); and the relation between germination rate (1/duration from sowing to emergence) and temperature for: (c) Sutton Bonington and (d) data of Irwin (1931). The equations of the fitted lines are (c) $y = 0.0135x - 0.0260$ ($P < 0.001$); (d) $y = 0.0079x - 0.0009$ ($P < 0.001$); the curves drawn in (a) and (b) were derived from the equations for (c) and (d) respectively.

The duration of the phase between sowing and emergence (t_g) usually decreased hyperbolically with temperature (Figs. 1a and 1b). This can be conveniently treated by defining a rate of germination ($1/t_g$) at each temperature, as this increases linearly with temperature (Figs. 1c and 1d). The temperature at which germination stops is here called the base temperature and is 1.9 (s.e. 0.96) °C for the 12 crops grown at Sutton Bonington. This is close to the value of 2.6 (s.e. 0.28) found in a study of 29 crops of barley grown at 3 locations in Australia by Angus *et al.,* (1980). From the relation

$$1/t_g = b(\bar{T} - T_b), \qquad (1)$$

where b is a constant, $\bar{T}$ the mean temperature during the phase, and T_b the base temperature, it follows that

$$t_g(\bar{T} - T_b) = 1/b, \qquad (2)$$

where 1/b is a thermal duration, day-degrees. For the crops grown at Sutton Bonington, this was 75 (s.e. 4.4) °C d above a base of 2.0 °C, almost identical to the figure of 79 (s.e. 2.5) °C d above 2.6 °C found by Angus *et al.* (1980). This combination of units is sometimes referred to as "accumulated temperature" or as a "temperature sum" or even a "heat unit", which it is not, as temperature is not a measure of energy. We prefer the expression thermal time (hence thermal duration), as it emphasises the fact that time, as it is perceived by a developing plant, depends on temperature.

Irwin's (1931) measurements suggest that T_b is closer to 0 °C (Fig. 1d). This is probably because his value for mean temperature was the average of the 09 00, 15 00 and 21 00 h readings of soil temperature at 100 mm depth.

The simple relation described by equation (1) does not hold for variation in sowing depth and soil moisture content. Deep planting slows the germination rate of cereal seeds, apparently because the epicotyl and mesocotyl must extend further before the soil surface is reached (Taylor and McAll., 1936; Lindstrom *et al.,* 1976). A dry soil will also slow the rate of germination and though this can be quantified (Lindstrom *et al.,* 1976) it is not considered further here.

Emergence to collar initiation

The duration of this phase (t_l) fell hyperbolically with temperature for the crops grown at Sutton Bonington. The corresponding development rate ($1/t_l$) increased linearly with temperature above a base of 0 °C (s.e. 2.5) over the range of 4-14 °C experienced. The thermal duration for this phase was 91 (s.e. 6.2) day-degrees.

Kirby and Appleyard (1980) examined the duration of the leaf initiation phase of ten spring barley cultivars, in photoperiods between 11 and 24 h. Their experiment was done in a glasshouse where a natural daylength of 9 h was extended by incandescent lamps. Their measurements show that, averaged over all cultivars, development was about 40% faster in photoperiods of 20 h compared with 11 h. The response of development rate to photoperiod varied, but in all cultivars except 'Mona' and 'Lise' there was a strong, generally linear, response over the 11 to 15 h range of photoperiods. To investigate whether the development rate for this phase depended on photoperiod in the field, a simple multiplicative interaction between temperature and photoperiod was assumed, of a type successfully used with wheat (Baker and Gallagher, in preparation).

The relationship has the form

$$1/t_l = c(\bar{P} - P_b)(\bar{T} - T_b), \qquad (3)$$

where c is a constant, $\bar{P}$ the mean photoperiod during the phase and P_b a base photoperiod below which development stops. The model assumes that the response of $1/t_l$ to photoperiod is linear over the range experienced in the field. It follows that a plot of $1/[t_l(\bar{T}-T_b)]$, here called a thermal development rate, against P should be linear and should intercept the photoperiod axis at P_b. Equation (3) is a special case of the more complicated model used by Angus *et al.* (1981). It is adopted here as being appropriate to the limited range of temperatures and photoperiods with which the analysis is concerned. There was a weak and non-significant ($P < 0.4$) correlation between the thermal development rate for this phase and mean photoperiod, indicating that development was faster in long days, as found by Kirby and Appleyard (1980). The regression equation showed an increase in development rate of about 40% in going from an 11 to a 20 h photoperiod, close to the increase found by Kirby and Appleyard (1980). The suspicion that there is a response to photoperiod in the field therefore remains.

Kirby and Appleyard (1980) also found that faster development caused by longer photoperiods during this phase was associated with the initiation of fewer leaves on the main-stem apex. As photoperiod increased from 11 to 20 h the number of leaves on the main-stem fell from 9.4 to 6.9, averaged over all cultivars. Other work in controlled environments has shown similar decreases in the number of leaves with increasing photoperiod (Guitard, 1960; Aspinall, 1966; Fairey *et al.,* 1975). In field experiments at Sutton Bonington, the main-stems of 'Proctor' produced nine leaves in all but the latest sowing, when there were eight (Scott and Dennis-Jones, 1976). Van Dobben (1952) also found that the number of leaves on spring barley main-stems fell by only one between early and very late sowings. The differences between experiments done in controlled environments and experiments done in the field may arise from the fact that in the field, over periods of several days, temperature, photoperiod and insolation change in concert. This apparently enables an increased rate of leaf initiation to compensate for a shorter duration, resulting in a stable number of leaves. This difference in behaviour between plants grown in the field and in the climate laboratory shows the difficulties that may arise when attempting to extrapolate results from one environment to the other.

Ear initiation

During this phase the spikelet primordia are initiated. Not all of these primordia bear grain; usually between 20 and 50% abort (Gallagher *et al.,* 1976), and this loss is considered later (p. 32). Once again, the development rate ($1/t_i$) was linerly dependent on temperature but apparently with a base temperature of about 4 °C (s.e. 2.2) (Fig. 2a).

There have been reports of shifts in base temperature with development stage for wheat (Robertson, 1970; Angus *et al.,* 1981), but this may not occur in spring barley. For instance, Takahashi and Yasuda (1960) observed the development of six spring barley cultivars planted in the field in each month of the year, but exposed to a 24 h photoperiod. Figure 3 shows, for two representative cultivars, that plant development rate increased linearly with temperature between 0 and 20 °C. The base temperature for both varieties was not statistically significantly different from 0 °C. Similarly, an analysis of leaf emergence rate on a range of barley cultivars sown on two occasions in the spring over two years gave an average base temperature not significantly different from 0 °C (Kirby *et al.,* 1982). The results from other work therefore suggested that the base temperature should be about 0 °C, lower than that derived from Figure 2a and less than the value of 6 °C (42 °F) conventionally adopted, though apparently arbitrarily (Monteith, 1981a). Scrutiny of Figure 2a shows a large variation in development rate for a series of four observations made at about 10 °C. The average photoperiods during the phase are marked on the graph and it seems that longer photoperiods accelerated development. It therefore seemed that the longer days which are usually, but fortunately not always, associated with warmer temperatures increased the development rate, and exaggerated the slope of the line in Figure 2a. This gave an artifically high base temperature.

Based on the results above, the base temperature was assumed to be 0 °C and the influence of photoperiod was examined using the approach summarized in equation (3). The thermal development rate increased linearly with mean photoperiod during the phase above a base of about 9 h (s.e. 1.5) (Fig. 2b). The data of Kirby and Faris (1970) for a crop of Proctor barley grown at Cambridge, England, and sown at about the same density as those at Sutton Bonington, enable a development rate to be calculated which is consistent with the other observations (Fig. 2b). From equation (3), it can be shown that a plot of 1/t against $(T - T_b)(P - P_b)$ should yield a straight line passing through the origin. Here we define a temperature adjusted for photoperiod (T') as

$$T' = (\overline{T} - T_b)(\overline{P} - P_b)/(24 - P_b). \qquad (4)$$

When development rate is plotted against this adjusted temperature a straight line results with an intercept of 0.05 °C (s.e. 0.60), not significantly different from 0 °C (Fig. 2c).

No other attempts appear to have been made to relate the duration of ear initiation of plants grown in the field to environmental factors in this way. Results from experiments done in controlled environments vary. Analysis of observations on the 10 cultivars grown by Kirby and Appleyard (1980) showed that all except 3 exhibited a linear response of development rate to photoperiods between 11 and 15 h. In 7 of the 10 the response to photoperiod appeared to be saturated beyond about 16 h, but in 'Maris Mink', 'Union', and 'CF 25', development rate increased linearly up to the maximum photoperiod of 20 h. For these cultivars P_b, obtained by extrapolation, was about 7 h. The observations of Fairey *et al.* (1975) can be interpreted as showing a linear response between 12 and 16 h photoperiods and a slower rate of increase between 16 and 24 h. By extrapolation, P_b appeared to be about 8 h. It is tempting to speculate that the tendency for a saturation type of response in controlled experiments is because the long photoperiods were achieved using an extension of weak, incandescent light. (Such extensions typically provide a negligible amount of energy for photosynthesis, and this is often deliberate, the aim being to separate effects of photoperiod from those of insolation). It is known that weak light can slow spikelet differentiation and prolong development in both wheat and barley (Friend *et al.*, 1962; Aspinall and Paleg, 1963).

The value of the base photoperiod of 9 h for this phase was determined imprecisely by extrapolation of the field results (Fig. 2b). None the less, it is close to the values which can be estimated from Kirby and Appleyard's (1980) data. It is also greater than 8 h, at which Guitard (1960), in an experiment done in controlled environments, found two

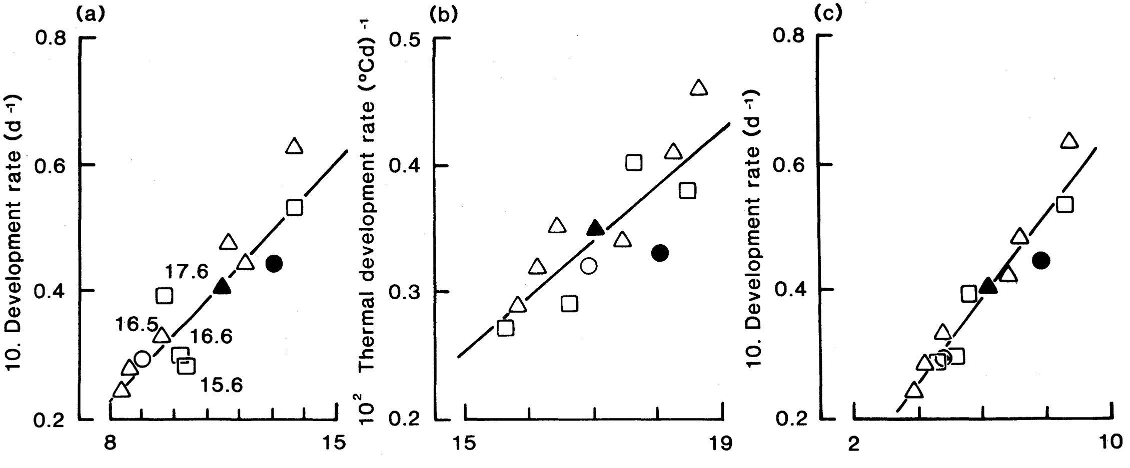

Figure 2: The relations between: (a) development rate ($10/t_i$) and temperature; (b) thermal development rate (100/day-degrees) and photoperiod; (c) development rate and adjusted temperature, all for the phase of spikelet initiation. Symbols: (▲) Kirby and Faris (1970); remainder as for Figure 1a. The equations of the fitted lines are:

(a) $y = 0.0543x - 0.205$ ($P < 0.001$);

(b) $y = 0.0450x - 0.421$ ($P < 0.001$);

(c) $y = 0.0637x + 0.003$ ($P < 0.001$).

See text for further details.

Canadian barley cultivars failed to develop.

The rate of initiation of spikelet primordia (which we shall call R_i) also responded linearly to temperature with a base of about 3 °C (s.e. 1.3), not significantly different from that for the development rate during this phase (Fig. 4a). The only other measurements of the response of R_i to temperature appear to be those of Borthwick *et al.* (1941) — though they did not calculate this variable. Their Table 1 gives information from which the rate of spikelet initiation can be calculated for vernalised 6-row barley, *Hordeum vulgare,* cv. 'Wintex' grown at three temperatures in a 16 h photoperiod. R_i responded strongly and apparently linearly between temperatures of about 4 and 18 °C (cf. Fig. 4a).

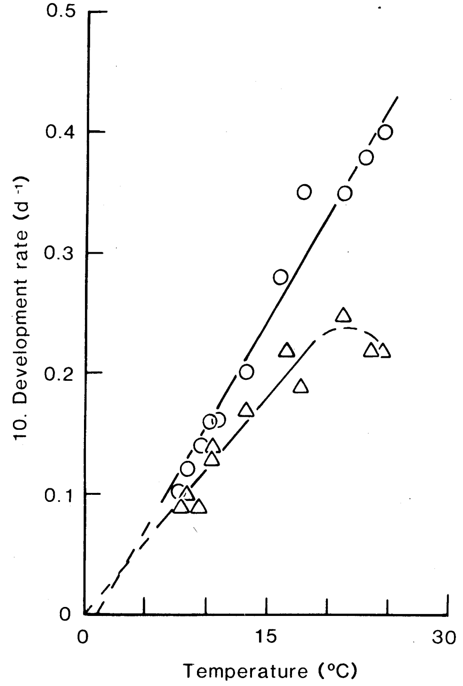

Figure 3: The relation between development rate (10/duration from sowing to flag leaf emergence) and mean air temperature for 'Shokubi mugi' (o) and 'Sachsender' (△) spring barleys grown in 24 hour photoperiods; data of Takahashi and Yasuda (1960). The equations of the lines are:

(o) $y = 0.0179x - 0.0244$ ($P < 0.001$); and

(△) $y = 0.0110x + 0.0013$ ($P < 0.001$) (observations beyond 23° were omitted from this regression).

Just as for development, a 'thermal rate' of spikelet initiation can be defined $(R_i/\overline{T})$ and this also responded linearly to photoperiod over the range experienced (Fig. 4b). Extrapolation gave a P_b of about 9 h (s.e. 1.7 h).

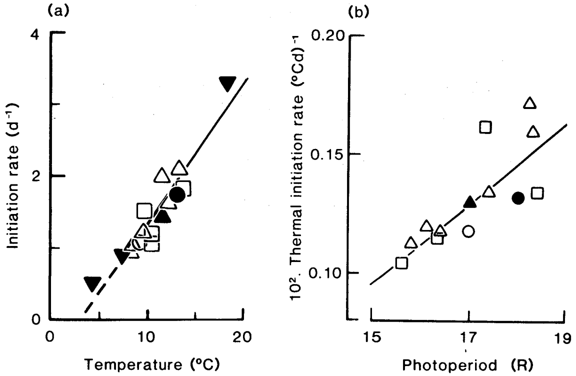

Figure 4: The response of: (a) spikelet initiation rate to temperature; and (b) spikelet initiation rate per unit of thermal time to photoperiod. The equations of the lines are:

(a) $y = 0.191x - 0.629$ ($P < 0.001$);

(b) $y = 0.0170x - 0.160$ ($P < 0.001$).

Symbols as for Figure 2; see text for further details.

Because the thermal rates of development and initiation both respond linearly to photoperiod and have a similar base photoperiod the maximum number of spikelets on the main stems will change little with variations of temperature and photoperiod resulting from late sowing (Monteith, 1977b). The measurements on which the analysis is based show a slight decrease in spikelet number from 40 with early sowing to 38 with late sowing (Scott and Dennis-Jones, 1976). A comparison of autumn- with spring-sown crops in Scotland showed the maximum number of spikelets to be stable (Russell *et al.,* 1982). Work in controlled environments has been mainly concerned with photoperiod, and results all show that the maximum spikelet number declines with increasing photoperiod (Aspinall, 1966; Fairey *et al.,* 1975; Kirby and Appleyard, 1980). This may be because R_i can be slowed by weak light. Aspinall and Paleg (1963) reported a linear increase of R_i with insolation up to the highest level of about 4.4 MJ PAR/m²/d used in their experiment, where the temperature was 20 °C and photoperiod 16 h. Could it be that in some experiments in controlled environments the *growth rate,* which is largely determined by insolation, is slow relative to the *development rate,* which is determined by photoperiod and temperature, and a shortage of assimilate results which slows R_i below its potential rate? It may be relevant that in the field, where radiation receipts per unit of developmental time (cf. Nix's (1976) 'photothermal quotient') are usually larger than in growth rooms, R_i increases linearly with photoperiod up to the longest daylengths experienced (Fig. 4b) — albeit with an increase in the variability of R_i.

Water stress has been shown to slow the rate of spikelet initiation and decrease the maximum spikelet number of barley grown in pots (Nicholls and May, 1963; Husain and Aspinall, 1970). In a field experiment, the number of grains per ear at harvest was strongly and negatively correlated with the mean soil moisture deficit during spikelet initiation

(Day *et al.,* 1978). But this was *not* associated with either fewer primordia per main-stem or a shorter ear at the time when the terminal spikelet was initiated. Subsequently spikelets at the tip and base of the ear died, so that by harvest the ears of main-stems subject to the most severe drought had about 20% fewer grains per ear than those from the fully irrigated treatment (Lawlor *et al.,* 1981). One explanation for these findings could be that early drought caused the leaves which unfolded subsequently to be small, and that this decreased the supply of assimilate to the rapidly growing ear during the ear growth phase.

Ear growth

During this phase, the morphogenesis of spikelets destined to become grain continues. The development of many of the spikelets at the tip of the ear stops before differentiation is complete, and the spikelets die. Up to half of the maximum number of spikelets initiated can be lost in this way (Gallagher *et al.,* 1976; Scott, this volume). The development rate ($1/t_e$) was linearly related to mean temperature during this phase over the limited range available from field experiments (12-17 °C). The base temperature was 0.2 °C (s.e. 3.81), indistinguishable from zero.

In contrast to the ear initiation phase, the thermal development rate of this phase was only weakly correlated with photoperiod ($P < 0.2$). This may be because the range of photoperiods experienced was so small (17.9-18.6 h). Kirby and Appleyard (1980) found that the duration of the ear growth phase decreased from about 34 d in their 11 h photoperiod to about 25 d in the 20 h photoperiod, a decrease of roughly 30%. The corresponding figures for the spikelet initiation phase were 49 d, 21 d, and 60%. These results may have been influenced by the different temperatures experienced during ear growth by plants in the different treatments. Ear growth occurred from mid-March to early April in the 20 h photoperiods and from mid-May to mid-June in the 11 h photoperiods. In these circumstances, low temperatures during ear growth may have partially compensated for the accelerating influence of long days.

Aspinall *et al.,* (1964) showed that water stress could shorten the duration of ear growth, but by less than three days.

Grain growth

The duration of this phase (t_k) is defined as the time from anthesis until grain growth stops. The end of grain growth can be determined by extrapolating the linear portion of the grain or ear growth curve until the final mass per grain, here called kernel mass, is reached (Gallagher *et al.,* 1976; Riggs and Gothard, 1976).

Preliminary analysis of measurements made at Sutton Bonington showed that t_k decreased by about 3.3 days per degree over the 14-19 °C range of temperatures experienced. Prince (1976) recorded ear emergence and grain growth of Proctor barley at a range of sites in two seasons, and his data show a decline in t_k of 3.4 days per degree rise in temperature. The observations of Andersen *et al.,* (1978) on spring barley grown in controlled environments at 10, 15, and 20 °C show the same rate of decline in t_k (see Vos, 1981). Within the bounds of error and despite the diversity of their origin, these data formed a coherent group and a joint regression line was fitted (Fig. 5a). The regression coefficient was -3.4 d/°C, similar to the value of -3.1 reported for duration of grain growth of a range of spring and winter wheats grown in the field by Wiegand and Cuellar (1981).

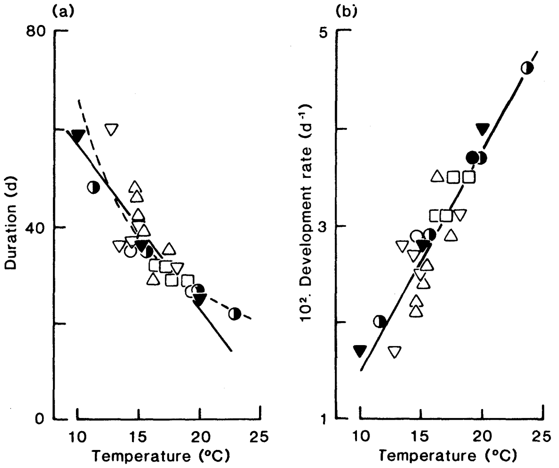

Figure 5: The relation between temperature and (a) the duration of grain growth and (b) the grain development rate (100/duration of grain growth) for data of: (▽) Prince (1976); (▼) Andersen *et al.* (1978); (◑) Gallagher and Thorne (1980); other symbols as for Figure 1 (a). The equations of the straight lines are:

(a) $y = -3.4x + 91$ ($P < 0.001$);

(b) $y = 0.23x - 0.79$ ($P < 0.001$);

the hyperbola in (a) was derived from the equation for (b). See text for further details.

The grain development rate ($1/t_k$) was also strongly and linearly related to temperature (Fig. 5b), and this relationship was preferred for three reasons. First, it is consistent with the way that other developmental phases have been treated. Second, other work has shown $1/t_k$ to be linearly related to mean temperature during grain growth (Gallagher and Thorne, 1980; Vos, 1981). Third, it accounts for slightly more variation (76 *v.* 71%). Gallagher and Thorne (1980) derived a duration of grain growth for 'Porthos' spring barley using fitted logistic curves (see Milford and Riley (1980) for an exposition of the technique), and their estimates of grain growth duration are shown for comparison in Figure 5. Extrapolating the line in Figure 5b gave a base temperature for grain growth of 3.4 °C (s.e. 1.7). Angus *et al.* (1981) showed an increase in base temperature for the anthesis-maturity phase in wheat and so the increase in base temperature for this phase in barley may be real, despite the uncertainty of the estimate. More precise studies would have to be done to confirm this.

There was no evidence that photoperiod had any influence on the thermal duration of grain growth for Proctor barley. Hough (1975) analysed observations from two years' trials of the European Brewing Convention, in which the cultivar 'Kenia' was grown in most of the countries of Western Europe. He suggested that long days might explain the rapid ripening of barley at high latitudes in locations such as Finland, but an experiment in a controlled environment showed that between 16 and 24 h daylength the duration of grain growth was stable (Dormling *et al.,* 1969). In this experiment the duration of grain growth did increase in a daylength of 8 h, but this may have been due to weak insolation. However the spectral composition of light in controlled environments is usually very different from that outside, and this can have pronounced effects of plant growth and development (Smith, 1976).

Drought can shorten the duration of grain growth (Aspinall, 1965; Lawlor *et al.,* 1981) but the response is hard to quantify. It may be that grain growth stops for want of assimilate after premature leaf death and exhaustion of stem reserves. A simpler explanation might be that the ears of drought-stricken crops are warmer than those of irrigated crops, as canopy temperatures of cereals increase with drought (Rackham, 1976; Sandhu and Horton, 1978; Ehrler *et al.,* 1978). If the relationship shown in Figure 5 holds, a 2 °C temperature difference between irrigated and unirrigated ears would shorten the duration of grain growth by nearly a week.

Hough (1975) found that the time from ear emergence to dead ripeness was inversely proportional to the potential transpiration rate and daylength. He preferred potential transpiration because he was concerned with the drying of the grain down to a suitable moisture content for harvesting. He also found a definite correlation between the rate of ripening (reciprocal of time from ear emergence to dead ripe) and air temperature ($r = 0.60$; $n = 74$), which supports the approach adopted here.

Summary and simplification

Table 2 summarises the importance of different weather variables in controlling the rate of barley development and the differentiation of leaves and spikelets. Any attempt to model the development of a barley crop accurately would have to incorporate such influences quantitatively — and perhaps others. Indeed, a comprehensive model advanced by Williams (1974) appears to require the estimation of 40 parameters.

Anticipating later analysis, however, progress will depend on the ability to predict the duration from sowing to the end of grain growth — here called the growth duration (t_a). Smith (1967) suggested that the number of hours of bright sunshine accumulated during longer phases such as t_a was stable, and a better indicator than either temperature or daylength. He also noted that the thermal time (day-degrees) accumulated between sowing and ripeness showed a strong tendency to decrease with increasing latitude. Smith's (1967) analysis may have been biased by his choice of 4.5 °C (40 °F) as a base temperature rather than 0 °C, which we believe to be more relevant for temperate cereals. Hough (1975) related the development rate between sowing and ear emergence simply to the daylength at crop emergence.

Because the preceding analysis showed both temperature and daylength to be important, we used both variables to predict the growth duration (t_a). The correlation of development rate ($1/t_a$) with mean temperature during growth was strong ($P < 0.001$), and we found

TABLE 2: Simple scheme to show how climatic factors may influence plant development during different phases and the number of leaves and spikelets initiated. Each + or − represents an increase or decrease in development rate or number with an increase of the weather factor.

Phase	Number	Temperature	Photoperiod	Drought
Sowing-emergence		+ + +		
Emergence-collar		+ + +	+	
	Leaves		−	
Collar-terminal spikelet		+ + +	+ + +	
	Spikelets	−	−	−
Terminal spikelet-anthesis		+ + +	+	
Anthesis-maturity		+ + +		+

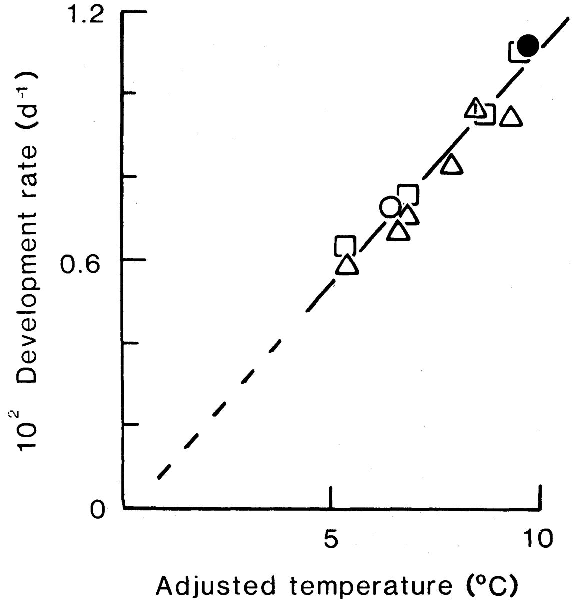

Figure 6: The relation between the reciprocal of duration from sowing to the end of grain growth (development rate) and adjusted temperature; symbols as for Figure 1(a). The equation of the line is:

$$y = 0.115x - 0.029 \ (P < 0.001).$$

$$100/t_a = 0.102\,\overline{T} - 0.448. \qquad (5)$$

But equation (5) gives a base temperature of 4 °C (s.e. 0.8) which, as mentioned above, is probably too high for temperate cereals. In addition the thermal development rate, $1/(t_a.\overline{T})$, was strongly correlated with mean photoperiod during growth ($P < 0.001$), with

$$1000/(t_a.\overline{T}) = 0.0705\,\overline{P} - 0.574, \qquad (6)$$

giving a base photoperiod of 8 h (s.e. 2.1). Combining equations (5) and (6) and plotting development rate against adjusted temperature showed a strong correlation, with a base temperature (T_b) not significantly different from 0 °C (Fig. 6). The photothermal duration (thermal duration adjusted for photoperiod) between sowing and the end of grain growth was 900 day-degrees (s.e. 14). Data from Prince's (1976) studies conformed with the observations made at Sutton Bonington (Fig. 6).

Caution

The foregoing has been based on an analysis of crops grown within a small range of latitude and the climate has been modified mainly by changing the sowing date. Temperature and photoperiod, with a few lucky exceptions (Figs. 4 and 5), will have been closely correlated. Angus *et al.* (1981) warned: "the confounding of temperature and photoperiod .... bedevils the interpretation of results from serial sowings at a single site". On the other hand, Hough (1975) warned that: "on the local scale, factors which have been dwarfed when considering international sites may become dominant". More tests are needed to establish the limits within which the simple analysis adopted here is valid.

GROWTH

The influence of climatic factors on crop photosynthesis, respiration, and dry matter production will be considered first; then the influence of these factors on the growth of plant organs important in determining yield will be examined.

Photosynthesis and respiration

The difference between gross photosynthesis (here defined as the sum of net photosynthesis and dark respiration) and respiration is almost equal to the growth rate of the plant or crop. This simplification neglects the mass of mineral nutrients taken up by the crop, which usually constitute about 5% of total plant dry mass at maturity. A crop which is well supplied with moisture is considered first. Early in the growing season, when the leaf area index (L) is less than about two, crop photosynthesis increases with the flux density of photosynthetically active radiation (PAR) up to about 200 W/m²; there is no increase of photosynthesis with brighter light (Line A C, Fig. 7). Bright sunshine is wasted because the photosynthesis of individual leaves is light-saturated (Fukai *et al.,* 1976; Biscoe and Gallagher, 1978). In addition, a fraction of light is wasted because the leaves cannot intercept it all when L is small.

Later in the season, when the green organs of crops intercept most of the incoming sunlight, the response of crop photosynthesis to radiation is stronger, and often light-saturation does not occur — even in very bright sunshine (line A B, Fig. 7; Monteith, 1968; Biscoe, Scott and Monteith, 1975; Fukai *et al.,* 1976; Leach, 1980). During periods of full crop cover, the daily net photosynthesis of crops is strongly correlated with daily insolation (Biscoe, Scott and Monteith, 1975; Fukai *et al.,* 1976). After ear emergence no new green tissue is produced, and because the maximum photosynthetic rate of organs declines with age (Biscoe, Gallagher *et al.,* 1975; Takeda and Udagawa, 1976), canopy photosynthesis responds less to light (Biscoe, Gallagher *et al.,* 1975; Monteith, 1981b). At the same time, senescence of green tissue decreases L and the photosynthesis-light response curves of crops resemble line A C in shape once more — though the dark respiration is usually faster (Fig. 7).

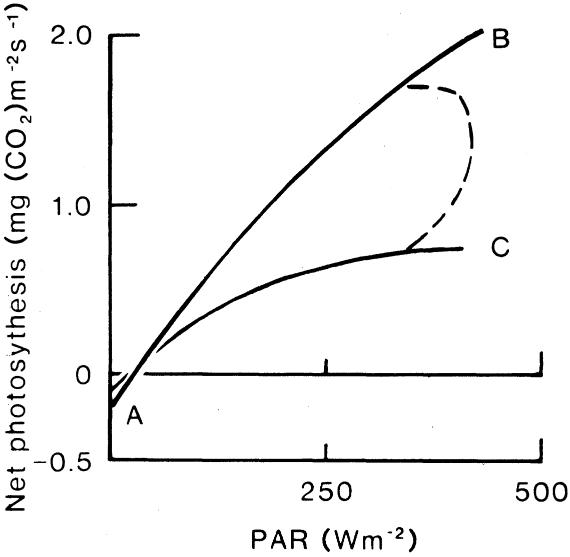

Figure 7: Scheme showing response of crop photosynthesis to photosynthetically active radiant flux density (PAR); see text for explanation.

Drought can modify these basic responses of crop photosynthesis to light. In dry weather, photosynthetic rates during late morning and afternoon are slower than at similar irradiances in the morning, sometimes the depression being as large as 50% (Biscoe, Scott and Monteith, 1975; Fukai *et al.,* 1976). The general pattern of photosynthesis with irradiance and time would be A B in the morning, falling to A C in the afternoon (Fig. 7), but the magnitude of depression, B - C, would depend on the severity of the drought. Legg *et al.* (1979) showed that such depressions are associated with decreases in the conductivity of leaves to carbon dioxide, caused by partial closure of the stomata.

The influence of temperature on the photosynthesis of temperate cereals is usually slight, a broad optimum extending over a 20 °C range in temperature being common (Murata and Iyama, 1963; Sawada, 1970). Sawada showed for wheat that the optimum temperature for photosynthesis varied with season. It rose from less than 10 °C in the winter to nearly 30 °C in the summer. However, very high temperatures, around 35 °C, may slow photosynthesis by about 25% (Murata and Iyama, 1963). Cold temperatures can also slow photosynthesis. Takeda (1976) and Fukai *et al.* (1976) showed that after heavy frosts the response of crop photosynthesis to light was sluggish during the following morning, but that recovery usually occurred later the same day. The general shape of the response curves following heavy frost is A C in the morning, moving to A B in the afternoon (Fig. 7).

Not all of the assimilate produced by photosynthesis is used in the production of new plant tissue. Assimilate is respired to provide energy for synthesising the complex molecules of which plant tissues are made, transporting materials about the plant, and maintaining the structure and function of existing tissue (Penning de Vries and Van Laar, 1977). For the present purpose, it is sufficient to know that the amount of carbon respired is often directly proportional to the amount of carbon fixed. This can be seen in a simple way from the measurements of Fukai *et al.* (1976), which showed that the ratio of night-time respiration to day-time net photosynthesis was about 1:8.

In a fuller analysis, Monteith (1968) presented observations for a crop of Proctor grown at Rothamsted, showing that over a seven-week period starting about three weeks before anthesis the ratio of total respiration to gross photosynthesis — the respiratory fraction — was about 0.57. In a similar exercise done nine years later, Biscoe, Scott and Monteith (1975) presented measurements showing that over the same developmental period the respiratory fraction was about 0.60. The data of Mogensen (1977) can be examined in the same way. By assuming a mean temperature of 16 °C during growth and a Q_{10} (coefficient of increase in the rate of respiration with temperature, expressed as a multiple by which the respiration rate is increased per 10 °C rise in temperature) for respiration of 2, Mogensen's (1977) data yield a respiratory fraction of about 0.54 over the same developmental period. This stability of the respiratory fraction is supported by Yamaguchi's (1978) work on rice, soyabean and maize, all of which had a respiratory fraction of 0.40 until partway through ear or seed growth. Thereafter the respiratory fractions of these crops increased quickly. The respiratory fraction also increased after anthesis in the barley studies mentioned above; before anthesis the average values for the respiratory fraction had been close to 0.45. This is similar to the respiratory fraction measured for barley in the 4-6 leaf stage and at a range of temperatures by Ryle *et al.* (1976). The conformity of all of these values is encouraging and suggests that during most of crop growth respiration is a stable proportion of gross photosynthesis. The growth rate of a crop therefore depends on its photosynthetic rate, which itself depends on crop cover and insolation (p. 29).

The practical result of this is that for much of the life of a cereal crop its growth rate is proportional to the amount of radiation absorbed by its green surfaces, the constant of proportionality being about 3.0 g DM/MJ PAR absorbed (Gallagher and Biscoe, 1978b). During an English summer, a crop which covers the ground completely will absorb about 7 MJ PAR/d and, assuming that it is well supplied with minerals and nutrients, it should therefore grow about 200 kg/ha/day. This value agrees both with measurements (Sibma, 1968) and theoretical estimates (Monteith, 1977a). Over the complete growing season the constant of proportionality falls from 3 to about 2 g/MJ (Gallagher and Biscoe, 1978a), the decrease being attributable to the weaker response of photosynthesis to light and the increasing respiratory fraction late in the season. Legg *et al.* (1979) showed that this seasonal value of 2 g/MJ could decline by a further 25% if severe drought was experienced (see above).

Because growth is proportional to absorbed light, a heavy crop can only be grown if leaf area expansion is fast and full green cover is maintained for a long period. An appreciation of the environmental factors governing the expansion and longevity of the leaf surface is clearly needed. In barley, this depends on the expansion and senescence of leaves on individual tillers, and, necessarily, on the process of tillering itself.

Leaf expansion and senescence

The rate of expansion and appearance of the leaves of temperate cereals increases rapidly with temperature above a base of about 0 °C (Biscoe and Gallagher, 1978; Kemp and Blacklow, 1982). With adequate water and mineral nutrition, the time taken for a crop to reach a given leaf area index depends primarily on temperature. The area of mature leaves also depends on temperature. Evidence from the field (Van Dobben and Hoogland, 1954) and growth rooms (Friend, 1966) shows that the area of leaves of the same ontogenic rank increases with temperature over the range usually experienced in temperate climates.

In contrast, the area of cereal leaves tends to be smaller in bright light, but the leaves are thicker, with bigger mesophyll cells, more veins per leaf, and a higher stomatal density (Friend *et al.*, 1962; Aspinall and Paleg, 1964; Friend and Pomeroy, 1970). These morphological characteristics are typically associated with a faster maximum rate of photosynthesis (Charles-Edwards and Ludwig, 1976), which tends to compensate for the smaller area of the leaves.

The data of Kirby and Appleyard (1980) showed that leaf appearance rate is faster in long photoperiods. However, Aspinall and Paleg (1964) found little difference in area between leaves grown in 16 h and 8 h photoperiods, although experiments with grasses and wheat have shown that long days increase leaf area (Langer, 1954; Friend *et al.*, 1962).

The rate of leaf expansion can be slowed by water stress (Biscoe and Gallagher, 1977) but little is known about how much this may restrict leaf expansion of crops sown in the autumn or the spring. With severe drought, leaves are certainly much smaller (Lawlor *et al.*, 1981) but whether this is due to unfavourable plant water status or reduced availability of mineral nutrients is unknown. Kemp (1980) showed the importance of an adequate supply of protein, and by implication mineral nitrogen, for leaf extension in wheat.

Little is known about the factors controlling leaf senescence. Drought certainly accelerates the senescence of cereal leaves, as does high temperature (Ford and Thorne, 1975; Biscoe and Gallagher, 1977; Legg *et al.*, 1979). The response to warm temperatures is probably related to the more general effect of temperature on development rate. Drought may accelerate senescence in two ways. The leaves and the other green tissues may be warmer during the day (p. 26), and drought may decrease the rate of uptake of mineral nutrients. Day *et al.* (1978) found that the uptake of phosphorus and potassium was greatly inhibited by drought. This could lead to enhanced rates of senescence if nutrients are translocated from older leaves to regions of active growth (Williams, 1955).

Roots

During early summer in Canterbury, an actively growing barley crop, with a leaf area index of three or more and rooted in moist soil, will lose about 4.5 mm water per day, i.e. 45 t water/ha/d. All this water has to be taken up through the plant roots. If the crop is growing well, say at 150 kg DM/ha/d, the roots will also have to extract about 1.5 kg of N and 2 kg of P and K/ha/d. It is hard to over-emphasise the importance of an adequate root system to meet the evaporative demands of the atmosphere and the requirement of a fast-growing crop for nutrients. To meet these requirements, a crop of barley will produce between 10 and 15 km of root per square metre of field surface by the time of ear emergence (Welbank *et al.*, 1974). It is also hard to over-emphasise the difficulties of studying the roots of field crops, and little is known about the response of root growth to environmental factors.

Root growth from the seed begins before shoot growth, and in temperate climates the roots of spring barley crops appear to grow down at a rate of about 20 mm/d. For winter crops, penetration proceeds at only about one third of this rate, presumably due to either low temperatures or slow assimilation (Gregory *et al.*, 1978). The growth of nodal roots is linked with the appearance of tillers, and environmental factors which favour prolific tillering are usually, but not always, associated with the establishment of many nodal roots (Brouwer, 1966). For instance, rapid drying of the topsoil can limit the penetration of nodal roots (Meyer and Alston, 1978). Most of the roots of barley are present in the top 0.3 m of soil, but some roots of temperate cereals usually penetrate to deeper than 1.5 m (Welbank *et al.*, 1974; Gregory *et al.*, 1978). These deep roots are few but they can be important in providing cereal plants with water during drought (Gregory *et al.*, 1978).

The response of root growth to environmental factors has often been explained in terms of a functional equilibrium. Thus, if water and nutrients are in short supply, root growth is favoured at the expense of shoot growth (Brouwer, 1966). The work of Lawlor *et al.* (1981) supports this concept. They found that at maturity the dry mass of roots to 1.0 m depth was almost identical in a fully irrigated and an unirrigated treatment, but that the root:shoot ratios were 0.05 and 0.10 respectively. In contrast, weak light, which is associated with slow evaporation and presumably a poor supply of assimilate to the roots, is associated with a small root:shoot ratio (Brouwer, 1966; Welsbank *et al.*, 1974).

Barley roots will not grow into a soil layer where the water potential is less than about -1.5 MPa (Briggs, 1978). This can cause problems in some environments when a crop is sown into a soil from which most of the water has been extracted by a recently harvested crop. This does not happen often in Canterbury, but may have been a problem on some soils in the dry autumn of 1982. It has also been shown that drought and high temperatures during early seedling growth can decrease the diameter of the xylem vessels of wheat (Richards and Passioura, 1981a). This response may help to ensure frugal use of soil water but its significance has yet to be established.

In general, knowledge about root growth in response to environmental influences and its significance for the yield of field crops is fragmentary. Much remains to be done.

Tillering

There are two main reasons why tillering is important. First, in most well-husbanded crops of barley the green area of the tillers is greater than that of the main-stems, so that they intercept much light and are responsible for much of the growth that occurs. Second, some of the tillers which are produced bear ears which increase the ears per plant component of grain yield (see Scott, this volume). The process of tillering in cereals and grasses has been regularly reviewed (Langer, 1963; Bunting and Drennan, 1966; Jewis, 1972; Gallagher and Biscoe, 1978a), but rarely researched. A summary of the present state of knowledge might run:

(i) Temperature. Tiller production is slow in cool temperatures but many tillers are produced, survival is high and many ears per plant are formed. Conversely, in warm temperatures the rate of tillering is fast but the maximum number of tillers formed and final number of ears per plant are small (Guitard, 1960; Dormling *et al.*, 1969). A possible reason is that warm temperatures accelerate development but do not increase photosynthesis (p. 30). The net effect of this is to decrease the growth made by the plant during the phases of both tiller production and tiller death.

(ii) Radiation. Large radiation receipts arising from either bright light or long days favour both tiller production and survival and result in the formation of many ears per plant (Guitard, 1960; Aspinall and Paleg, 1964; Aspinall, 1966; Dormling *et al.*, 1969; Willey and Holliday, 1971). These responses are presumably due to the extra assimilation per unit of developmental time associated with stronger insolation.

(iii) Photoperiod. Kirby and Appleyard (1980) found that more ears per plant were formed in long photoperiods, although some of the cultivars they examined exhibited only a small or a negative response. In general, the response of tillering to photoperiod seems to be related more to light energy than to any photomorphogenetic effects (Aspinall and Paleg, 1964; Aspinall, 1966; Dormling *et al.*, 1969; Fairey *et al.*, 1975).

(iv) Drought. Dry weather between sowing and terminal spikelet formation decreases the maximum number of tillers that a plant produces, and in general decreases the number of ears/m^2 at harvest (Kirby, 1968; Rackham, 1972; Lawlor *et al.*, 1981). The cause of these effects is not certain. A small maximum number of tillers per plant is usually associated with a small DM per plant around the time of maximum spikelet number. Day *et al.* (1978) found that ears/m^2 was most closely correlated with soil moisture deficit between terminal spikelet and anthesis; large deficits were associated with few ears per plant and slow growth (Lawlor *et al.*, 1981). These workers also have evidence suggesting that drought causes tiller death even after anthesis. This evidence is supported by an experiment done in a glasshouse in which severe drought around the time of ear emergence decreased the number of ears per plant by about half (Morgan and Riggs, 1981). More information is urgently needed about the causes and timing of tiller death.

Ear growth

Environmental factors controlling the total number of spikelets initiated have been dealt with (p. 26). This section will consider the growth of the ear between the initiation of the terminal spikelet and anthesis — the period during which spikelet growth and death occur and the number of grains per ear is largely determined. No studies appear to have been made of the influence of environmental factors on the actual rate of DM growth of ears during this phase. The summary and interpretation below are therefore based more on inference than direct evidence.

(i) Temperature. Cool temperatures increase spikelet survival and the number of grains per ear (Guitard, 1960; Tingle *et al.*, 1970). These results are supported by the statistical analysis of Hough (1975), which showed that grain number per ear was negatively correlated with temperature. The reason for this may be the same as that advanced to account for better tiller survival at low temperatures, that more assimilate is produced during the developmental phase.

(ii) Radiation. As with tiller survival, large radiation receipts favour spikelet survival and are usually associated with high numbers of grains per ear (Guitard, 1960; Tingle *et al.*, 1970; Willey and Holliday, 1971; Scott and Dennis-Jones, 1976).

(iii) Photoperiod. The effect of this factor is variable. Fairey *et al.* (1975) found no significant influence of long days (achieved by extending a 12 h bright period with weak incandescent light) on spikelet number at heading. Using a similar technique, Kirby and Appleyard (1980) found a 26% decrease in grains per ear as photoperiod increased from 13 to 20 h, though the response of individual cultivars varied from 8% to 35%. Nicholls and May (1963) also found spikelet number to decrease in a long photoperiod. In the field, Hough (1975) found a weak negative correlation between photoperiod at crop emergence and grain number per ear. He did not examine the specific influence of daylength during the ear-growth phase. Tingle *et al.* (1970) found that daylengths of 16 h gave about 10% more fertile spikelets than those of 24 h, and 83% more than those of 8 h, but as insolation varied with photoperiod in this experiment the results are hard to interpret.

(iv) Drought. Several studies have shown that drought can decrease grain number per ear (Aspinall *et al.*, 1964; Rackham, 1972; Day *et al.*, 1980; Morgan and Riggs, 1981). In treatments that were subject to drought from terminal spikelet onward, Day *et al.* (1978) found a 15% decrease in grain numbers per ear. But they also found that over all treatments, grains per ear was most closely correlated with soil moisture deficit *before* the terminal spikelet was initiated (see p. 36 for discussion). Aspinall *et al.* (1964) found that water shortage, both during ear growth and ear emergence, decreased the number of grains per ear on main-stems by about 15%. These results are supported by those of Morgan and Riggs (1981), who found that stress between ear emergence and about 14 d after heading decreased the number of grains per ear by nearly 50%. The larger response was probably because Morgan and Riggs (1981) grew their plants in small pots.

Grain growth

The growth of barley grains follows a sigmoidal pattern, though for about 60% of the duration of grain growth the curvature is not pronounced and the grain growth rate is stable (Riggs and Gothard, 1976). About 90% of the total increase in grain dry matter occurs during this period of steady growth. This means that final grain size can be conveniently described as the product of an average rate of grain growth and a duration. Environmental control of the duration of grain growth was considered above (p. 27), and influences on the rate of grain growth will now be considered.

(i) Temperature. Grains of temperate cereals grow faster at higher temperatures (Pope, 1943; Sofield *et al.*, 1977; Chowdhury and Wardlaw, 1978; Gallagher and Thorne, 1980). Such faster growth is usually more than compensated by a shorter duration of growth (p. 27), and kernel mass falls at higher temperatures. Results from experiments with barley in controlled environments show that kernel mass decreases by between 0.8 and 1.75 mg/°C change in mean temperature during grain growth (Dormling *et al.*, 1969; Chowdhury and Wardlaw, 1978; Gallagher and Thorne, 1980). Wiegand and Cuellar (1981) found that kernel mass in wheat declined by about 1.4 mg/°C in studies done in controlled environments, but by about 2.9 mg/°C in field experiments.

There is little evidence on the response of barley to high temperatures in the field. However, Day *et al.* (1978, 1980) grew 'Julia' spring barley under full irrigation in two seasons in which the mean temperature during grain growth differed by about 3°C. In the cooler season grains were about 8 mg heavier than in the warm season, suggesting that kernel mass decreased by about 2.5 mg/°C. In these field experiments the effect of temperature may have been influenced by differences in sunshine, humidity and sowing date, but the comparison suggests that, as with wheat, warm temperatures in the field have a greater effect than in controlled environments. Part of the reason for this may be the greater diurnal range of temperatures experienced by crops in the field. The results of Gallagher and Thorne (1980) showed an optimum temperature for the growth rate of barley grains of about 30 °C. Some support for this comes from Pope's (1943) work on the rate of extension of barley caryopses shortly after fertilisation. His results indicate a sharp optimum for extension rate at about 30 °C (Fig. 8). If the response of the development rate for this phase to temperature is linear, and measurements suggest that it is (p. 27), then days when temperature exceeds about 30 °C for significant periods will depress grain size because faster development of the grains will not be compensated by faster grain growth.

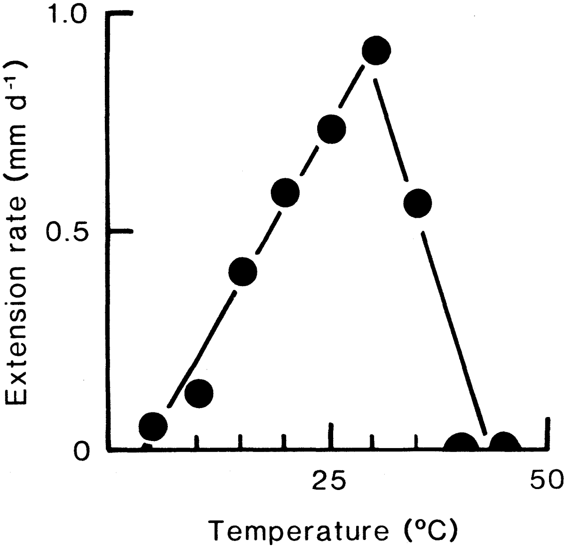

Figure 8: The relation between caryopsis extension rate and temperature during the six days following pollination; from data of Pope (1943).

(ii) Radiation. Dull conditions during grain growth are usually associated with smaller grains. In an experiment done in controlled environments, kernel mass was about 10% smaller with an insolation of 5.4 compared with 7.9 MJ (PAR)/m^2/d (Gallagher and Thorne, 1980). This was due to both a slower rate and a slightly shorter duration of grain growth. Similar changes in kernel mass have resulted from shading crops in the field, and decreasing day-length in controlled environments (Guitard, 1960; Dormling *et al.*, 1969; Willey and Holliday, 1971).

(iii) Photoperiod. The study of Kirby and Appleyard (1980) appears to be the only one in which the influence of photoperiod on grain size was not confounded with changes in insolation. Averaged over all cultivars, they found a 45% decrease in kernel mass as photoperiod increased from 11 to 20 h; this was associated with a 41% decrease in the time from sowing to ear emergence. In general, these changes in kernel mass were not associated with changes in the number of grains per plant. It is known that the environment before anthesis can a dominant influence on grain size independently of its effects after anthesis (Prince, 1976). Scott *et al.* (1983) also showed that differences in grain size between cultivars are established before anthesis. Could it be that the slow development in short photoperiods before anthesis in Kirby and Appleyard's (1980) experiment led to the formation of large ovaries which went on to produce big grain? This is a question worth studying.

(iv) Drought. The influence of drought on kernel mass depends on the severity of the drought and the timing of the dry spell. The combination of fast potential evaporation and little rain usually causes kernel mass to decline (Bidinger *et al.*, 1977; Day *et al.*, 1978), but can cause an increase (De Vos and Toussaint, 1966; Kirby, 1968) or have little effect (Day *et al.*, 1980). In general drought seems to have little effect on grain growth rate; its main influence is to shorten the duration of grain filling (Aspinall, 1966; Lawlor *et al.*, 1981).

One reason why drought has little influence on grain growth rate may be the ability of barley plants to draw on reserves of carbohydrate stored mainly in the stem (Gallagher *et al.*, 1975; Bidinger *et al.*, 1977; Austin *et al.*, 1980; Lawlor *et al.*, 1981). In dry seasons in temperate climates, such reserves may account for about half the grain dry mass at maturity (Austin *et al.*, 1980). In more arid climates the available reserves seem to be smaller (Bidinger *et al.*, 1977), but it is not known whether this difference is related to differences in climate or genotype.

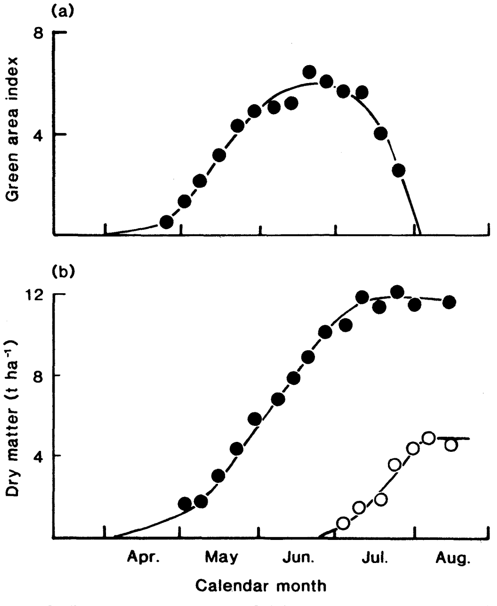

Figure 9: Temporal change of (a) green area index and (b) total shoot (●) and grain dry matter (o) for a representative crop of Proctor barley grown at Sutton Bonington.

TABLE 3: Simple scheme to show how climatic factors may influence growth processes and yield components.

		Temperature				
Process	Size/number	Cold	Warm	Radiation	Photoperiod	Drought
Photosynthesis		–	–	+ + +		– –
Respiration		–	+		(as for photosynthesis - see text)	
DM growth rate				+ + +		– –
Leaf appearance rate		– – –	+ + +		+ +	
Leaf expansion rate		– – –	+ + +	–	+	– –
	Area/leaf	–	+ +[1]	–		– –
Leaf death rate		– –	+ +		+	+
Root growth rate		– –	+ +	+		+
Tillering rate		– –	+ +	+		– –
	Maximum tiller no./plant	+ +	– –	+ + +	+	– – –
Tiller death rate		– –	+ +	– – –	+	+ + +
	Ear no./plant	+ +	– –	+ +	–	– –
Ear growth rate		– –	+ +	+	+	–
	Grains/ear	+ +	– –	+ +	–	– –
Grain growth rate		– –	+ +	+	–	
	Kernel mass	+ +	– –	+	--	?

[1] decreasing beyond about 20 °C mean temperature.

Summary and simplification

Table 3 summarises qualitatively the response of the processes of growth considered above to different weather variables. Because of the uncertainty about the responses — sometimes the sign, let alone the magnitude, is unknown — it would be unwise to build a comprehensive simulation model and expect it to make accurate predictions of yield and yield components. Such a model-building exercise might well be worthwhile to identify those processes and relationships about which little is known, but which have a major effect on yield. However, if in the first instance an estimate of yield is all that is required, measurements made on well-husbanded crops at Sutton Bonington suggest a crude way of circumventing the problem of complexity.

Figure 9 shows a typical set of measurements describing both the total and grain DM of a crop of Proctor barley. The total shoot DM at maturity was about 11.5 t/ha. Most of this DM was produced during a period of 68 days when the growth rate was stable at about 170 kg/ha/d (Fig. 9). This growth rate is about 85% of the maximum of 200 kg/ha/d estimated theoretically for crops completely covering the ground and well supplied with water and mineral nutrients (Monteith, 1977a). The difference between the theoretical and the achieved growth rates is almost certainly due to incomplete light interception by the real crop, particularly at the beginning and the end of the linear growth phase. The growth of the crop in Figure 9 can be split into three periods: sowing to the start of fast growth (I); fast steady growth (II); the end of fast growth to the end of grain growth (III). During periods I and III, green crop cover is poor and growth rates slow. During period II, crop cover is nearly complete and the crop grows at a steady rate close to the potential one. Using Monteith's (1981a) nomenclature, some of the time in periods I and III is *lost*, due to slow establishment of the leaf surface and senescence respectively. Monteith (1981a) showed how the amount of time lost during period I depends on temperature, but here a further simplification is made. An average crop growth rate ($\overline{C}$) is defined as

$$\overline{C} = M_t/t_a, \qquad (7)$$

where M_t is the total shoot DM produced and t_a is the (actual) growth duration from sowing until the end of grain growth. For the example in Figure 9, $\overline{C}$ is about 85 kg/ha/d, roughly half the rate during the period of fast growth because the actual growth duration is about twice the duration of fast growth. For 12 crops of Proctor barley grown at Sutton Bonington over a range of seasons and sowing dates, the mean value for $\overline{C}$ was 95 kg/ha/d (s.d. 11.6). This may be compared with a value of 130 (±16) kg/ha/d calculated for nine C_3 crops with record or near record yields, abundantly supplied with nutrients and water and grown in climates with strong insolation (Monteith, 1978). The crops grown at Sutton Bonington probably had a slower average growth rate because they received and intercepted less light; on occasions they may also have been short of some mineral nutrients, and may have suffered from drought.

The stability of $\overline{C}$ for crops grown over a wide range of weather conditions suggests that, if the influence of environment on growth duration is accurately described by the relationship of Figure 6, then it should be possible to predict the effect of gross differences of climate on total dry matter production. The grain yield could then be predicted if the fraction of the total DM present in the grain (the harvest index) were known. A summary of measurements of harvest index made on crops of Proctor barley grown in a range of environments gave a mean value of 0.46 (s.e. 0.022) (Gallagher and Biscoe, 1978b). Measurements on 16 crops of Julia spring barley grown under different irrigation treatments in two seasons at Rothamsted show a mean harvest index of 0.48 (s.e. 0.035) (Day *et al.*, 1978, 1980). The difference in average harvest index between Proctor and Julia may be real and arise from genetic differences (Riggs *et al.*, 1981) such as a difference in mean crop height. Harvest index was not correlated with yield for either variety ($P > 0.05$).

The next section examines how the stability of the average crop growth rate and harvest index can be exploited in a simple model to predict some effects of climate and sowing date on yield.

MODEL AND SYNTHESIS

BASIC PRINCIPLES

A model is needed to synthesise knowledge about the response of barley to environmental factors to provide predictions of yield responses to climatic and agronomic factors. Here, a model based primarily on the foregoing simplifications is used for synthesis. Yield (Y) is equated simply to the product of an average growth rate ($\overline{C}$), a growth duration (t_a), and a partitioning factor (the harvest index, F_h), so that

$$Y = \overline{C} \times t_m \times F_h. \qquad (8)$$

The maximum duration of growth (t_m) depends on temperature and photoperiod (Fig. 6). The photothermal time which has to elapse between sowing and the end of linear grain growth was set at 900°C d (p. 29). In subsequent calculations, the photothermal time was calculated using monthly averages of temperature and photoperiod and no adjustments were made for variety. $\overline{C}$ was set at 95 kg/ha/d, the average for the crops grown at Sutton Bonington, and F_h at 0.47, the average for several crops of Proctor and Julia.

INFLUENCE OF DROUGHT

Drought can be thought of as decreasing the growth duration and this notion is explained and quantified below. Essentially the approach depends on an analysis developed by Penman (1952, 1970a), reviewed and refined by French and Legg (1979), and extended by Monteith (1981a). The analysis depends on three important definitions and four assumptions now presented.

Definitions

Potential Evaporation Rate (E). This is the rate of evaporation from a green crop, fully covering the ground, of large horizontal extent, actively growing and well supplied wth water. E can be estimated from meteorological observations using a formula outlined by Penman (1952), an appropriate version of which was stated in SI units by French and Legg (1979).

Potential Soil Moisture Deficit (D). At any time during growth, D is the difference between the sum of E and the sum of irrigation and rainfall, thus

$$D \doteq \Sigma E - \Sigma (I + R) \qquad (9)$$

For most autumn and spring sown crops, D is close to or reaches zero during early growth, i.e. the soil is close to or reaches field capacity. D is not allowed to be negative; when excess rain falls it is assumed to be lost through drainage. It is important to note that: "D is a measure of the amount by which atmospheric demand for evaporation exceeds rainfall plus irrigation, it is independent of the availability of water in the soil .... for small deficits the potential and actual deficits should be equal. As the potential deficit increases there comes a time when the crop is no longer able to extract water at the potential rate, so the actual deficit increases more slowly than the potential deficit and eventually reaches a limit. *If the drought continues the actual deficit remains constant but the potential deficit increases.*" (French and Legg (1979), our italics). When calculating D some allowance is usually made for incomplete crop cover during early growth.

Maximum Potential Soil Moisture Deficit (D_m). This is the maximum value that D attains during the development of a crop. It is not necessarily the value of D at maturity.

Assumptions (after French and Legg, 1979)

1. When water is freely available in the soil, the growth rate, expressed as increase of total DM, is proportional to the evaporation rate and hence to E.
2. When D reaches and exceeds a *limiting deficit* (D_l), growth stops; when there is further rain or irrigation it is freely available and the crop grows at the full rate until the extra water is all used. The value for D_l depends on both crop and soil type; it is large for deep-rooted crops and for soils with a large water-holding capacity (Penman, 1970a, 1970b; French and Legg, 1979).
3. Yield is proportional to total dry matter production. It follows that the loss of yield is proportional to $D_m - D_l$. The total DM yield is given by

$$Y = k\,\Sigma E \qquad \text{when } D_m < D_l$$

and

$$Y = k\,(\,\Sigma E - (D_m - D_l)) \text{ when } D_m > D_l, \text{ where k is a constant.}$$

4. Implicit in Penman's analysis is that there are no critical phases or sensitive periods, i.e. phases of crop development when a given degree of drought — defined by D — will depress yield more than if that same drought occurred during another phase. This *definition*, concerned with plant physiology, should not be confused with the *idea*, concerned with meteorological probabilites, that a crop is more likely to suffer a severe drought and need irrigating during certain phases of development. On average, in climates with which this analysis is concerned, D_m can be expected to increase until some time during grain growth. Crops frequently need watering near the time

of booting, as in many soils D is approaching or has exceeded D_l at this stage. This does not mean that the crop is more susceptible to drought at this stage. Recent research on barley shows that yields are depressed by drought at any stage (Day *et al.*, 1978). Indeed, Mogensen (1980) reported that a given degree of drought, measured by the ratio of actual to potential evaporation, decreased yield more if experienced during the jointing and shooting phases rather than during later phases when the crop is traditionally assumed to be more sensitive to drought.

Penman's analysis, therefore, makes crude simplifications and ignores much of the conventional wisdom behind the response of crop yields to drought, and its usefulness might justifiably be questioned. Because his analysis is central to the model developed here, some tests of it are described below.

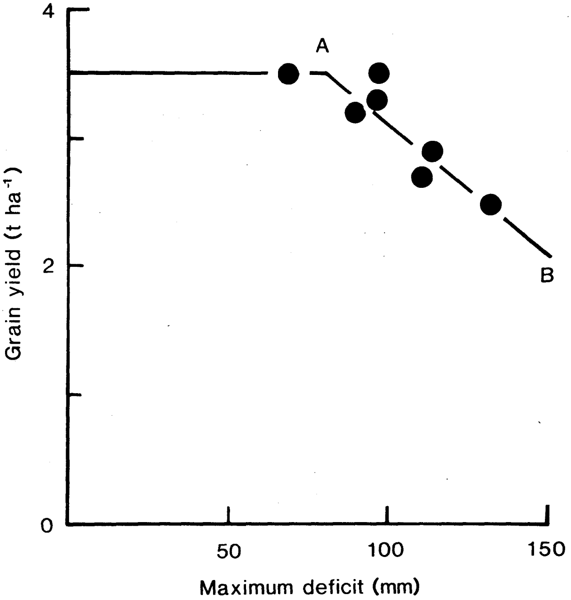

Figure 10: the relation between grain yield and maximum potential soil moisture deficit derived from data of de Vos and Toussaint (1966). The lines were fitted by eye. See text for further details.

Tests

Penman's analysis has been carefully tested for a range of crops grown on sandy and clay soils in England. For barley grown on sandy soils, D_l was found to be about 50 mm, and on clay soils about 100 mm (Penman, 1970b; Day *et al.*, 1978). French and Legg (1979) used a more refined statistical procedure and showed that growth did not stop at the limiting deficit, but continued more slowly.

De Vos and Toussaint (1966) studied the response of barley yields to seven irrigation treatments on a sandy soil in a sunny, dry season in the Netherlands. Assuming that their $E_o = 1.4$ E enables Penman's analysis to be applied to their results and compared with the Rothamsted work. Figure 10 shows that Penman's response model fitted the data well, giving a value for D_l of about 80 mm. The maximum expected response to irrigation, given by the slope of the line A B in Figure 10, is about 28 kg (grain)/ha/mm and similar to the maximum value of 25 kg/ha/mm reported for experiments on a sandy soil by Penman (1970b).

A preliminary analysis of Drewitt and Smart's (1981) measurements suggested that Penman's analysis described the response of barley yield to drought at Winchmore adequately. The value of D_l was about 50 mm and the maximum expected response to irrigation about 12 kg/ha/mm. This response is only about half of the maximum values for sandy soils in England and the Netherlands, but is close to the average English value of 16 kg/ha/mm (Penman, 1971). These maximum values assume that water is supplied uniformly and efficiently when needed; the actual response to water applied using border dyke and some spray irrigation systems will be an order of magnitude smaller.

Extension

Monteith (1981a) has recently introduced the concept of "lost time". Put simply, it is the amount of time for which a crop stops growing because of drought. If the potential evaporation rate is stable during the period when most growth is made, and it usually is, and if Penman's analysis holds, then the time lost due to drought (t_d) is given by

$$t_d = (D_m - D_l)/\overline{E}, \tag{10}$$

where $\overline{E}$ is the average rate of potential evaporation during the growing season. The model represented by equation (8) can now be modified to account for drought and becomes

$$Y = (t_m - t_d) \times \overline{C} \times F_h \tag{11}$$

Tests

Predictions made by the simple model represented by equation (11) were first compared with the yield of a crop of Proctor barley receiving nitrogen fertiliser, which was grown at Rothamsted Experimental Station by Watson *et al.* (1958). Rain in May brought the soil up to field capacity and D_m for this crop reached only 108 mm by the end of July. Assuming E to be 3 mm/d and D_l for barley at Rothamsted to be 100 mm (Day *et al.*, 1978), only three days of growth were lost due to drought. The yield estimated from equation (11) was 5.8 t/ha and the measured yield was 5.6 (s.e. 0.13) t/ha; an encouraging start.

The model was then used with the same values for all parameters to predict some of the yields of the barley crops grown at Rothamsted in 1976 and 1979 with different irrigation treatments, and described by Day *et al.* (1978, 1980). The crops examined all received nitrogen fertiliser. In 1976, E was assumed to be 3.5 mm/d because the weather was dry and sunny, but during April was set to one half of this value to allow for incomplete crop cover. In 1978, the equivalent period of incomplete cover was from sowing (18 April) until the end of May, as the weather was cooler. Figure 11 shows that predicted and measured yields for these crops grown at Rothamsted were in reasonable agreement, but that there were some systematic deviations. The yields of the well-irrigated crops in 1976 (11, 4 and 12; Fig 11) were all underestimated. This may be because the average growth rate of these crops was faster than the value of 95 kg/ha/d assumed in the model, on account of the bright sunny weather in 1976. In 1979 the model again underestimated the yield of the fully irrigated treatment (Fig. 11). Part of the reason for this was the high harvest index of 0.50 recorded in 1979 (cf. 0.46 in 1976 and 0.47 in the model). But, in addition, it seems as if these well irrigated crops were growing about 10% faster than the average for unirrigated crops at Sutton Bonington. The yield of the unirrigated crops in 1979 was underestimated by about 30% (Fig. 11). This may be because the generally slower evaporation in 1979 meant that growth did not stop when D_l was reached, but continued more slowly, as French and Legg (1979) found in their analysis. Doubtless the Rothamsted workers will provide an answer soon. Despite these failings, the model successfully predicted the better yields that Day *et al.* recorded in 1979 compared with 1976. Encouraged by the agreement found in these preliminary tests, we used the model to examine some effects of climate and sowing date on yield.

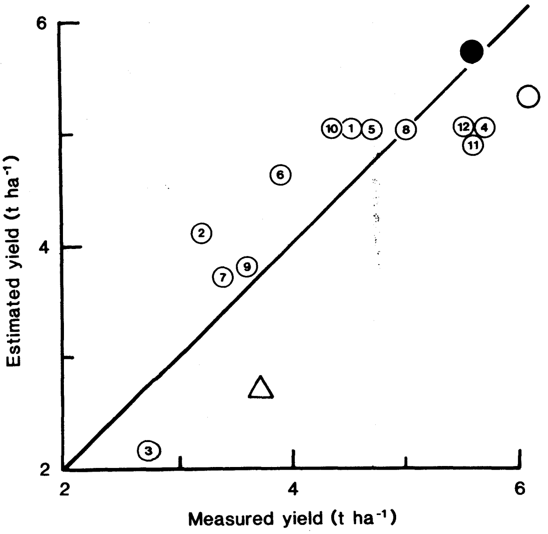

Figure 11: The relation between estimated and measured grain yields for crops of barley grown at Rothamsted: (●) Watson *et al.* (1958); (ⓝ) Day *et al.* (1978), number refers to treatment; (○) fully irrigated and (△) unirrigated crops of Day *et al.* (1980) which received nitrogen fertiliser. The line x = y is drawn for comparison.

PREDICTIONS

Sowing date

Many field experiments have attempted to answer the question of when to sow spring barley. Francis (1974) reported results from experiments done at six sites during three years, with several varieties sown around three dates: 4 March, 25 March and 26 April. The model was used to estimate the average yields to be expected from sowing at these dates using climatic data from the School of Agriculture at Sutton Bonington. The model overestimated the actual yields by about 35% (Table 4a). This may be because the husbandry was not ideal; outbreaks of disease were reported, and some crops lodged; and the crops were grown on a range of soil types and in different rotations. But when yield is expressed relative to the yield obtained from early sowing, the predictions from the model are closer to the measurements, though the model exaggerates the decline in yield from early to late March sowing (Table 4a). This is probably because the model takes no account of the extra time taken to expand the leaf area in early spring when temperatures are low. Table 4b shows that in another series of experiments reported by Munro *et al.* (1974), where barley was sown at five sites in four years, the relative decline in yield from late March to late April sowing is predicted well by the model. Kirby (1969) reported the results of an experiment with Proctor barley which was sown on 12 March or 26 April at Cambridge. The decline in yield relative to the early sowing is predicted accurately, but once more the model overestimates the absolute yields of the crops (Table 4c).

TABLE 4: Comparison of measurements and estimates of the response of yield to sowing date: data of (a) Francis (1974)[1]; (b) Munro *et al.* (1974); (c) Kirby (1969). Numbers in parenthesis are yields expressed relative to the yields from the earliest sowings.

		Yield t/ha	
	Sowing Date	Measured	Estimated
(a)	4/3	4.6 (1.00)	6.4 (1.00)
	25/3	4.3 (0.95)	5.5 (0.87)
	26/4	3.5 (0.77)	4.7 (0.71)
(b)	28/3	5.0 (1.00)	5.4 (1.00)
	25/4	4.4 (0.88)	4.6 (0.85)
(c)	12/3	4.0 (1.00)	6.2 (1.00)
	26/4	3.3 (0.83)	4.9 (0.79)

[1] Results for Proctor and 'Impala' sown at Bridgets and Impala at Arthur Rickwood in 1967 were not included in the analysis as poor seedbeds appear to have caused a 20% loss in yield from the early sowings.

These results suggest that the decline in yield with late sowing is largely due to faster development, with average growth rate and harvest index remaining relatively stable. However, it is known that on very sandy soils there are yield advantages of up to 20% to be gained from sowing in January and February rather than in March (Selman, 1977). The model would not predict these increases in yield, as it seems likely that they are related to better root growth.

TABLE 5: Response of yield to sowing date in Canterbury. The measurements are for Zephyr sown in 1977 (Drewitt and Muscroft-Taylor, 1978); the estimates are based on climatic records. Numbers in parentheses are yield and duration expressed relative to the values from the September sowing.

Sowing Date	Measured Yield t/ha	Measured Growth Duration days	Estimated Yield t/ha	Estimated Growth Duration days
Early September	4.7 (1.00)	146 (1.00)	6.4 (1.00)	143 (1.00)
Early October	4.8 (1.02)	119 (0.82)	5.5 (0.86)	123 (0.86)
Early November	4.6 (0.98)	106 (0.73)	5.0 (0.78)	112 (0.78)

TABLE 6: Comparison for average yields from drilled trials at Cambridge, England and Edinburgh, Scotland, in 1976 and 1977 (Ellis and Kirby, 1980) with estimates made from the model developed in the text and long term climatic records. Figures in parenthesis are yields expressed relative to the yields at Cambridge. See text for further details.

	Yields t/ha Cambridge	Yields t/ha Edinburgh
Trials	4.85 (1.00)	5.98 (1.23)
Estimate (water non-limiting)	5.3 (1.00)	5.7 (1.08)
($D_l = 100$mm)	4.7 (1.00)	5.7 (1.21)

The model was next applied to Canterbury conditions and used to predict the response of yield to sowing on 1 September, 1 October and 1 November (Table 5). As for English conditions, the *predictions* showed a strong advantage from early sowing. In contrast, the *measurements* of Drewitt and Muscroft-Taylor (1978) showed no such advantage. The predictions of growth duration for the two earlier sowings agreed well with the measurements, but the growth duration of the latest sowing was over-estimated. This may be because the effects of warm temperatures during grain growth are not given sufficient weight in the model. It is surprising that the measured decrease in growth duration of 30% brought no yield penalty. The model overestimated the actual yields, but other work at Winchmore shows yields of 6 t/ha to be quite possible (Drewitt and Smart, 1981). More recent experiments at Winchmore have shown an advantage from sowing in October rather than November (Drewitt, this volume). It is tempting to wonder whether, if the experiments were repeated, there might in some seasons be an advantage to sowing in September as the model predicts. Such is the nature of empirical research.

Climate

Statistical studies have frequently shown that cool summers are associated with large barley yields (Hooker, 1907; Jones, 1979). It is also known that within a small range of latitude cooler geographical regions have larger yields than warmer regions. An example of this is found in the United Kingdom; long-term statistical records show that Scottish yields are typically between 15 and 20% greater than English yields (Whitehouse, 1977). In an experimental study, Ellis and Kirby (1980) showed a 20% advantage to Scotland in drilled trials. To investigate the possible reason for these differences, the model was run using climatic data from Northumberland to represent the Scottish climate (because the climate is similar and records were readily available, not because Scottish meteorological records are unreliable!) and from Cambridge, and assuming a sowing on 1 April. This showed that differences in temperature could account for only about half of the observed differences in yield (Table 6). This was because the cooler northern temperatures which would prolong development were partially compensated by longer days accelerating development. The model predicted that the duration of growth in Scotland would be about six days longer than in England. Kirby and Ellis (1980) found a difference in the time to ear emergence of about a day in 1976, an exceptionally warm season, and seven days in 1977, a more typical season. If this latter difference is typical and maintained until the end of linear grain growth, the prediction of phenology by the model is acceptable.

Another cause of the difference in yield between England and Scotland may be that much of the English barley crop is grown in the south-east of the country, which is frequently subject to drought. A limiting potential soil moisture deficit of 100 mm — a reasonable average for the soils on which barley is grown in south-east England — was therefore introduced into the model and D_m was estimated from long-term records (Smith, 1976). Adding drought into the model in this way accounted for the 10% difference in yield that was unexplained previously by differences of photoperiod and temperature alone (Table 6). The result of this analysis is slightly different from Monteith's (1981a) suggestion that temperature alone might explain the difference between Scottish and English yields, but he was concerned to demonstrate a principle and to avoid complexity. It is likely that the better wheat and barley yields in Southland compared with Canterbury are due to slower development (cooler temperatures) and less severe drought.

In 1982, Canterbury experienced one of the most severe droughts in its history, and this section would be incomplete without attempting to use the model to quantify the losses in yield that can be caused by drought in Canterbury. The model was therefore used to estimate the response of barley yield to irrigation in three seasons, to compare with the experimental measurements of Drewitt and Smart (1981).

Calculations were made with the model using the same values for all parameters as in England. Penman's formula (French and Legg, 1979) was used to calculate potential evaporation. Measurements of evaporations from well-watered crops at Palmerston North (McNaughton *et al.*, 1979) showed that Penman's equation over-estimated actual evaporation; but it is not clear exactly how their calculations of evaporation were made, or whether net radiation was measured or estimated using an empirical, and sometimes inaccurate, formula (French and Legg, 1979; Wales-Smith, 1981). Heine and Ryu (1980) measured evaporation from a wheat crop in Canterbury and found that this was close to that calculated from Penman's formula during fast growth early in the season. Partly for this reason, but mainly to be consistent with the calculations made for English crops, we used the standard version of Penman's formula (French and Legg, 1979). The limiting deficit was set to 50 mm, a figure appropriate to the stony Lismore soils. The model is not very sensitive to the value of limiting deficit selected: a change of 25 mm changes the growth duration by about 6 days and yield by about 0.25 t/ha.

Figure 12 shows that the model tended to over-estimate yields in the wetter seasons, 1979 and 1980, but under-estimated yields in the dry (more typical?) season, 1978. For particular seasons therefore, the fit is poor, but the model seems to be giving a good *average* prediction of the influence of drought on these otherwise well-husbanded barley crops. It is surprising that the average crop growth rate of 95 kg/ha/d derived from the English measurements seems to hold in Canterbury with its sunnier climate where growth would be expected to be faster. But in the absence of any measurements of barley growth rates in Canterbury, this remains a matter for conjecture. Despite this possible anomaly, the results of these calculations indicate that the principles involved in the model, simple and crude though they may be, are adequate to describe the likely response to irrigation over a run of seasons. Further experiments are needed to investigate whether the predictions can be extended to other regions and soil types and, more importantly, if the principles on which the model is based are correct.

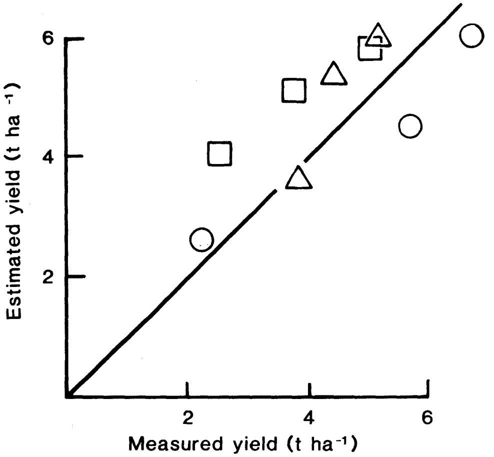

Figure 12: The relation between estimated and measured yields for crops of barley receiving different irrigation treatments in 1978 (○), 1979 (△) and 1980 (□); data of Drewitt and Smart (1981). The line x = y is drawn for comparison.

EXTENSION AND IMPLICATIONS

EXTENSION

The model which has been developed is simple. Its use is restricted to crops well supplied with nutrients, free from disease and (probably) grown in a restricted range of latitude and climate. The model is didactic rather than mechanistic. It could be extended to account for the effects of temperature on leaf expansion early in the season, but the need to take account of the influence of mineral nutrition and disease on growth and yield is more pressing.

Mineral nutrition

There is some evidence to suggest that it would be possible to describe the effect of a shortage of mineral nutrients on crop growth and yield in terms of lost time. The results of many experiments with small grains show that growth and yield are proportional to the uptake of a limiting nutrient until a plateau is reached when some other nutrient or factor is limiting yield (Van Keulen, 1977; Spiertz, 1980). In the absence of disease, and with adequate supplies of water and nutrients, this other factor is climatic — usually the radiation received by the crop (Van Keulen, 1977). When crop yield is limited by climate alone, as a first approximation the *minimum* demand of that crop for a nutrient is given by the product of the total dry matter production and the minimum concentration of that nutrient in plant tissues at maturity. If the demand of a crop for a nutrient exceeds the supply of that nutrient from the soil during crop development, then crop growth and yield will be restricted. In effect, an amount of time for growth will be lost due to nutrient deficiency and this time will be proportional to the difference between nutrient demand and supply. This is analagous to the time lost due to drought, which is proportional to the difference between atmospheric demand for moisture during growth and the supply of moisture from irrigation, rainfall and the soil (p. 35).

Where other factors in addition to nutrients limit crop growth, it is possible that the law of limiting factors would apply; growth duration would be determined by the factor in shortest supply, responsible for most lost time. This approach would probably account for the positive interactions found when different nutrients are supplied in combination. Though conceptually simple, the application of the concept of lost time in this way to shortages of nutrients ignores several practical problems, including the difficulty of estimating the rate of supply of a given nutrient from a particular soil, the efficiency with which applied nutrients are taken up by plants, and the interaction between the distribution of nutrients and moisture in the soil profile. None the less, the concept of lost time as applied to crop nutrition is probably still worth examining. It may provide crop and soil scientists with a useful and unifying framework for studying the effects of shortages of both soil nutrients and moisture on crop growth and yield. The idea of applying the concept of lost time in this way is included here as part of a wider appeal for simplicity, the simplicity that we believe is needed to make progress.

Disease

Another potent factor in decreasing yield is disease. Little is known about the interactions between crop, environment and pathogen, though it is known that mildew *(Erysiphe graminis)* can decrease the size of the root system of barley (Ayres and Zadoks, 1979; Scott and Griffiths, 1980). Presumably, such infections would decrease D_l for a diseased crop and make it more susceptible to drought. It is also known that disease can decrease leaf size in barley as well as the area of green leaf (Niffenegger *et al.,* 1965; Gaunt, this volume). As growth is proportional to the amount of light absorbed by the green surfaces of a crop (p. 30) then, in the absence of drought and effects of plant metabolism the loss of yield due to disease will be proportional to the difference in light absorption by green tissue between a healthy and a diseased crop. Such a difference would be laborious to measure directly, but using infra-red photography, or measuring the reflection of near infra-red radiation by crop canopies, it may be possible to measure the effect of disease on light absorption indirectly. The task of predicting the spread of disease will, none the less, remain.

Extension of models to take account of factors such as nutrients and disease will doubtless prove more difficult than outlined above, but the exercise needs doing, to help overcome the limitations of the advice that can be given from empirical experiments.

IMPLICATIONS

The relevance of the physiological knowledge reviewed in this paper is now examined in relation to farming practice, barley breeding and agronomic research.

Farming practice

There is good evidence that the yield of barley is strongly related to the amount of radiation absorbed by the green surfaces of a crop. In general, farmers should aim at establishing green crop cover early and maintaining it for as long as possible. Early sowing, providing that the soil is suitable for drilling, should help to achieve this aim. In England early drilling has consistently proved the key to larger yields on sandy soils which are prone to drought (Selman, 1977). There are three main reasons for the advantage. First, a longer period of growth is achieved. Second, early sowing appears to promote better root growth so that more moisture can be extracted from the soil, although there is little direct evidence for this. Third, the slower development before anthesis and the slightly cooler temperatures during grain growth are associated with bigger grains. In this respect, it should be noted that early sowing has always been recommended to growers of malting barley, providing the seedbed is good (Hunter, 1952).

If barley has to be sown late due to constraints of the farming system or rainy weather, then it is usually as well to sow more seed. This is because the faster development associated with late sowing usually depresses the value of all yield components except plants/m^2, and sowing more seed helps compensate for this (Kirby, 1969; Cannell, 1969; Jessop and Ivins, 1970). This certainly holds in areas of higher rainfall. In dry areas, the problem is more complex and it may be advisable not to alter seed rate. This is because yield will probably be limited by water supply. A low sowing density slows evaporation early in the season because the leaf area is slow to expand; it also provides a larger volume of soil and water to each plant. Both of these effects enable growth to continue for longer and bigger grains to be produced than if the water supply had run out earlier.

The limitations on yield caused by drought hardly need to be amplified here. It is sufficient to say that when water is needed the value of irrigation should be about 12 kg grain/ha/mm of water applied to and used by the crop, i.e. not including that wasted by drainage, evaporation, run-off or irregular distribution. It should be possible to tell when water is needed if the limiting potential soil moisture deficit is known from research or guessed from information about soil type and rooting depth. For barley, this limiting deficit will vary from less than 50 mm on shallow light soils to about 150 mm on deep moisture-retentive soils.

Plant breeding

Donald (1968) suggested that the selection programmes of plant breeders are essentially a combination of two philosophies, "defect elimination" and "selection for yield". He also pointed out that crop physiological knowledge had reached a stage at which it should be possible to predict which characters would enable a plant to yield well in a given environment. Donald called a hypothetical genotype with an ideal combination of morphological and physiological characters a crop *ideotype*, a type of plant "expected to yield a greater quantity or quality of grain .... when developed as a cultivar", and went on to describe a wheat ideotype designed to give high yields in an environment where nutrients and moisture were plentiful. These ideas were subsequently used in a barley breeding programme (Donald, 1979). Barley was chosen for this programme simply because single-stemmed varieties were immediately available and the "uniculm" habit was a central feature of Donald's (1968) cereal ideotype. In the context of this paper, two questions are relevant: Is Donald's cereal ideotype suited to the New Zealand environment? Has new knowledge suggested any changes to the ideotype? To answer the first question, it is probably necessary to distinguish two broad types of environment within New Zealand: those with adequate water (often supplied by irrigation) and abbreviated here to moist; and those subject to drought, abbreviated here to dry. These environments may have different requirements in terms of a crop ideotype which will consistently yield well. The word consistently is important. It will be assumed here that in a dry environment a variety producing a reliable yield would be more desirable than a variety producing yields which fluctuate markedly with season, albeit with the same mean long-term yield. Bearing the two environments in mind, the second question raised above will be answered by reconsidering Donald's original ideotype, the features of which were:

1. *A short strong stem.* Donald stipulated this characteristic both to help prevent lodging and to promote large ear size by decreasing the competition between the developing ear and the stem for resources needed for growth. Short, strong stems would certainly be needed in the moist environment for the reasons above, and probably in the dry environment for other reasons (see 5 and 8 (c) below).

2. *Erect leaves.* This was originally included because erect leaves are associated with a more even distribution of sunlight over the total leaf area, which should result in a faster rate of canopy photosynthesis, particularly in conditions of bright light with the sun high in the sky. However, in a comprehensive review, Trenbath and Angus (1975) concluded that: "In cereals achieving their maximum LAI when solar elevations are lower, e.g. during spring in a Mediterranean-type climate, models and experimental data agree in suggesting that leaf inclination is unimportant." Indeed, for the moist environment a prostrate habit during early growth which ensured that the ground was soon covered by leaves would probably be an advantage (Monteith, 1981b). Thereafter, leaves should be more erect, but this would not seem to be an urgent priority. In fact, the leaves appearing at the top of the canopy where the light is brightest are erect as a result of their growth pattern, as are the leaf sheaths and the ears, all of which are capable of fast photosynthesis (Biscoe, Gallagher *et al.*, 1975).

For a variety adapted to a dry environment, erect leaves would be more advantageous. This is because their irradiance would be smaller than for near horizontal leaves of the same area; this should result in slower transpiration and, in times of drought when stomata close, cooler leaves (Trenbath and Angus, 1975). A canopy of erect leaves would also intercept less radiation and, at least early in the season before LAI is greater than three, this should result in slower evaporation from the crop, leaving more water in the soil for use later in the growing season. This interpretation neglects evaporation from the soil, but it should be a simple matter to use a model to predict the magnitude of any advantage over a run of seasons.

3. *Few small leaves.* Donald preferred small leaves, because he believed that their dispersion would be more regular and would allow faster photosynthesis; and few leaves, because he believed that this characteristic would be associated with a larger ear. Donald's contention about leaf number has subsequently been substantiated by work showing a gradual decline in leaf number from more than nine leaves per mainstem for varieties bred in the last century to about eight for recently bred varieties (Riggs *et al.*, 1981). There appears to be little direct information about the precise effects of leaf size. For the moist environment, leaf size should be larger than in a dry environment, in particular leaves might be wider to ensure full light interception. It would also be interesting to know if there were varietal differences in leaf dispersion, as a regular dispersion should lead to faster growth in the moist environment. For the dry environment narrow leaves would be preferable, mainly because sensible cooling is faster, and this would be important in preventing over-heating during stomatal closure (Gates, 1980). A clumped distribution of leaves might also be advantageous for the dry environment as this would slow evaporation from both crop and leaves.

4. *A large ear* (many florets per unit of dry matter). Donald believed that this characteristic would be important in producing a large harvest index in the uniculm ideotype with which he was concerned. But he also feared that any effects might be hard to detect because of interactions with the ears per plant and kernel mass components of grain yield. His fears were well-founded, as in a comparison of a wide range of barley varieties, Riggs *et al.* (1981) found no significant correlation between yield per ear and either harvest index or yield. None the less, in principle Donald was probably correct, at least for favourable environments; the number of grain-bearing florets per ear should not decrease markedly in response to a short period of unfavourable environmental conditions. On the other hand, in a dry environment, what Donald called 'conservative' behaviour with respect to grain formation is probably needed. By this he meant that the yield components determining the number of grains per plant should show such reduction in relation to past and current environmental conditions as to offer a high probability that the load of growing grain would be within the photosynthetic capacity of the plant to bring it to maturity. This ability seems important if well-filled grains are to be produced in an environment that is subject to drought.

5. *An erect ear.* This characteristic was required so as to achieve good illumination of the photosynthetic tissue of the ear. Most barley cultivars have an erect ear while they are green and photosynthetically active. Thereafter, for many New Zealand regions, an important consideration must be to breed for an ear disposition and form to minimize wind drag and the possibility of ear-shedding in strong winds. Perhaps a short thick peduncle and an arcuate rather than a hooked ear are needed.

6. *The presence of awns.* The desirability of this trait was simply related to the significant contribution made by awns to the assimilate needed for grain growth. In barley, this may be manifest in large kernel mass and hectolitre mass rather than bigger yields (Shannon and Reid, 1976). Most barley cultivars have awns, but the amount of awn tissue per ear differs between cultivars (Johnson *et al.*, 1975). These workers found that breeding lines differed in both the rate at which awn photosynthesis declined with age and the amount of photosynthesis per unit of awn mass — on this basis, dense ears (i.e. ears with many spikelets per unit of length) had a poorer photosynthetic efficiency. Faris (1974) studied four 6-row barley lines, isogenic except for awn lengths which were 0.4, 2.8, 45.1 and 100 mm respectively. He found that in moist conditions the line with awns of 45 mm yielded best. There is therefore little firm evidence for suggesting changes to awn length in the moist environment, though if large grain were an objective of a breeding programme, long awns would probably be a desirable trait (Faris, 1974; Shannon and Reid, 1976).

For the dry environment, long awns with a slow rate of senescence would seem desirable, as the value of awns in dry environments is well established (Vervelde, 1953; Biscoe *et al.,* 1973). Because of their small width, sensible transfer of heat from awns to the atmosphere is fast, and awns will not rise much above air temperature even if their stomata close.

7. *A single culm.* Donald preferred a uniculm plant for two main reasons. First, in multiculm varieties, more tillers are formed than eventually bear grain, and the barren tillers may be considered a wasteful diversion of assimilate and mineral nutrients, only some of which are translocated back to the parent plant before death. Donald felt that this waste of resources might limit the size of ears on tillers which did bear grain. Second, the loss of water through transpiration from tillers destined to be sterile is wasteful and this is probably significant in drier environments. Work by Kirby and Jones (1977), in which tiller buds were removed surgically, supported the idea that tillers that are destined to be barren divert resources which would otherwise be used to produce longer ears on the main-stem and surviving tillers. They also found (Jones and Kirby, 1977) that restricted tillering led to greater grain yield and better water use efficiency when water was in short supply.

Riggs *et al.* (1981) showed that an important characteristic associated with the higher yields of modern barley cultivars was better tiller survival; with little difference in the maximum numbers of tillers formed by old and new cultivars, the newer ones produced more ears/m^2. For a moist environment, high tiller survival or better tillering efficiency (Gallagher and Biscoe, 1978a) would seem to be an important target for breeders. The extreme of a uniculm habit is probably desirable only in environments where pest attacks can be prevented and plant establishment is always good. For a dry environment the advantage would seem to lie with a cultivar producing two tillers at most. This should slow evaporation from the crop early in the season, and leave more water for the plants to use during grain growth.

8. *Other characters. (a) Maturity.* A cultivar bred for a dry environment should have an early maturity date. This is to enable grain growth to occur in early summer, when potential evaporation is slower and drought less severe. One problem with this might be susceptibility to frost damage during certain phases of reproductive development. This problem may be easily and quickly studied in a controlled environment, and, if necessary, cultivars could be screened for tolerance to frost.

(b) Leaf area duration. The persistence of green leaves after anthesis is often associated with heavy grain yields (e.g. Evans, Wardlaw and Fischer, 1975). Donald thought that pursuit of a large leaf area duration after anthesis *might* be a worthwhile goal. This is almost certainly true for dry environments, as the main reason why barley yields poorly in drought is that green tissues die prematurely (Legg *et al.*, 1979). Little is known about the physiology of senescence of cereal leaves in the field (most plant physiologists prefer to study the senescence of cotyledons in the dark!) and the work of Pattterson and Moss (1979) and Patterson *et al.* (1980) on the senescence of wheat leaves in the field appears to be unique. Genetic differences in the rate of leaf senescence of barley have been reported but their influence on yield may be complicated by pleiotropic effects (Quizenberry, 1982). More information is needed about genetic variation in leaf and ear senescence in relation to drought. For the dry environment, cultivars are needed which do not shed their leaves if subjected to drought, and possibly they should be able to roll their leaves and expose a surface of high reflectivity in response to dry spells. These traits should lessen the radiation absorbed by leaves, slow transpiration, and help to minimise differences between leaf and air temperature, and thereby slow senescence.

(c) Stem sugars. Donald believed that the ability to accumulate a large amount of sugar in the stem and translocate this subsequently to the ear might be a characteristic associated with better yields. This characteristic may be less desirable in moist environments where photosynthesis after anthesis should be fast and leaf area duration long. Photosynthate produced before anthesis would probably be used to better effect if it were used to form large ears with many grains.

In dry environments though, it would seem essential that the plant be able to accumulate much water-soluble carbohydrate in the stem, to be used for grain growth if drought caused slow photosynthesis after anthesis. This can be regarded as an expensive insurance policy. A large premium is paid by the plant each year in the form of sugar accumulated in the stem, mainly before anthesis. A claim is made only in dry years, when the sugar in the stem is used to ensure that grains grow to a certain minimum size. This behaviour means that sugars in the stem would be wasted in wetter seasons when photosynthesis after anthesis is adequate to fill the grain. Unless these stem sugars are respired away when not needed — and Pearman *et al.* (1981) reported this to occur in wheat — then this behaviour results in a variable harvest index: large in dry, unfavourable seasons, and small in moist, favourable seasons. Analysis of published measurements shows that harvest index is positively correlated with kernel mass (Day *et al.*, 1978, 1981; Donald, 1979; Kirby and Appleyard, 1980) with a regression coefficient of between 0.005 and 0.01 increase in harvest index per mg increase in kernel mass. It would be instructive to know whether cultivars or lines exist which do not have this correlation.

Recent studies with wheat have shown that there are genetic differences in the ability to store sugars in the stem (Innes and Blackwell, 1981a). It would be interesting to find such differences in barley, and to see where this line of research leads.

(d) The root system. Donald simply pointed out that his uniculm ideotype would place greater reliance on the seminal root system. Grown in pots 1.2 m deep, Donald's (1979) uniculm line produced 66% more root DM than the standard-tillered lines. There was, however, no difference in the distribution of the roots down the soil profile. Recently, the desirability of different rooting patterns and morphology has been carefully examined (Meyer and Alston, 1978; Passioura, 1981). It is clear that the best pattern and morphology for roots vary with soil type and the environment. For dry environments it would seem that

a slow but steady growth of roots is needed throughout the life of the plant, the aim being to ensure a more gradual and thorough exploitation of soil moisture resources. Most measurements show a slowing down of root extension at about the time of anthesis (Biscoe, Clark *et al.*, 1975; Day *et al.*, 1978; Gregory *et al.*, 1978) which may be unfortunate, as grain yield in dry environments is crucially dependent on water supplies after anthesis (Fischer, 1981; Passioura, 1981).

Another useful characteristic for dry environments would be a greater hydraulic resistance to the flow of water from the root surface to the stem, which might be achieved by decreasing the number of nodal roots, or the diameter of the main xylem vessels (Richards and Passioura, 1981b).

The following characteristics were not specifically dealt with by Donald:

(e) Leaf photosynthesis. In moist environments the LAI of crops will be large, and the young leaves at the top of the crop will be erect (p. 41) so the *average* irradiance of leaves will not be great. The young leaves in the brightest light at the top of the canopy will also have the fastest maximum rate of photosynthesis and will be light saturated only at irradiances greater than about 200 W/m^2 PAR (Biscoe *et al.*, 1975; Charles-Edwards and Ludwig, 1976). There may therefore be little point in breeding for faster rates of leaf photosynthesis. Indeed, the history of the domestication of wheat has been one of steadily decreasing the maximum photosynthetic rate of individual leaves (Evans and Dunstone, 1970).

In contrast, an ideotype for a dry environment probably should have high rates of individual leaf photosynthesis. This is because the total leaf area of the sparsely tillering, small-leaved crop will be small, and the irradiance of leaves large, despite their erect habit. In these circumstances, fast leaf photosynthesis will be needed, to ensure that light energy is not wasted and high water-use efficiency is achieved (Fischer and Turner, 1978).

(f) Grain growth. Kernel mass seems to be low in crops which develop at high temperatures, because the rate of kernel growth shows an optimum with respect to temperature whereas the development rate of the grains increases linearly with temperature (p. 27). There is no doubt that if air temperatures exceed about 25 °C for a long period, the grain size of temperate cereals is less (Sofield *et al.*, 1977; Chowdhury and Wardlaw, 1978). It seems important to find whether there are differences between genotypes in the response of grain growth to temperature, and to study the influence of short periods of warm temperatures on grain mass. For much of the South Island of New Zealand, cultivars are needed in which kernel mass will not be decreased by short episodes of high temperature such as occur during afternoons when a north-west wind is blowing.

(g) Grain quality. As always, any barley cultivar should malt well and have a large hectolitre weight. Cultivars with a more favourable balance of amino acids are needed for feeding animals and poultry.

Caution

Many crop ideotypes have been advanced, both to stimulate thought and to provide guidance for plant breeders. In practice, the warning given by Fischer (1981) should be heeded: "The intention may be good but frequently insufficient consideration is given to the full ramifications of recommended traits in the context of dryland crops, and little or no attention is given to the verification of these recommendations". None the less, as our understanding of crops and their environment improves, it should be possible to explore the yield response of different ideotypes to a range of New Zealand environments using simulation models. This type of research is cheap in resources and would seem an essential first step before embarking on a breeding programme to produce an ideotype; it would certainly expose areas of ignorance where further research might be profitable. If theoretical studies of this type can identify ideotypes suitable to particular New Zealand environments, it may become possible to engineer the required combination of genes selected from the resources of international centres for crop improvement and genetic conservation.

Agronomic research

There is a continued need for experiments, not to produce yet more empirical results on how agronomic practices affect yield, but rather to provide a better *understanding* of the factors controlling yield. Such experiments must be multidisciplinary and include study of the soil as well as crop husbandry, physiology and microclimate. This will undoubtedly mean that fewer experiments will be done. But this need be no great loss if the improved understanding gained from such work can be used to build models which will accurately predict the yield resulting from different husbandry practices, soil types and climates. Such models will be more complex than the one described here. Hopefully, they will be able to predict the size of the various yield components and indicate the likely quality of the grain produced. Used in conjunction with long-term weather records, such models should be able to establish the outcome of different husbandry practices over many seasons, information that should be valuable in determining the profitability of different farming systems.

In more practical terms, studies should be made of the influence of sowing date on yield so as to explain the discrepancy between theory and experiment in New Zealand (p. 38). Similarly, work is needed to test more rigorously the validity of Penman's irrigation response model under New Zealand conditions (p. 39). The possibility of genotype x environment interactions of the type implied in defining barley ideotypes for dry and moist environments would also repay study.

With respect to the last two projects, it is pertinent to recall a well-established law known to all experimentalists. Put in its general form it is that: "Whenever you do not want an event to occur, it will, and at the worst possible moment". For experiments investigating drought the event is rain. To be able to study the influence of drought on crop yield efficiently and systematically, large mobile rain shelters are needed, such as those used successfully by Arkin *et al.* (1976), Day *et al.* (1978), Foale *et al.* (1979) and Innes and Blackwell (1981b).

CONCLUSION

It is salutary to end in a similar way to that in which we began.

"From the facts emerging in this analysis the interrelations of the processes determining growth are shown, and the interaction of the climatic complex with the internal factors. This analysis is in the nature of a preliminary survey of the physiological aspects of the problem of the adaptation of the plant to the environment. As suggested in the introductory remarks, the way is indicated towards a true agricultural physiology, which may restate in precise terms much that at present is empirical knowledge. The study of the plant as a whole is needed to test conclusions drawn from laboratory experimentation with single organs where previous history has been assumed to be unimportant, and on single phases of the total life-cycle, whose chief characteristic is an intrinsic unity" (Gregory, 1926).

We hope that Professor Gregory would not be too disappointed with the progress made along the way he so clearly indicated more than fifty years ago.

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DISCUSSION

Gaunt: Do you consider that in our environment the root growth is adequate to tap all the moisture available?

Gallagher: It is an important point. It is clear from sowing date experiments that later sown crops have less root development and as a consequence cannot tap as much soil water. In drier seasons the decline in yield with delayed sowing is magnified. I would imagine if fungi slow down root growth that will mean there is less water available to the plants and they are more susceptible to drought.

Coles: It is suggested that over the last 20 years the only improvement in yield that breeders have made is to increase harvest index. Given that it seems likely that we have reached the limit in improved harvest index with Southern cultivars, where in physiological terms can a breeder look in terms of your equation for further yield improvement?

Gallagher: I don't think we have gone all the way with harvest index: I put it at 0.47 and in absolute terms that gives a reasonable prediction for the crops that were grown. I think the limit is about 0.60, possibly 0.65.

We certainly need to continue with disease resistance. For the soils here we want consistency of performance and we might get more consistency if we had cultivars with deeper roots, but you are probably selecting for this via yield normally. Perhaps faster leaf expansion in the spring, but this results in smaller leaves and if you select for bigger leaves you get slower leaf appearance. You could select for greater photosynthetic rates but for various reasons I'm not sure that this is going to be a winner. Maybe I am suggesting that the advance of yield may cease by the turn of the century.

Wall: There is a belief in farming circles that you shouldn't sow barley too early; the ground should be warm at drilling as any check to growth is detrimental. What is your comment on this especially with regard to root depth and do you know any physiological reason why early sowing harms potential yield?

Gallagher: Physiological reasons, no. Sowing date experiments in the U.K. show the earlier the better. I would estimate that in Canterbury you lose 15% of the yield by delaying until 1st Oct. compared with 1st Sept. but that doesn't take into account seedbed conditions. Obviously if you sow into a saturated seedbed the results are not going to be very good but on sand-land farms in the U.K. if they can drill the equivalent of July they will, and in a dry year they will get a yield advantage. So if you can drill in good conditions I say the earlier the better — dare I say it — but May is the time to be drilling.

Kearney: Has there been any work done on soil temperature to determine what is "early"?

Gallagher: In terms of emergence rate there is a linear response between 0 and 20 °C. The warmer the temperature the faster the emergence, leaf appearance and tillering. So provided the soil temperature is at or above 0 °C seedlings will emerge.