Rates and Cardinal Temperatures for Processes of Development in Wheat: Effects of Temperature and Thermal Amplitude

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Abstract. This paper addresses three issues relating to development in wheat. Whether thermal amplitude changes rates of leaf appearance and phenological development, whether the responses of leaf appearance to a wide range of temperature can be acceptably described in terms of rates and cardinal (base and optimum) temperatures, and whether similar rates and cardinal temperatures can be applied to parallel processes of development. The two studies used a total of 22 naturally-lit growth chambers and 44 treatments, and the disparate wheat cultivars Sunset, Condor, Rosella and Cappelle Desprez. All plants were vernalised and then grown under photoperiods extended to 18 h. In the first study, thermal amplitudes varying between 0 and 14°C around a common mean of 19°C did not change rates of leaf appearance and had no consistent effect on phenological development at any stage to anthesis. Consequently, conclusions from data collected under one amplitude at this mean temperature can be extrapolated with confidence to another. In the second study, with six mean temperature regimes of 10–25°C, rate of leaf appearance was significantly increased progressively by increasing temperature up to 19°C. All cultivars had an optimum temperature for this process which approximated 22°C but they differed in their base temperatures which ranged from –5.7 to –1.9°C. Optimum and base values for the concurrent phase of phenological development ranged between similar extremes, but the rankings of base values amongst genotypes differed markedly for leaf appearance and phenology. For the process of culm extension, temperature significantly, but not linearly, affected final length but not internode number. Length was unchanged by temperatures between 10 and 16°C but was significantly reduced above 19°C. Cultivars differed in their respective optimum and base temperatures for rate of elongation, ranging from *ca* 19 to 21°C and from 2 to 5°C. The concurrent phenological process had a higher optimum of 22–25°C but again a similar range in base temperature with differing cultivar rankings. We conclude from the second study that cardinal temperatures for leaf appearance, culm elongation and phenology were different, and for each process there were cultivar differences.

Introduction

The aim of the present paper was to examine the effects of temperature on the rate of appearance of leaves in wheat. The specific questions asked were:

(*1*) Is it solely mean daily temperature that controls the rates, or does the range between maximum and minimum for the same mean also have an impact?

(*2*) What is the pattern of response to a wide range of mean temperatures? Can it always be described by a simple linear relationship between standard cardinal temperatures such as are used in thermal time models to describe phenological development?

(*3*) If the use of common cardinal temperatures is feasible, do the same values of base and optimum apply to other processes occurring at the same time in ontogeny or do different processes have different cardinal temperatures?

(*4*) Do the same cardinal temperatures apply to divergent genotypes?

Thermal Amplitude

It may seem rather elementary to ask whether development is driven by mean temperature *per se*, particularly as most controlled-environment studies assume this, and most computer models which calculate plant time via thermal time summations, use it. But rather surprisingly, the experiments to test it are sparse.

There is no doubt that thermal amplitude does have a significant influence on some physiological attributes. For example, the effect on break of seed dormancy is well documented (e.g. Benech Arnold *et al.* 1988). Similarly, rate of germination can be changed by thermal amplitude. Thus, in pearl millet, the greater the thermal amplitude between 0 and 8°C, the faster the rate of development (Garcia-Huidobro *et al.* 1982*a*, 1982*b*, but see Wagenvoort and Bierhuizen 1977 for findings of no effect of amplitude with several vegetable species).

Aside from the studies on germination, there are few studies on the effect of temperature amplitude. However, those that are available on the rate of phasic development appear to justify the assumption that mean temperature *per se* does drive development. Went (1944) hypothesised that day and night temperature differentially affect plant development, however, there has been little support for his hypothesis. Moe (1990) found no effects of thermal amplitude on phasic development in the long-day plant *Campanula isophyla*, though there were large effects on stem elongation. Ellis *et al.* (1990) with tomato, and Summerfield *et al.* (1992) with rice, also found no support for the hypothesis. Ellis *et al.* (1988), working with barley, did support Went's hypothesis, but reached their conclusions by comparing results from discrete experiments. To the best of our knowledge, no appropriate results have been published for wheat.

We argued that before we could extrapolate any conclusions from controlled-environment constant temperature regimes to other temperature environments, and particularly to the field where thermal amplitude varies daily, it must be established whether thermal amplitude alters rate of development (the reciprocal of duration) and, in particular, whether leaf emergence rate is changed.

Leaf Appearance Rates and Cardinal Temperatures

Leaf appearance rate is a major component of crop leaf area development which finally determines the interception of radiation and potential crop growth (Gallagher and Biscoe 1978; Fischer 1983; Slafer *et al.* 1990; Loomis and Connor 1992). Consequently, it has been the subject of many studies, particularly in wheat (Baker *et al.* 1980; Kirby *et al.* 1982; Delecolle *et al.* 1985; Kirby and Perry 1987; Hay and Delecolle 1989; Masle *et al.* 1989*a*, 1989*b*; Stapper and Fischer 1990; Cao and Moss 1991*a*).

There is no doubt that, of all environmental factors, temperature has the greatest influence on this rate. Although several methods have been described to quantify temperature effects on crop development (Major *et al.* 1975), the daily summation of mean temperatures between the two thresholds of base and optimum temperature (cardinal temperatures), called thermal time (with units of degree days,°Cd), is probably the most widely accepted

(Monteith 1984). This has been used extensively to analyse, or predict through computer simulations, the dynamics of leaf appearance (e.g. Gallagher 1979; Baker *et al.* 1980; Kirby *et al.* 1982; Bauer *et al.* 1984; Stapper 1984; Delecolle *et al.* 1985; Kirby *et al.* 1985; Baker *et al.* 1986; Hay and Delecolle 1989; Kirby *et al.* 1989; Cao and Moss 1991*a*, 1991*b*; Hay and Kirby 1991; Kirby 1992; Cao and Moss 1994; Slafer *et al.* 1994).

The method is also useful for making rough calculations. For example, if it is known that a new leaf appears every 100°Cd under particular conditions, that information can be used to guess that it will take 5 days at a mean temperature of 20°C and 10 days at a mean of 10°C (assuming that the base temperature is 0°C and the optimum is greater than 20°C). By extension, seven leaves will take about seven times as long to appear (e.g. Rawson 1988 and see Slafer and Rawson 1995*a* for a discussion of the calculation of the parameters used). The great strength of the method is its convenience, not that it holds any physiological significance, and that it seems to work acceptably in a range of environments.

The method has been applied primarily to the results of field studies. As most computer simulations of leaf appearance rate are intended for use in the field, this is clearly appropriate. However, there is a potential weakness in attempting to calculate cardinal temperatures from field data. In the field, environmental variables such as temperature, radiation and photoperiod, covary, but in different combinations at different locations. If the responses to temperature are affected by the responses to the other variables, the cardinal temperatures calculated may be at worst, site-specific, or at best, not portable between very different locations. A further related problem is that these environmental variables also independently affect phenological development which in turn may modify leaf appearance rates.

One way to ensure that the cardinal temperatures calculated are free from interference from environmental variables other than temperature, and free from feed-back from phenological development, is to calculate them for plants grown under long photoperiod and after vernalisation. In such plants, phenological development will be occurring at the fastest rate possible for the genotype. Such a data set would also answer the question about whether cardinal temperatures are inherently the same for different genotypes, as the potential variation between genotypes arising from varying response to photoperiod and vernalisation would have been negated.

Cardinal Temperatures to Describe Different Processes

It has been suggested that the cardinal temperatures for phenological stages rise steadily with plant development. Thus, base values increase from below zero at germination

to above 7°C during grain filling, while optimum values rise from less than 22°C to more than 25°C (see discussions by Angus *et al.* 1981; Del Pozzo *et al.* 1987; Porter *et al.* 1987; Ellis *et al.* 1988; Morrison *et al.* 1989; Slafer and Savin 1991; Slafer and Rawson 1995*a*). What apparently has not been addressed is whether the same cardinal temperatures can be applied to different processes occurring in parallel during development. Thus, is the same base temperature applicable for leaf appearance rate during early vegetative growth as for phenological development between plant emergence and terminal spikelet? Similarly, are the cardinal temperatures for stem elongation the same as for the simultaneous process of phenological development between terminal spikelet and anthesis? Clearly it would simplify the prediction of the durations of different processes if cardinal temperatures for one process could be assumed from the cardinal temperatures of another.

The Studies

We conducted two independent studies although both had the same four contrasting genotypes with the same pretreatments, in both, all plants were grown under long photoperiod in sunlit growth chambers, and in both all environmental treatments were duplicated in separate chambers. The two studies meant that we could look for internal consistency of response of genotypes, and the duplication of chambers meant that we could have confidence that the results were not chamber-specific.

In the thermal amplitude study we used one mean temperature but varied the amplitude around that mean in five combinations between 0 and 14°C. All combinations used a smooth and continuous sine wave-shaped change in temperature between the maximum and minimum for the day. This was an attempt to come closer to the field pattern than the step changes of temperature which are more commonly used in controlled-environment studies. The study used 10 growth chambers.

In the study which examined leaf appearance rate and cardinal temperatures for various processes and stages of development we used six constant temperature regimes between 10 and 25°C. This study used 12 growth chambers.

Materials and Methods

Genotypes

Cultivars were chosen to represent different developmental sensitivities to environmental factors. They were Sunset and Condor (Australian spring wheats), Rosella (Australian semi-winter wheat), and Cappelle Desprez (French winter wheat). Sunset is practically insensitive to either photoperiod or vernalisation while Condor is moderately sensitive to photoperiod and slightly sensitive to vernalisation. Rosella and Cappelle Desprez are respectively moderately and strongly sensitive to both photoperiod and vernalisation (for more details see Slafer and Rawson 1995*b*).

Common Pretreatments and Growing Conditions

Seeds were sown in a presoaked 50/50 mixture of vermiculite/perlite at a rate of three seeds per 100×150 mm pot (vol. 1.18 L), and retained at room temperature for 1 day. The pots were then transferred for 50 days to a cool-room (*ca* 4°C) with low-intensity fluorescent lamps (150 μmol m^{-2} s^{-1}) providing a light period of 8 h. The beginning of the experiment was defined as the day when the pots were removed from the cool-room to sunlit chambers in the Canberra phytotron (Morse and Evans 1962). In those chambers the total light period consisted of 9 h of natural radiation that was artificially extended for 9 h with low-intensity incandescent lamps of about 10 μmol m^{-2} s^{-1} PAR. All pots were supplied with complete Hoagland nutrient solution each morning and with water each afternoon. The studies were carried out in duplicate chambers for each temperature regime, and within each chamber cultivars were arranged in three blocks, i.e. there were six blocks in total. Within a block each treatment consisted of four pots. Pots were arranged in a square pattern throughout the study, and were touching their neighbours, so that there were about 300 plants m^{-2} initially.

Photosynthetically active radiation inside the glasshouses from early March to the end of June when all experiments were done averaged 26.5, 21.5, 13.9 and 10.7 mol m^{-2} day^{-1} for March, April, May and June, respectively.

Plant Handling and Measurements

Every 2 days after the appearance of the third leaf on the main culm, one plant was randomly selected for dissection (see Gardner *et al.* 1985 for stages of apex development) within each pot (six plants per treatment). Different pots were used at consecutive harvests, so that the sampling procedure was also a thinning mechanism throughout plant development. At terminal spikelet initiation, plants were reduced to one per pot. For each of the four plants left per replicate (i.e. 24 plants per treatment), the dates of appearance of the tip of the glume of the uppermost spikelet above the flag-leaf sheath (heading) and the extrusion of the anthers out of the central spikelets (anthesis) were recorded.

Two plants per replicate of each treatment were tagged with coloured rings 1 week after the coleoptiles emerged from the soil. The number of leaves per main culm was recorded on tagged plants every 2–3 days following the method of Haun (1973). Regression analyses were used to estimate rates of leaf appearance (RLA) for each cultivar. For that purpose, the number of leaves on the main stem was regressed against time for each treatment, and RLA was estimated as the slope. Phyllochron was then calculated for each treatment as the slope of the relationship between days after beginning the experiment and leaf number. This was preferred to calculating it as the reciprocal of RLA, since this procedure yields estimates of both phyllochron and its standard error.

Differences Between the Thermal Amplitude and Cardinal Temperature Studies

In the thermal amplitude studies, five different day/night temperatures with a common average of 19 ± 0.6°C were used. The regimes were 19/19, 21/17, 22.5/15.5, 24/14 and 26/12°C, which represent daily thermal amplitudes of 0, 4, 7, 10 and 14°C. In all cases, temperature was varied following a 12 h sine wave.

In the cardinal temperature studies, constant temperatures of 10, 13, 16, 19, 22 and 25 ± 0.6°C were used. Stem height was an additional concern to that of leaf emergence and phenology and was estimated as follows. After anthesis, the length of the main-culm was measured from the soil surface to the base of the spike and the number of elongated internodes (those longer than 1 cm) was counted in each of the four plants per sub-plot. Although culm elongation can begin soon after floral initiation (e.g. Aitken 1961; Hama Rashid and Halloran 1984), in the present studies it started after the appearance of the terminal spikelet, judging from the dissections. In fact, several results from field experiments show that the stage of 'spike at 1 cm' (when the spike is 1 cm above the crown) coincides with initiation of the terminal spikelet (Kirby et al. 1985; Masle 1985; Kirby 1990; Stapper and Fischer 1990). Thus, we have considered here the rate of culm elongation simply as the ratio between final culm length and the duration of the phase from terminal spikelet appearance and anthesis.

Analyses

Analyses of variance considering temperature or thermal amplitude (depending on the study), cultivar, and their interactions, were performed on all the variables in both studies. Regression analyses were used to estimate the effect of temperature on rates of leaf appearance, or on phenological development, or on stem extension. Base temperatures were calculated from the intercept and slope of these regressions as in Slafer and Savin (1991). The standard errors for base temperatures were calculated following the method for predicting a value of X corresponding to a particular value (in this case the origin) on the Y-axis, as described in Snedecor and Cochran (1971).

A proper statistical procedure to estimate optimum temperature (the temperature for the maximum rate of development or growth) would be to use a 'split line model' (see Potter and Ross 1979; Thomas et al. 1980). This model allows an accurate determination of the breakpoint of the relationship between rate of development and temperature that corresponds to the optimum temperature. However, this procedure could not be used here as there were never more than one to two data points beyond the optimum temperature. Optimum temperature was estimated to be that corresponding value on the X-axis where the line for the regression of increasing rate with temperature intercepted the line (fitted by eye) of decreasing rate with temperature. This procedure is not precise and allows us to identify only general trends rather than exact values of optimum temperatures. Thus, we present data calculated for this cardinal temperature at a resolution of only 0.5°C.

Results

Thermal Amplitude and Leaf Appearance Rates

Cultivars differed significantly in the final number of leaves produced on the main shoot, from 5.5 to 5.8 in the spring wheats Sunset and Condor, to 6.4 in Rosella, and to 8.1 in the winter wheat Cappelle Desprez. Thermal amplitude did not significantly change these leaf numbers. In each of the 20 treatments, numbers of leaves emerged at any time was significantly linearly related with plant age,

with coefficients of determination always being higher than 0.97. The rates of leaf appearance, derived by the procedure, were unchanged by thermal amplitude in any of the genotypes (Table 1), so phyllochron followed no trend with thermal amplitude. Interestingly, in this study in which environmental conditions encouraged rapid phenological development (i.e. the mean temperature was close to the optimum), there were minimal differences in phyllochron between genotypes.

Thermal Amplitude and Phasic Development

Averaging across temperature regimes, genotypes differed in time from the beginning of the experiment to anthesis by 2 weeks, with Sunset and Condor each taking 40 days, Rosella 43 days and Cappelle Desprez 54 days. However, across cultivars, the effects of thermal amplitude on this duration were minimal with mean values for progressively increasing amplitude being 43, 46, 44, 45 and 44 days for 0, 4, 7, 10 and 14°C respectively. Sunset and Cappelle Desprez took slightly but significantly longer to reach anthesis at 4°C amplitude than in other thermal regimes, but we have no explanation for this behaviour.

We next tested whether thermal amplitude might differentially affect the duration of different developmental phases, analysing separately the phase of leaf and spikelet primordia initiation (i.e. from the beginning of the experiment to terminal spikelet initiation) and the phase of stem elongation (from terminal spikelet initiation to anthesis, cf. Kirby 1990; Stapper and Fischer 1990). The analysis showed that thermal amplitude did not systematically change the durations of these phenophases in any genotype (data not shown).

It was concluded that the effects of thermal amplitude at this mean temperature on both phasic development and leaf appearance rate were negligible, and did not follow any particular pattern, so they can be ignored. By corollary, conclusions from data collected under one amplitude can be extrapolated with confidence to another.

Final Leaf Number and Leaf Appearance Rate—Response to Temperature

In the second experiment, as in the first, cultivars differed in their final number of leaves, with Sunset, Condor, Rosella and Cappelle Desprez averaging 5.5, 5.9, 6.4, and 8.2 leaves on their main culms respectively. These numbers did not change significantly with temperature regimes between 10 and 25°C, with the exception of Cappelle Desprez. But even in that cultivar the effect was less than 0.8 leaves for the whole range of temperatures used.

In each of the 24 treatments, leaf number was linearly related to plant age with all r^2 values for the regressions being 0.98 or higher for the 6–13 data points used. Table 2 shows the slopes of the regressions. Some of the

Table 1. Rates of leaf appearance with changed thermal amplitude (TA)

Rates (RLA, leaves per day) were determined as the slope of the regression between leaf number and time for the four genotypes grown at long photoperiod after 50 days vernalisation. Mean phyllochron (Phyll,$^\circ$Cd leaf^{-1}) is also calculated assuming a base temperature of 0°C and ignoring the optimum temperature

Regime (°C)	TA (°C)	Sunset		Condor		Rosella		Cappelle Desprez		Mean Phyll
		RLA	se	RLA	se	RLA	se	RLA	se	
19.0/19.0	0	0.184	0.012	0.196	0.012	0.189	0.011	0.198	0.006	99
21.0/17.0	4	0.172	0.008	0.196	0.009	0.178	0.011	0.192	0.002	103
22.5/15.5	7	0.190	0.009	0.189	0.006	0.182	0.006	0.181	0.003	102
24.0/14.0	10	0.174	0.011	0.197	0.006	0.187	0.005	0.183	0.003	102
26.0/12.0	14	0.182	0.003	0.194	0.006	0.196	0.008	0.195	0.006	99
Mean Phyll		105	2	98	1	102	2	100	2	101

Table 2. Parameters of the linear regression between the number of emerged leaves on the main stem and time in four wheat cultivars grown in six temperature regimes

Phyllochron was calculated as the reciprocal of the slope, expressed in days and then in degree days by multiplying that value by the corresponding temperature. Coefficients of variation were 5, 7, 4 and 2% for the slopes of the four respective cultivars

Temperature	10	13	16	19	22	25	Mean
Slope (leaves day^{-1})							
Sunset	0.112	0.116	0.152	0.184	0.192	0.181	0.156
Condor	0.125	0.134	0.168	0.196	0.210	0.183	0.169
Rosella	0.122	0.138	0.173	0.189	0.219	0.192	0.172
Cappelle Desprez	0.117	0.131	0.159	0.197	0.223	0.193	0.170
Mean	0.119	0.130	0.163	0.192	0.211	0.187	0.167
Phyllochron (day leaf^{-1})							
Sunset	8.92	8.60	6.57	5.42	5.20	5.54	6.71
Condor	7.98	7.46	5.96	5.10	4.77	5.46	6.12
Rosella	8.22	7.23	5.78	5.30	4.56	5.21	6.05
Cappelle Desprez	8.53	7.65	6.30	5.08	4.49	5.17	6.20
Mean	8.41	7.74	6.15	5.23	4.76	5.35	6.27
Phyllochron (°Cd leaf^{-1})							
Sunset	89	112	105	103	115	138	110
Condor	80	97	95	97	105	137	102
Rosella	82	94	92	101	100	130	100
Cappelle Desprez	85	99	101	96	99	130	102
Mean	84	101	98	99	105	134	103

relationships had curvilinear components, but they explained less than 3% of the variation in leaf number. The slopes were significantly affected by temperature. The general trend was for an increase in the rate of leaf appearance with increase in temperature up to 22°C. As a consequence phyllochron was reduced as temperature was increased. This trend in phyllochron was not completely removed by calculating its value in degree days above a base temperature of 0°C and ignoring an optimum value (Table 2). Sunset had a consistently longer phyllochron than other cultivars, in keeping with the findings in the experiment on thermal amplitude (Table 1) and in agreement with field observations over several sowing dates made by Stapper (pers. comm., 1994) comparing Sunset with Condor and Rosella.

The analysis of the relationship between rate of leaf appearance from Table 2 and temperature showed that the common assumption of linearity between a base and an optimum temperature applied for all genotypes (Fig. 1). However, cultivars differed in the sensitivity of their rates of leaf appearance to temperature as demonstrated by differences in the slopes of the relationships (Table 3). Sunset and Condor were the least sensitive cultivars and Cappelle Desprez the most.

Base temperatures for rate of leaf appearance also differed between cultivars, ranging from −5.7 to −1.9°C. These base temperatures were significantly different from 0°C in two of the four cultivars (Table 3). If the regressions were forced through the origin (as is necessary if we accept that a base temperature of 0°C might be appropriate) the
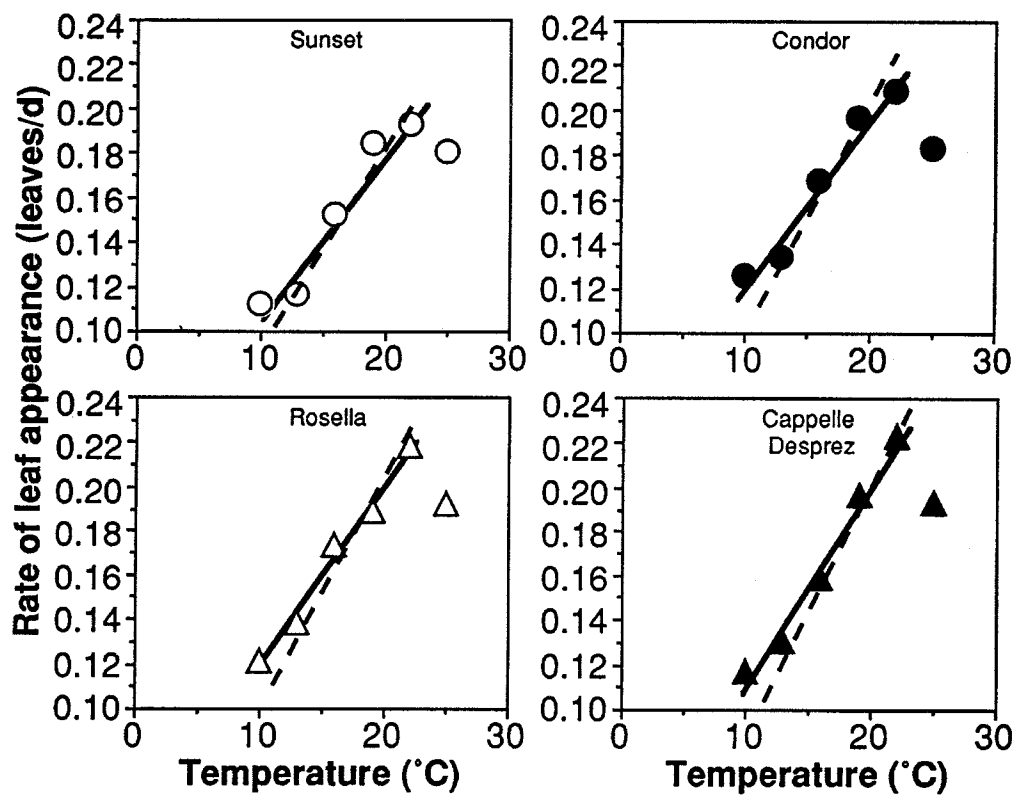
Fig. 1. Relationship between rate of leaf appearance on the main shoot and temperature for Sunset, Condor, Rosella and Cappelle Desprez. Lines were fitted by regression analysis (see Table 3). Plain and broken lines represent the regressions (for temperatures excluding 25°C) fitted with free intercept or forced through the origin, respectively.

Table 3. Parameters of the positive linear regressions shown in Fig. 1
The regressions between rate of leaf appearance and temperature (excluding 25°C, $n = 5$) were calculated either with a free intercept, or forced through the origin. P is the probability level for the regression, se is standard error for the parameter, phyllochron (Phyll) was calculated as the reciprocal of the slopes, optimum temperature was estimated by eye

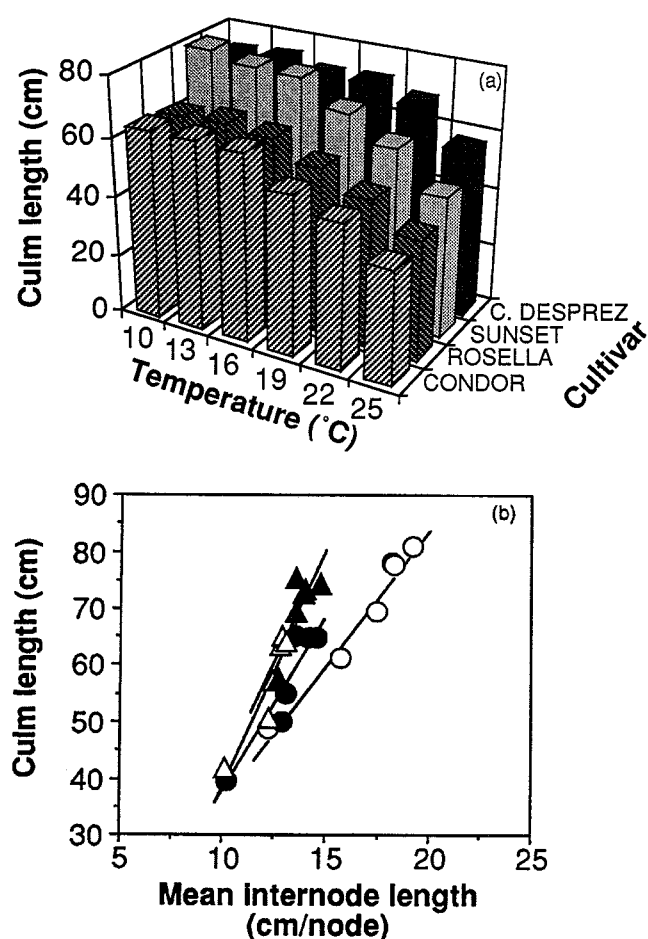| Cultivar	Intercept (leaves day^{-1})		Slope (leaves °Cd)		r^2	P	Base (°C)	Optimum (°C)	Phyll (°Cd)
		Regressions with free intercept							
Sunset	0.029		0.0076		0.971	0.006	−3.87	22	131
se		0.018		0.0011			2.72		
Condor	0.044		0.0077		0.985	0.002	−5.66	22	130
se		0.013		0.0008			1.89		
Rosella	0.037		0.0082		0.994	0.005	−4.57	22	122
se		0.009		0.0005			1.06		
Cappelle Desprez	0.018		0.0092		0.990	0.001	−1.90	22	108
se		0.013		0.0008			1.52		
		Regressions forced through the origin							
Sunset	0		0.0093		0.944	0.011	0	21	107
se			0.0033						
Condor	0		0.0102		0.925	0.016	0	20	98
se			0.0004						
Rosella	0		0.0104		0.955	0.008	0	21	96
se			0.0003						
Cappelle Desprez	0		0.0102		0.983	0.002	0	22	97
se			0.0002						

Fig. 2. Final culm length of the four cultivars grown in the study under six different temperatures (*a*) and the relationship between culm and mean internode length (*b*). Symbols as described in the Fig. 1 caption. Lines were fitted by regression. The pooled standard errors were 2.3 and 0.6 cm for final culm length and mean internode length, respectively.

slopes were increased and the phyllochron reduced (Table 3). Using regressions with a forced intercept resulted in phyllochron values for the four cultivars which were more similar than when regressions with free intercepts were used. However, the forced regressions were not entirely satisfactory as they underestimated the rates of leaf appearance at low temperature and overestimated them at high temperature (Fig. 1). It was evident that the rates of leaf appearance at the highest temperature (25°C) were lower than those at temperatures in the range 19–22°C for all the cultivars (Table 2; Fig. 1). Consequently, optimum temperatures were *ca* 22°C for all cultivars if the regression was fitted with a free intercept, and between 20 and 22°C if the regression was forced through the origin.

Main Culm Length and Culm Elongation Rate—Response to Temperature

Extension rates of culms were analysed to see whether cardinal temperatures could reasonably be derived from the relationships with temperature. As expected, cultivars differed significantly ($P < 0.001$) in culm length with the two standard-height cultivars, Cappelle Desprez and Sunset, always taller than the semi-dwarf cultivars, Condor and Rosella, regardless of temperature (Fig. 2*a*). Although temperature significantly affected the length of the main culm of all cultivars, the relationship was not linear, i.e. culm length was not modified by temperatures up to 16°C but was significantly reduced by increases in temperature above 19°C (Fig. 2*a*). The effect of temperature on culm length appeared to be related to its effect on the length of the elongating internodes (Fig. 2*b*) as there was no effect on the number of elongating internodes. This, in turn, could be related to the fact that final leaf number was essentially insensitive to temperature and node numbers are related to leaf numbers (see also Slafer and Rawson 1994*b*).

The traditional linear thermal-time model could be applied to the relationship between rate of culm elongation and temperature (Fig. 3). As shown by the slope of the regression, cultivars differed in their sensitivity to temperature. Cappelle Desprez and the semi-dwarfs (Rosella and Condor) were the most and the least sensitive cultivars, respectively. Sunset had intermediate sensitivity, but since it was the cultivar with the largest intercept (and therefore the lowest base temperature) its rate of culm elongation was the highest at 10°C (Fig. 3). Base and optimum temperatures for rate of culm elongation ranged between cultivars from *ca* 2 to 5°C (base) and from 19 to 21°C (optimum, Table 4). In contrast to the situation described for rate of leaf appearance, when the regressions were forced through the origin (i.e. through a base temperature of 0°C) the regression coefficients were decreased and the rates of culm elongation overestimated at low temperatures and underestimated at high (below-optimum) temperatures.

Comparisons of Cardinal Temperatures and Rates for Concurrent but Different Processes

We next compared the base temperatures and then the rates within two pairs of concurrent processes. We assumed for the purposes of these comparisons that leaf appearance and the early phenological stages to terminal spikelet appearance were concurrent processes. We also assumed for our second pair of concurrent processes that culm elongation occurs largely during the phenological phase between terminal spikelet appearance and anthesis (Kirby *et al.* 1985; Masle 1985; Kirby 1990; Stapper and Fischer 1990). Within the limitations of these assumptions, base
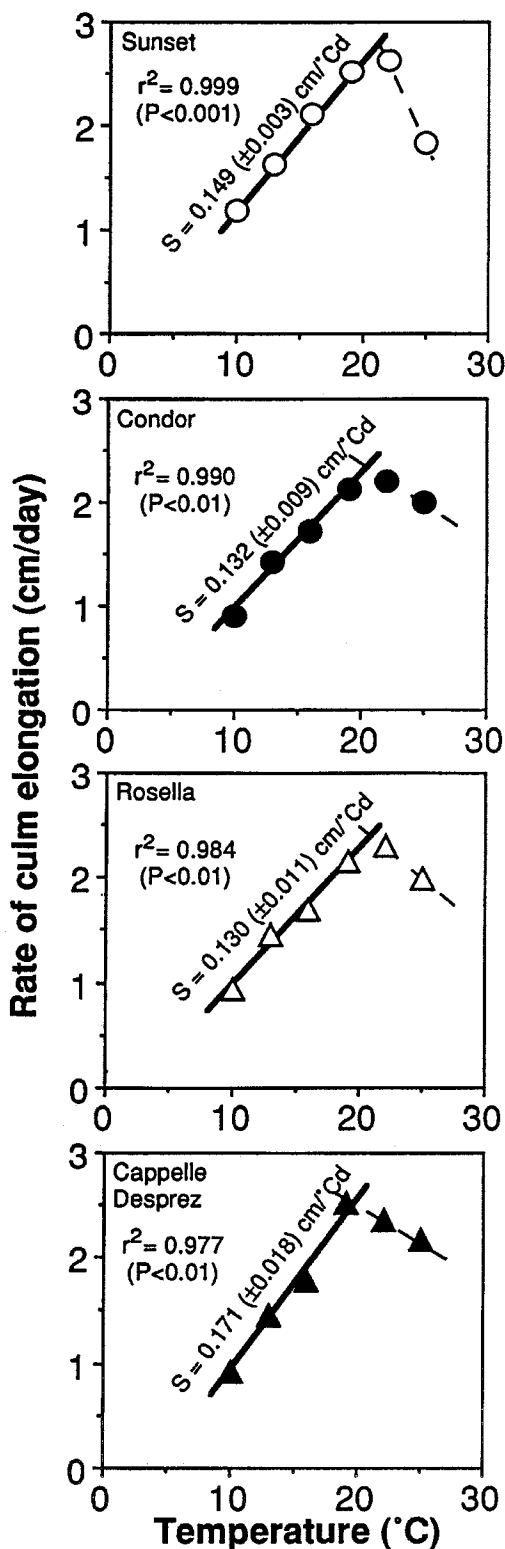
Fig. 3. Relationship between rate of culm elongation and temperature for Sunset, Condor, Rosella and Cappelle Desprez. Solid lines were fitted by regression analysis and broken lines were fitted by eye. S represents slope.

temperatures for concurrent processes were roughly similar if the means of the cultivars were compared across processes, but rather different if the values for individual cultivars were compared (Table 4). Thus, the base temperature for phenological development for Cappelle Desprez was much more negative than that for leaf appearance, but the reverse applied for Condor. Similar conclusions can be drawn from comparisons between base temperatures for culm elongation and its parallel phenological phase (Table 4).

If we now make comparisons between rates of development of the two pairs of concurrent processes we see that, in general, there were linear relationships between rates of leaf appearance and rates of apex development towards terminal spikelet initiation (Fig. 4). But again, comparisons at the level of the cultivar showed variation. Thus, the linearity was stronger in Rosella and Cappelle Desprez than in Sunset and Condor (Fig. 4). In the two spring cultivars particularly, there was even some hysteresis, due to different optimum temperatures for the processes of apex development and leaf appearance (Table 4).

For the second pair of concurrent processes, the overall relationships between rates of phenological development and culm elongation were curvilinear (Fig. 5). The curvilinearity arose because of differing optimum temperatures between the processes (Table 4). Thus, for the relatively cool temperatures from 10 to 16°C, which were below the optimum of both processes, the relationships were effectively linear. However, between 19 and 25°C, the rising temperatures reduced the duration of the phase from terminal spikelet initiation to anthesis more than they accelerated the rate of culm elongation, which resulted in shorter stems at anthesis (Fig. 2a).

Discussion

Does Thermal Amplitude Affect Development?

Ritchie (1991) and Cutforth et al. (1992) stressed that, to reach a more mechanistic approach to modelling wheat development and yield, it is important to understand how environmental factors affect the duration of phasic development, final leaf number, and the rate at which leaves appear. From our limited data, it seems that diurnal thermal amplitude is of little consequence to the rate of development of wheat, supporting results with rice (Summerfield et al. 1992) but not complying with expectations in barley (Ellis et al. 1988). Our data also showed that the final number of leaves was insensitive to thermal amplitude, as by inference, was the rate of leaf primordia initiation.

The application of this finding is that conclusions from data collected under one amplitude at this mean temperature can be extrapolated with confidence to another. This general approach is already used by physiologists who use mean temperatures to describe the responses of processes to

Table 4. Base and optimum temperatures for concurrent processes

Phenology refers to rates of processes associated with reproductive development, where TS is terminal spikelet appearance. Data for leaf appearance and culm extension are from this paper and for phenology are reworked from Slafer and Rawson (1995a)

	Start to TS		TS to anthesis	
	Phenology	Leaves	Phenology	Culm
	Base temperature			
Sunset	2.22	-3.87	4.28	2.05
Condor	0.58	-5.66	4.64	2.75
Rosella	-2.40	-4.57	4.12	2.57
Cappelle Desprez	-8.23	-1.90	2.78	4.69
Mean	-1.96	-4.00	3.96	3.02
	Optimum temperature			
Sunset	19.5	22	22.0	21
Condor	19.5	22	>25	20.5
Rosella	21	22	>25	21
Cappelle Desprez	20	22	>25	19
Mean	20.0	22.0	>24.3	20.4
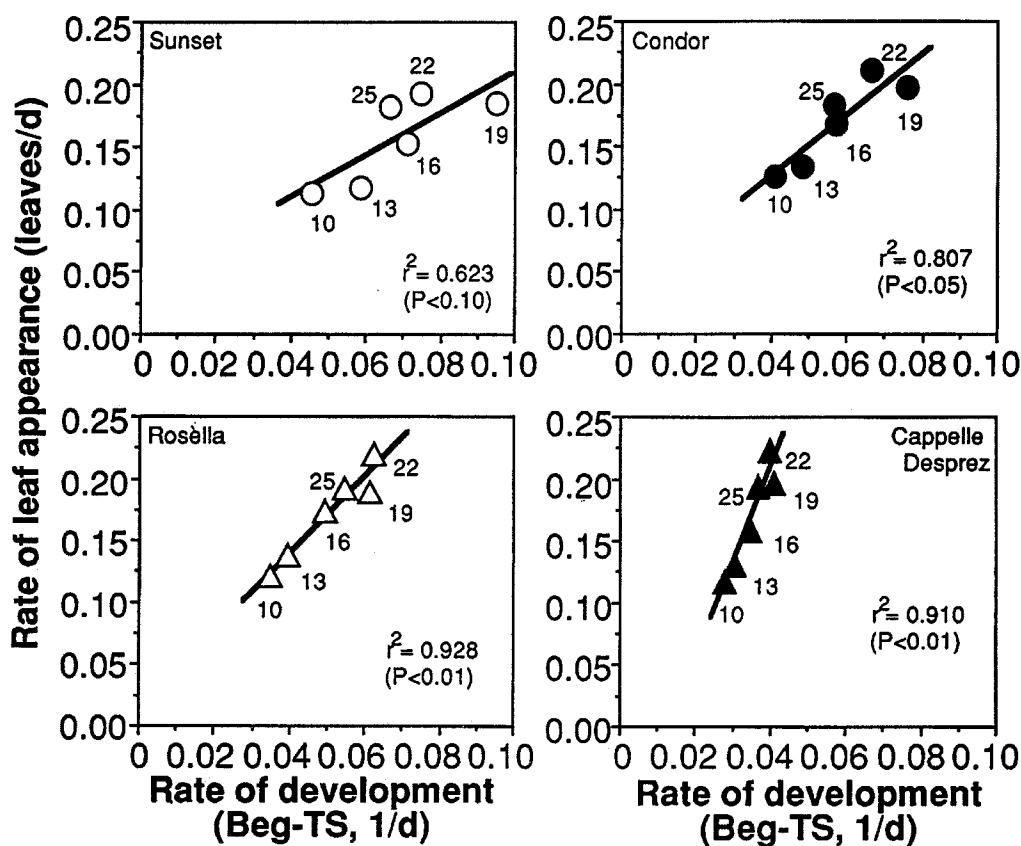
Fig. 4. Relationship between rate of leaf appearance on the main culm and rate of development between the beginning of the experiment (Beg) and terminal spikelet appearance (TS) for Sunset, Condor, Rosella and Cappelle Desprez. Lines were fitted by regression analysis. Numbers represent the temperature corresponding to each point.
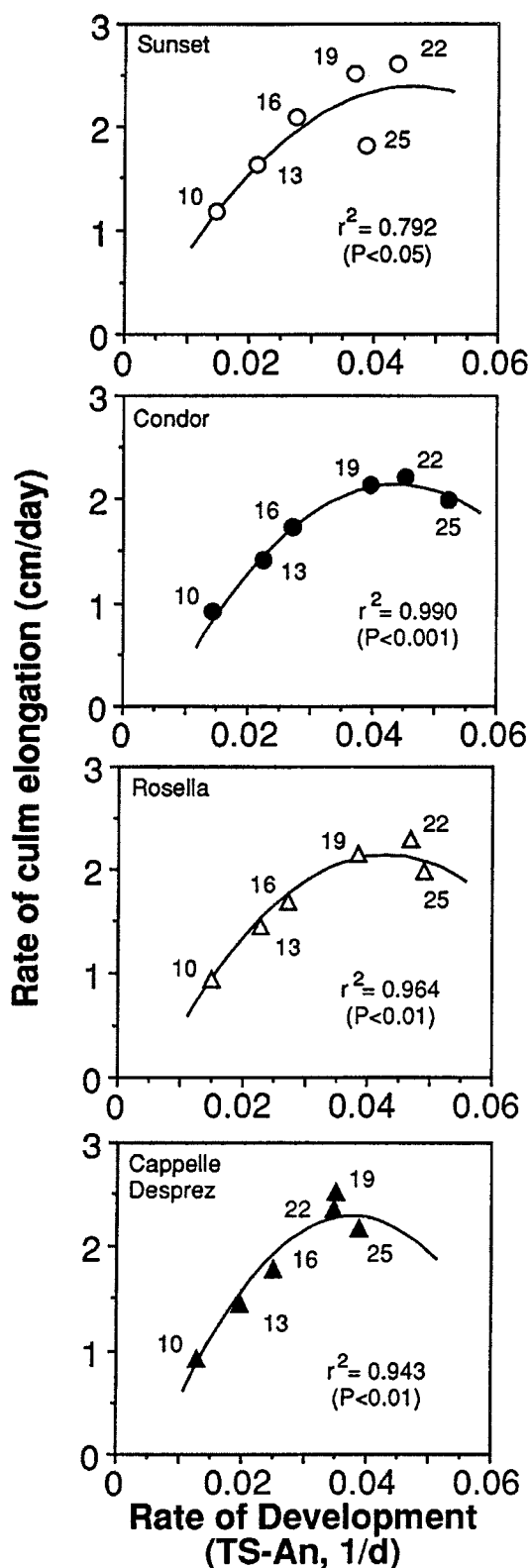
Fig. 5. Relationship between rate of culm elongation and rate of development from terminal spikelet appearance (TS) to anthesis (An) for Sunset, Condor, Rosella and Cappelle Desprez. Lines were fitted by regression analysis. Numbers represent the temperature corresponding to each point.

temperature. It is used by modellers who, when calculating thermal time summations for processes, commonly use the mean of maximum and minimum temperatures for a daily accumulation, irrespective of amplitude. So this finding will have little actual impact except to make some researchers feel more comfortable with the approach they already use.

It has the message for greenhouse managers that it is not essential to maintain near-constant temperatures to achieve particular rates of development for wheat. Allowing an amplitude around the same mean will give the same result, more closely mimic the field environment, and save energy in maintaining glasshouse temperature at the same time.

We do emphasise that the results reported here were from one mean temperature and consequently the conclusions cannot be extrapolated with impunity. Development in wheat is strongly affected by the interactions between vernalisation and photoperiod with temperature (Rawson 1993a; Rawson and Richards 1993; Rawson and Zajac 1993; Slafer and Rawson 1994a). If thermal amplitude is such that a vernalisation response is being satisfied by lower night temperature in one case and not in another, thermal amplitude will change the rate of development. Furthermore, if thermal amplitude at low mean temperatures results in a higher maximum day temperature, this could result in faster growth in C_4 species and changed rate of development in a light-limited environment (see Rawson 1988, 1993b).

Leaf Appearance: Are there Common Cardinal Temperatures?

In our second study we used temperature regimes with 0°C amplitude to examine the responses of development to temperatures between 10 and 25°C. Our results can be compared with those of Cao and Moss (1989b) who also used wheat grown in controlled conditions. However, the results have to be assessed in context. They only considered the first four leaves whereas we calculated rates of leaf appearance from all main shoot leaves. This difference in methodology should be of no consequence as in our studies there was no apparent change in phyllochron interval during the course of plant development. Of more importance is that they used a 14 h daylength. If daylength (Cao and Moss 1989a) and its interaction with temperature (Cao and Moss 1989c) can affect the rate of leaf appearance, the response to temperature could be interacting with the response to daylength, possibly preventing accurate estimates of base and optimum temperatures. In our study, we attempted to remove responses to vernalisation and photoperiod by our pretreatments and growth conditions.

Cao and Moss (1989b) reported that their optimum temperatures, beyond which the rate of leaf appearance was reduced, ranged from 21 to 24°C. This agrees with the results obtained here (Table 4). They also reported a base temperature of 0°C for all their cultivars which does not

support our finding. However, their calculation of base temperature was done by using a quadratic regression between rate of leaf appearance and temperature, including in the regression the supraoptimal temperatures. This procedure has two important consequences; first, an overestimation of the base temperature for the rate of leaf appearance under suboptimal temperatures, and second, an effect of temperature on the thermal time accumulated between the appearance of successive leaves. This is not acceptable if the basis for the use of thermal time is to remove the effect of temperature. If linear regressions are fitted only to the data they obtained under clearly suboptimal temperatures (from 7.5 to 15°C), the coefficients of determination of the linear regressions were always very high ($r^2 > 0.99$). The estimated base temperatures from these regressions would be lower than 0°C and different amongst the cultivars they used, in agreement with the present study.

We know of no published studies that have found differences between genotypes in base temperatures for the rate of leaf appearance. Any differences in the parameters determining leaf appearance have been limited to the slopes i.e. the amount of thermal time required between the appearance of successive leaves (e.g. Kirby et al. 1985; Baker et al. 1986; Kirby and Perry 1987; Cao and Moss 1989a; Hay and Delecolle 1989). Base temperature is usually assumed to be, or calculated to be 0°C. The estimation of base temperature has often been based on data from field studies with changing temperatures, photoperiods and differing degrees of vernalisation. An iterative procedure is used which regresses leaf number against thermal time, using a range of different base temperatures and observing the residual variation (e.g. Gallagher 1979). This methodology has practical convenience, but it has the limitation in determining base temperature that base temperature is one of the determinants of the response. The other difficulty of determining base temperatures from field data is that the effects of vernalisation and photoperiod are difficult to separate from the effects of temperature. So we suggest that although our findings on differing base temperatures between cultivars are not supported by others, there are often enough potential errors in the calculations to mask the variations in base temperature that might exist.

Our data suggest that base temperatures may differ between cultivars by around 4°C. The consequences of this difference in predicting phyllochron interval at one temperature from observations at another are quite large. For example, if it takes 5 days for each leaf to appear at 20°C, this is equivalent to $20 \times 5 = 100$°Cd if the base temperature is 0°C, and $25.7 \times 5 = 128$°Cd if the base is −5.7°C (see Condor in Table 4). If these data are then used to predict phyllochron interval at 10°C, assuming a base of 0°C, a new leaf will appear every $100/10 = 10$ days. However, if the real base was −5.7°C, a new leaf should

actually appear every $128/15.7 = 8.1$ days. This error would extend to 17 days if the data were used to estimate the date of appearance of the flag leaf of a nine leaf plant.

Culm Elongation and Response to Temperature

As expected, cultivars differed significantly in culm length with semi-dwarf cultivars always being shorter than standard-height cultivars. The main reason for the difference was the average length of the internodes, not internode number (see Rawson and Evans 1971; Stapper and Fischer 1990, for confirmation). Comparing the two standard-height cultivars, Cappelle Desprez was, on average, taller than Sunset, but a clear cultivar by temperature interaction was evident, in that Sunset was slightly, but significantly, taller than Cappelle Desprez at the lowest temperatures (Fig. 4). This cultivar by temperature interaction on culm length was mainly a reflection of the differential sensitivities of their rates of culm elongation to temperature. Both cultivars were sensitive, but Sunset had a lower base temperature (2 vs 4.7°C) and a smaller sensitivity (0.15 vs 0.17 cm [°Cd]$^{-1}$) than Cappelle Desprez (Fig. 5).

There were no differences between the semi-dwarf cultivars used here either in sensitivity or in cardinal temperatures. Rates of culm elongation were less sensitive to temperature than those of the standard-height cultivars. Temperatures of 19°C or higher reduced the length of the main culm in all cultivars by a direct effect on the average length of the elongated internodes. The lack of major effects of temperature on the number of elongated internodes reflects the insensitivity of final number of leaves to temperature (see also Slafer and Rawson 1994b). Therefore, the main reason for reduced culm length under the highest temperature can be found in the difference in optimum temperature between the rate of culm elongation and rate of phenological development between terminal spikelet initiation and anthesis. Stapper and Fischer (1990) found that when cultivars of wheat were sown on different dates their final culm length was reduced as anthesis was delayed. This was mainly, but not completely, due to a reduced number of elongated internodes (which could be a response to photoperiod; Slafer et al. 1994a), but also possibly due to the higher temperatures occurring with late anthesis in the field (M. Stapper, pers. comm.).

Associations Between Processes

Temperature had little effect on the final number of leaves on the main stem. By contrast, the duration of the primordia initiation period was strongly affected by temperature in all cultivars used here, as well as in other cultivars (Slafer and Rawson 1994a). Therefore, the rate of leaf primordia initiation and the rate of development towards floral initiation were almost equally affected by temperature (see confirmatory studies of Rawson 1970;

Rawson and Zajac 1993; Slafer and Rawson 1994*b*). Consequently, we can conclude that there are only tenuous links between the rate of leaf primordia initiation and phyllochron, supporting the proposition of Rawson (1993*a*), at least when temperature is the only factor affecting development. This differs from the proposed co-ordination between leaf primordia initiation and leaf appearance when both photoperiod and vernalisation responses are involved (Kirby 1990; Rawson and Zajac 1993; Slafer *et al.* 1994).

Almost all processes analysed were sensitive to temperature in all cultivars and there was variation in sensitivity in all comparisons. For example, cardinal temperatures differed for the processes of leaf appearance, culm elongation and phasic development and cultivars differed for each process. Consequently, to use standard cardinal temperatures for purposes of prediction in crop simulation models would lead to inaccuracies. Results which reinforce this conclusion have recently been published for rice (Ellis *et al.* 1993). Generally, the later the phase of development or process, the higher the base temperature. This trend substantiates what has been suggested from field studies (Angus *et al.* 1981; Del Pozzo *et al.* 1987; Porter *et al.* 1987; Slafer and Savin 1991). Such confirmation is important because many factors besides temperature change with the advancement of development in the field. So it is difficult to link observed trends solely with temperature. Furthermore, for most temperate field crops, mean temperature rises with plant development. Thus, an increase in base temperature in later developmental stages could be interpreted as a consequence of that increased average temperature under which the base temperature is estimated. Our results are free from both constraints, having been collected from plants which were grown at constant temperature throughout development, and under constant long photoperiod.

Acknowledgments

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