TEMPERATURE, CO$_2$ AND THE GROWTH AND DEVELOPMENT OF WHEAT: CHANGES IN THE MEAN AND VARIABILITY OF GROWING CONDITIONS

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Abstract. The experiment described here resulted from simulation analyses of climate-change studies that highlighted the relative importance of changes in the mean and variance of climatic conditions in the prediction of crop development and yield. Growth and physiological responses of four old cultivars of winter wheat, to three temperature and two carbon dioxide (CO$_2$) regimes (350 or 700 ppmv) were studied in controlled environment chambers. Experimental results supported the previous simulation analyses. For plants experiencing a 3 °C increase in day and night temperatures, relative to local long-term mean temperatures (control treatment), anthesis and the end of grain filling were advanced, and grain and dry matter yields were reduced by 27% and 18%, respectively. Increasing the diurnal temperature range, but maintaining the same mean temperature as the control, reduced the maximum leaf area (27%) and grain yield (13%) but did not affect plant development. Differences among the temperature treatments in both phyllochron interval and anthesis date may have resulted from differences between measured air, and unmeasured plant, temperatures, caused by evaporative cooling of the plants. Thermal time (base $\approx$ 0 °C), calculated from air temperature, from anthesis to the end of grain filling was about 650 °C d for all cultivars and treatments. Doubling ambient CO$_2$ concentration to 700 ppmv reduced maximum leaf area (21%) but did not influence plant development or tiller numbers.

1. Introduction

Present levels of CO$_2$ are about 350 ppmv and, in the absence of measures to counter the burning of fossil fuels, are expected to reach about 500 ppmv by the middle of next century (Houghton et al., 1990). The direct influence of rising ambient CO$_2$ concentration (C_a) is expected to increase crop phytosynthesis and yield with C$_3$ plants, including wheat, showing greater stimulation than C$_4$ plants (Kimball, 1983). However, associated with rising C_a, has been a progressive rise

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in the earth's mean temperature (Houghton et al., 1992) and this secondary effect may prove detrimental to plant growth and agriculture (Parry, 1990).

Assessment of the impacts of climate change on resource systems, such as agriculture, has involved the linkage of meteorological data with crop simulation models. In the broadest sense, crop simulation models transpose a distribution of weather sequences into a distribution of plant dry matter and harvestable yield. Initially, climate change impact scenarios were constructed by applying changes in mean meteorological variables to historical weather data (Giorgi and Mearns, 1991). Some analyses also postulate an increase in weather variability (Mearns et al., 1992).

Correlation between the frequency of occurrence of extreme events, such as drought, is higher with changes in the variability of climate than with changes in its mean (Katz and Brown, 1992). As a consequence, recent research has incorporated changes in inter-annual (Wilks, 1992) and diurnal (Mearns et al., 1995) variability into climate change scenarios. Crop-climate models also contain many non-linear responses to weather variables, such as the relationship between maintenance respiration rate and temperature (McCree and Amthor, 1982). For these two reasons, in our view, climatic-change impact assessments that rely solely on changes in mean conditions are flawed and will, simply via their methodology, underestimate impacts. Semenov and Porter (1995) assessed the impact of changing inter-annual temperature and precipitation variability on wheat yields using the stochastic simulation system AFRC3S, which is the wheat simulation model AFRCWHEAT2 (Porter, 1993) linked to a stochastic weather generator (Rascko et al., 1991). A similar reduction in grain yield was produced by increasing mean daily temperature and its interannual variation (Semenov and Porter, 1995).

In the present controlled environment (CE) study we have compared the effects of changing daily mean temperature and increasing diurnal temperature variance on the growth and development of wheat plants. Mearns et al. (1995) predicted that changes in diurnal temperature range may vary spatially and seasonally, with decreased variability in winter, but localised increases in summer. Analyses indicate that most of the rise in global temperature over the past 40 years can be attributed to increasing minimum, usually night, temperatures and consequently a decrease in diurnal variation (Horton, 1995). The mechanisms responsible for this decrease are not fully understood, but may be related to the combined effects of increased cloud cover over continents with increased sulphur emissions (Hansen et al., 1995). Increases in the diurnal temperature range have been reported in locations such as the Pacific islands, including parts of New Zealand (Salinger, 1995), and it is an increase in diurnal variation that is the focus of the present study.

Plant growth and development respond to their environment via a combination of linear and non-linear relationships. For example, when separated into phases, rates of development respond linearly to temperature and photoperiod (Porter and Delécolle, 1988). Growth processes, such as photosynthesis, initially respond linearly, with respect to incident photosynthetically active radiation (PAR), but then

reach a plateau, at about 120 W m^{-2} for wheat (Marshall and Biscoe, 1978). Even with developmental processes, there are conditions in which the general linear response of a process may decline (Monteith, 1987).

Crop simulation models represent crop responses to their environment via a combination of mechanistic and empirical components. In AFRCWHEAT2, the response to different CO_2 concentrations is modelled via changes in the light response curve (Weir et al., 1984; Porter, 1993), whereas CERES-Wheat uses an empirically based increase in radiation use efficiency of 25% (Adams et al., 1990). For this study we used AFRC3S to design the experimental treatments and to examine the relative differences in crop response to temperature and CO_2 treatments.

Previous experimental analyses of changes in the variability of temperature (Robson, 1973; McCree and Amthor, 1982) and increases in CO_2 (Lawlor and Mitchell, 1991) have concentrated on specific growth periods. For this study we examined the effects until crop maturity.

Plants were grown in four controlled environments: (1) Ambient CO_2 (350 ppmv) and with a diurnal temperature cycle that followed a measured seasonal cycle, or (2) with the mean daily temperature elevated by 3 °C, or (3) at ambient mean temperature but with its diurnal variance increased, or (4) at elevated CO_2 and with the same diurnal temperature cycle as for the control.

2. Materials and Methods

2.1. SIMULATION ANALYSIS

This experiment aimed to link previous simulation analyses, based on 30 years data (Semenov et al., 1993; Semenov and Porter, 1995), to an experimental procedure that would enable assessment of the effects on winter wheat of changes in the mean and variance of temperature and increased CO_2. Treatments were designed following a simulation analysis of growth and development for a single season using cv Avalon winter wheat and the AFRCWHEAT2 model.

2.2. TREATMENT DETAILS

(1) *Control (CE1)*. Seasonal temperatures and photoperiods were imposed for an entire winter wheat growth season. Temperatures were the mean daily maximum and minimum values at Long Ashton Research Station from 1973 to 1982 (Porter, 1987). The CO_2 concentration was 350 ppmv.

(2) *Elevated mean temperature (CE2)*. Conditions were the same as for CE1 except daily maximum and minimum temperatures were 3 °C higher.

(3) *Increased diurnal variation (CE3)*. The aim to double the standard deviation of the mean (1973–82) seasonal temperature distribution was not achieved because the chambers had a lower limit of 4 °C. Thus, night temperatures were held
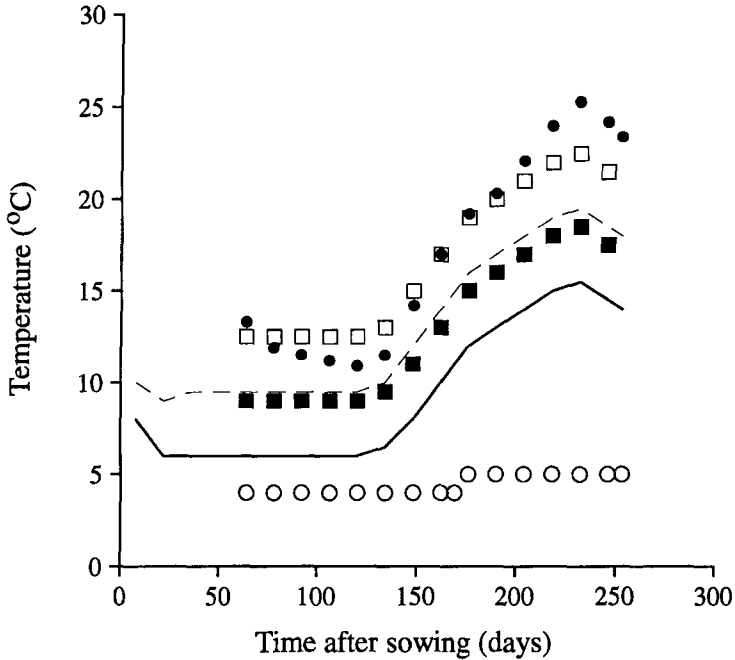
Figure 1. Temperature profiles for controlled environment (CE) treatments. All treatments followed the same regime as CE1 (day - - -, night —) up to 66 days after sowing. CE1: Control, mean diurnal temperature range for Long Ashton Research Station, U.K., ambient CO_2 (350 ppm); CE2, CE1, temperatures +3 °C day (□), and night (■), ambient CO_2; CE3, 4–5 °C night temperature (○), day temperature (●) adjusted to give the same daily mean as CE1, ambient CO_2; CE4, CE1, temperatures, 2 × ambient CO_2 (700 ppm).

at this level and day temperatures were adjusted (taking account of changes in photoperiod) to maintain the same mean daily temperature as in CE1. The CO_2 concentration was 350 ppmv.

(4) *Elevated CO_2 (CE4).* Conditions were the same as for CE1 except the CO_2 concentration was 700 ppmv.

The temperature regime for each treatment is shown in Figure 1. Accumulated thermal time was calculated using daily mean temperatures (adjusted for photoperiod) from the commencement of treatments and was therefore the same in CE1, CE3 and CE4.

2.3. CONTROLLED ENVIRONMENT ROOMS

The four controlled environment rooms (3.0 × 2.5 × 2.0 m) each contained two fans above the light source. Air was drawn through the plants, heated or cooled, and blown back into circulation down the sides of the room. The air temperature was monitored by an OS 9000 operating system (Measurement Systems Ltd, 4b Faraday Rd, RG13 2AD, U.K.) using thermostats at the canopy level that ensured

targeted temperatures were achieved. Room temperatures were switched between day and night over approximately one hour.

All rooms were fertilised with CO_2 to ensure ambient (350 ppmv) and twice ambient (700 ppmv) conditions were maintained. The CO_2 concentration was monitored at six minute intervals using an infra red gas analyser (Analytical Development Company, EN11 0AQ, U.K.). The CO_2 concentration was maintained by injecting pure CO_2 (0.85 cm^3 min^{-1}) into the air intake ducts of the cooling system, and the air in each room was recirculated to ensure good mixing.

Light was supplied by 56, 2.4 m white fluorescent tubes placed along the width of the rooms and 2 m above the ground. Sixteen evenly spaced 60-W tungsten lights were suspended below the fluorescent tubes to provide light in the red region. Fluorescent tubes were replaced regularly to minimise the effects of a natural, rapid 'drop off' in their output potential with time. Saturing light levels are ≈ 120 Wm^{-2} PAR (Marshall and Biscoe, 1978); however, PAR levels in the rooms never exceeded 65 Wm^{-2}.

A border row of wheat plants was introduced into each room after vernalisation to minimize border effects and the experimental pots were re-randomised three times during the experiment to further reduce border effects.

2.4. PLANT MATERIAL

Four former commercial winter wheat cultivars, introduced in 1953, Capelle-Desprez (CD), 1935, Holdfast (H), pre-1900, Prince Albert (PA) and, 1908, Little Joss (LJ), and described by Austin et al. (1980), were used in the experiment. Seeds were sown on 1 December 1993 into seedling trays containing John Innes compost, (sand : peat : loam, 1 : 2 : 3) and an Osmocote slow release fertiliser. Trays were placed in an unheated glasshouse for germination.

Germination occurred about 6 days after sowing and 30 days later, seedlings were transplanted into 225 mm diameter pots (280 mm depth), to a population of 240 plants m^{-2} (10 plants per pot). Plants were then vernalised in a CE room for 30 days at a 9.5/6.0 °C day/night temperature. On February 4th, 1994, 12 blocks of four pots (each containing one cultivar) were placed in a randomised block design into each of four rooms and the four treatments commenced. Pots were watered twice weekly to minimise moisture deficits.

2.5. MEASUREMENTS AND SAMPLING

Post-vernalisation, plants were harvested at 7- or 14-day intervals until maturity. Five plants per cultivar were randomly selected from each treatment and cut at ground level for measurements of tiller number, photosynthetic leaf area, and total above ground dry weight. Additional pots of glasshouse grown plants were added to the chambers to maintain the plant population until terminal spikelet, when maximum tiller number should be set (Hay and Kirby, 1991). Tiller production

and death were assessed for primary and secondary tillers separated from the main stem. Leaf areas were monitored using a Delta-T meter (Delta T Services, Ltd., 128 Burwell Rd, CB5 0EJ, U.K.). After ear emergence, plants were monitored daily to record 50% anthesis, as the time when 50% of the ears had dehisced anthers. Post-anthesis, ears were hand threshed for measurement of grain dry weights. From these data the beginning and end of grain-filling (maturity) and the rate of change of harvest index during this time, were calculated (Moot et al., 1996). Leaf emergence was monitored twice weekly on the main stems of five randomly selected plants from each cultivar in each treatment. A leaf was considered fully emerged when the ligule was visible.

2.6. DATA ANALYSES

Data analysis for all variables used the Genstat statistical package (Payne et al., 1987). Logistic functions were fitted to dry matter data against time, for each cultivar in each treatment. The relative growth rate (RGR), maximum dry matter produced, and time to the maximum growth rate (mid-point of the logistic curve) were estimated. Gaussian functions were fitted to changes in tiller number and leaf area data over time. From these, the maxima ($dy/dt = 0$) and time after sowing to the maxima were estimated. The rate of change (dy/dt) was approximated from the line connecting the time between 50% of the maxima and the maxima. Leaf emergence rates were estimated as the reciprocal of regression coefficients from analysis of leaf number against thermal time (accumulated temperature above $0\,^{\circ}C$). Parameters from all functions and anthesis and maturity data were analysed by analysis of variance to determine treatment and cultivar main effects using the interaction as the residual. Mean separation of significant differences was via least significant difference tests.

3. Results

3.1. SIMULATION RESULTS

3.1.1. *AFRCWHEAT2*

Simulation analyses for *cv* Avalon under control and elevated CO_2 conditions predicted anthesis 191 days after sowing and the end of grain-filling 35 days later (Table I). These stages were predicted to be earlier for increased mean temperature of 3 $^{\circ}C$, corresponding to CE2, but the increased diurnal variation, corresponding to CE3, was predicted to delay anthesis without affecting the end of grain-filling (Table I). Grain yield was predicted to be 375 gm^{-2} under the control conditions but reduced by 16% and 11% by an increase in the mean and variability of temperature, respectively (Table I). In contrast, CO_2 was predicted to increase both grain yield and total dry matter (TDM) by about 30%.

Table I

Predicted number of days after sowing (DAS) to anthesis and end of grain-filling, and yield results from the AFRCWHEAT2 crop simulation model for *cv* Avalon winter wheat grown in four environments (CE1–CE4). Environmental details were given in Figure 1. Yield change is relative to the control (100%)

	Anthesis (DAS)	End of grain-filling (DAS)	Dry matter (g m^{-2})	Grain yield (g m^{-2})	Yield change (%)
Environment					
CE1	191	226	842	375	100
CE2	178	204	751	315	84
CE3	198	225	814	332	89
CE4	191	226	1086	491	131

3.2. EXPERIMENTAL RESULTS

3.2.1. *Anthesis, Grain-filling and Yield*

Plants grown with an increased mean temperature (CE2), took fewer days to reach anthesis and the end of grain-filling than those in other treatments (Table II). However, the thermal time to anthesis (1774 °C d) and the end of grain-fill (2421 °C d) was higher ($p < 0.05$) for CE2 than other treatments. The lag phase from anthesis to the start of grain-filling lasted about 6 days in the control and increased CO_2 treatments, CE1 and CE4 (Table II), but was accelerated to 2.7 days for the increased mean temperature treatment and delayed to 11.6 days by the increased diurnal variation. Relative to the control, grain yield was decreased by 27% in CE2 and increased by 7% by CO_2 enrichment (Table II).

3.2.2. *Leaf Emergence Rates*

Regression analyses of leaf number against thermal time were all linear with a coefficient of determination (R^2) of at least 0.96. Analysis of variance indicated differences in the leaf emergence rate among treatments and cultivars (Table III). The accumulated thermal time between leaves for the control (123 °C d) was similar to that under increased CO_2 but less ($p < 0.01$) than that found under different temperature regimes, 143 °C d for CE2, and 134 °C d for CE3 (Table III). Final main stem leaf number averaged 12.6 leaves for all treatments (Table III).

3.2.3. *Tiller Number*

The temporal pattern of tiller production was similar in all treatments. Tiller number per plant began to increase ca. 60 days after sowing and reached a maximum after ca. 125 days (Figure 2). Primary tiller numbers were constant at ca. 5 plant^{-1} from 106 to 164 days after sowing in all treatments, and then declined to their final number (ca. 3.3 plant^{-1}), about 200 days after sowing (Figure 2). The lower maximum tiller number in CE2 (Table IV) was due to the production of fewer

Table II

Time [days after sowing (DAS) and accumulated thermal units (Tt)] to anthesis and end of grain-filling (EGF), duration of the lag phase, and grain yield for wheat plants of four cultivars grown in controlled environments (CE1-CE4). Environmental details were given in Figure 1. Yield change is relative to CE1 (100%). Note: (1) Results are for environments over cultivars, and cultivars over environments. (2) s.e.d. is the standard error of the difference. (3) Values within columns with a letter subscript in common are not significantly different by least significant difference tests ($\alpha = 0.05$, 9 df)

	Anthesis		EGF			Yield	
	DAS	Tt	DAS	Tt	Lag phase (d)	Grain (g plant^{-1})	Change (%)
Environment							
CE1	208_b	1467_b	247_a	2163_b	6.1_{ab}	3.0	100
CE2	202_c	1774_a	234_b	2421_a	2.7_b	2.2	73
CE3	210_{ab}	1518_b	247_a	2157_b	11.6_a	2.6	87
CE4	212_a	1534_b	251_a	2227_b	6.4_{ab}	3.2	107
Cultivars							
Cappelle-Desprez	204_b	1505_c	240_b	2152_b	7.4_{ab}	2.4	
Little Joss	205_b	1525_c	242_b	2188_b	2.6_b	2.7	
Prince Albert	213_a	1666_a	248_a	2293_a	10.9_a	2.5	
Holdfast	209_a	1597_b	250_a	2236_a	6.4_{ab}	3.3	
s.e.d.	1.5	28.3	2.2	36.7	2.63	0.40	

secondary tillers. All secondary tillers in CE2 had senesced by 164 days after sowing, which was about 16 days earlier than in other treatments (Figure 2).

3.2.4. *Dry Matter Accumulation*

There was a high degree of variability within dry matter samples for *cv* Prince Albert, particularly during the maturation phase (Moot et al., 1996), and this prevented the fitting of logistic curves for this cultivar. For the remaining cultivars, the RGR was estimated to be ca. $0.04 \, \mathrm{g \, g^{-1} \, d^{-1}}$ in each treatment (Table V). Time to the maximum growth rate was longer ($p < 0.01$) in CE3 (195 days) than in CE2 (169 days), and was ca. 182 days for both control and CO_2 treatments. The maximum dry matter produced in CE2 ($11.6 \, \mathrm{g \, plant^{-1}}$) was estimated to be lower ($p < 0.05$) than in other treatments (Table V). In the elevated CO_2 conditions there was a post-grain maturity increase in dry matter of about 20% (Figure 3).

3.2.5. *Leaf Area*

Changes in leaf area over time were described from fitted Gaussian curves (Figure 4). The maximum leaf area produced, and its rate of production were highest ($p < 0.01$) in CE1 and CE2 (Table VI). However, all calculated rates (Table VI) may have underestimated the expansion and overestimated the decline in leaf area, due to the imperfect symmetry in the response over time (Figure 4). Green leaf

Table III

Summary of regression analysis of leaf number against thermal time (Tt), and final leaf number for wheat plants of four cultivars grown in controlled environments (CE1–CE4). Environmental details were given in Figure 1. Note: (1) Results are for environments over cultivars and cultivars over environments. (2) s.e.d. is the standard error of the difference. (3) Values within columns with a letter subscript in common are not significantly different by least significant difference tests ($\alpha = 0.05$, 9 df)

	Initial leaf number (per plant)	Coefficient (leaves per °C d)	Tt (°C d per leaf)	Final leaf number (per plant)
Environment				
CE1	4.2$_a$	0.0081$_a$	123	12.5
CE2	3.6$_b$	0.0070$_c$	144	12.7
CE3	4.0$_a$	0.0075$_b$	134	12.6
CE4	4.0$_a$	0.0077$_{ab}$	129	12.6
Cultivars				
Cappelle-Desprez	3.7$_c$	0.0076$_a$	131	11.8$_b$
Little Joss	4.0$_{ab}$	0.0078$_a$	128	12.8$_a$
Prince Albert	4.2$_a$	0.0071$_b$	140	13.0$_a$
Holdfast	3.9$_b$	0.0078$_a$	129	12.9$_a$
s.e.d.	0.09	0.00013		0.17

area in the elevated CO$_2$ conditions was maintained for about 25 days longer than in other treatments (Figure 4).

4. Discussion

Both simulation and experimental results showed that altering the variance of temperature had the same order effect on the development and growth of wheat as changing its mean value. These results support the conclusions of Semenov and Porter (1995), who highlighted the importance of representing changes in both the mean and variability of climatic conditions in order to predict the impact of climatic change on crop development and yield. Thus, the experiment provides an all too rare link between simulation and experimental investigations.

Crop development rate was predominantly affected by temperature (Table II). Anthesis and maturity were advanced by several days for plants that experienced a 3 °C increase in mean temperature. Furthermore, plants in the three treatments that experienced the same mean daily temperatures reached anthesis and maturity on similar days, despite the increased diurnal variation in CE3 (Table II). Differences in development may have occurred if treatments had been imposed prior to vernalisation, when the extended period of lower temperatures in CE3 would
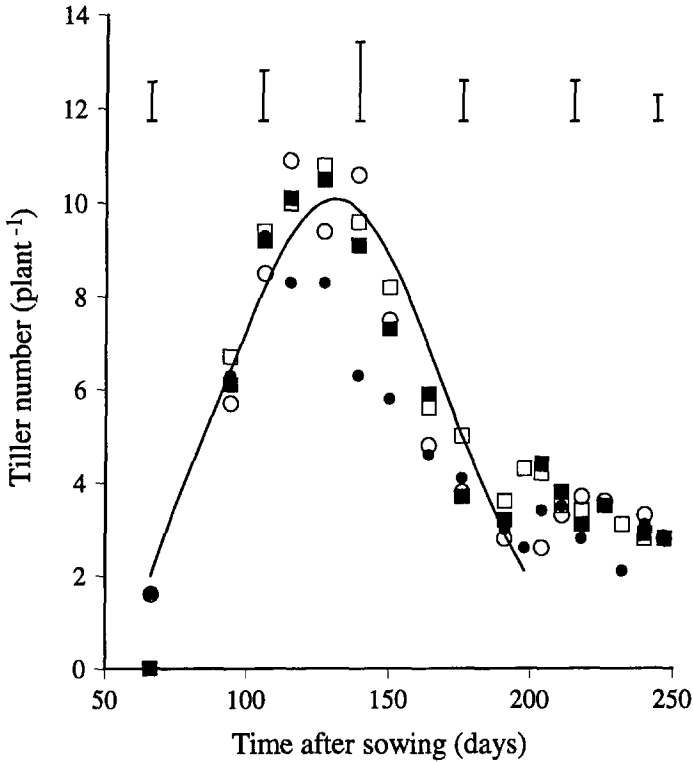
Figure 2. Tiller number against time after sowing for plants grown in four controlled environments
(CE1 □, CE2 ●, CE3 ○, CE4 ■), and the fitted Gaussian curve for CE1 (—). Treatments details
were given in Figure 1. Vertical lines represent standard errors of the mean across cultivars.

have reduced the time needed for vernalisation, and the higher temperatures would
accelerate post-vernalisation development (Semenov and Porter, 1995).

Temperature also influenced the time between anthesis and end of grain–filling,
which was 7 days shorter for plants in CE2, compared to the control (Table II).
Despite this difference, thermal time between these stages was comparable among
treatments (669 ± 29.9 °C d) and cultivars (644 ± 15.1 °C d), and in line with the
value of 650 °C d commonly reported for this period (Hay and Kirby, 1991) and
utilised in crop simulation modelling (Amir and Sinclair, 1991). The consistency
of the thermal time interval for this period supports conclusions that temperature is
the most important factor governing later stages of crop development (Porter and
Delécolle, 1988).

The total thermal time from the beginning of treatments until maturity was
highest for CE2 (2421 °C d), caused by an increase in time to anthesis (Table II).
Anthesis date in winter cultivars is affected by vernalisation and photoperiod,
which influence final leaf number (Hay and Kirby, 1991), but these were the same
for all treatments. The consistency of final leaf number (Table III) also suggests
that any effects of photoperiod or vernalisation were the same among treatments.

Table IV

Estimates of maximum (Max), days after sowing (DAS) to the maximum (Mean), rate of change (Rate), and final (FN) tiller number, derived from Gaussian curves fitted to observed tiller numbers over time. Results are for wheat plants of four cultivars grown in controlled environments (CE1–CE4). Environmental details were given in Figure 1. Note: (1) Results are for environments over cultivars and cultivars over environments. (2) s.e.d. is the standard error of the difference. (3) Values within columns with a letter subscript in common are not significantly different by least significant difference tests ($\alpha = 0.05$, 9 df)

	Max (tillers plant^{-1})	Mean (DAS)	Rate (tillers plant^{-1} d^{-1})	FN (tillers plant^{-1})
Environment				
CE1	10.3$_a$	131	0.118$_{ab}$	3.3$_a$
CE2	7.9$_b$	124	0.079$_b$	2.8$_b$
CE3	10.2$_a$	127	0.124$_a$	3.3$_a$
CE4	10.1$_a$	129	0.121$_{ab}$	3.6$_a$
Cultivars				
Cappelle-Desprez	8.9$_b$	130	0.098	3.0
Little Joss	10.9$_a$	126	0.127	3.5
Prince Albert	8.5$_b$	128	0.095	3.0
Holdfast	10.4$_a$	126	0.122	3.5
s.e.d.	0.65	2.47	0.0174	0.17

The increased thermal time to anthesis for plants in CE2 was probably caused by differences between the measured air temperature and the temperature perceived by the plants. Specifically, air temperatures may have overestimated the thermal time accumulated in CE2, relative to other treatments. Absolute humidity was the same in all treatments but, in these non-water limited environments, the higher air temperature in CE2 would have increased the vapour pressure deficit and allowed greater evaporative cooling of plants. Thus, the difference between air temperature and plant temperature would probably have been greater in this treatment, leading to an overestimation of accumulated thermal time based on air temperature. Similarly, prior to stem extension, when the meristem is below ground (Hay and Kirby, 1991) soil temperatures may be more appropriate for driving development (Gallagher and Biscoe, 1979; Jamieson et al., 1995) and the routine application of water may have moderated soil temperatures among treatments. Given the co-ordination between phenological events and leaf emergence (Hay and Kirby, 1991), the longer phyllochron (Table III) and reduced maximum tiller number (Table IV) found for CE2, was consistent with these proposed discrepancies in temperatures.

Differences in the coupling of air and plant temperatures may also be responsible for confounding the results of previous developmental studies. For example,

Table V

Estimates of relative growth rate (RGR), time to maximum growth rate (MGR), and maximum dry matter produced (DM), derived from logistic curves fitted to observed dry matter data over time. Results are for wheat plants of three cultivars grown in controlled environments (CE1–CE4). Environmental details were given in Figure 1. Note: (1) Results are for environments over cultivars and cultivars over environments. (2) s.e.d. is the standard error of the difference. (3) Values within columns with a letter subscript in common are not significantly different by least significant difference tests ($\alpha = 0.05$, 9 df)

	RGR $(g\,g^{-1}\,d^{-1})$	MGR (days after sowing)	DM $(g\,plant^{-1})$
Environment			
CE1	0.037	180_{ab}	14.3_a
CE2	0.047	169_b	11.6_b
CE3	0.038	195_a	15.2_a
CE4	0.042	184_{ab}	16.2_a
s.e.d.	0.0060	6.2	1.01
Cultivars			
Cappelle-Desprez	0.036	181	11.9_c
Little Joss	0.038	183	14.3_b
Holdfast	0.049	182	16.8_a
s.e.d.	0.0049	5.4	0.88

Hay and Kirby (1991) summarised results from Rawson (1970) and Wall and Cartwright (1974), and reported that higher air-temperature treatments resulted in slower development, in terms of thermal time, in 17 out of 26 comparisons. However, Rawson (1970) reported daily applications of Hoaglands solution and watering, and this probably influenced soil temperatures more than the targeted air temperatures.

In contrast to the results from leaf emergence and anthesis, the constancy in the thermal time interval between anthesis and physiological maturity, among treatments, cultivars and experiments, suggests air temperature was a good indicator of the temperature to which plants responded during this later phase. Post-anthesis, both stomatal (Marshall, 1978) and canopy (Hatfield, 1985) resistances have been shown to increase in wheat, thus, reducing evaporative cooling and the differential between air and plant temperature. Clearly, detailed measurements of air, soil, and apical meristem temperatures are required to corroborate this interpretation and to determine their importance for predicting plant development (Jamieson et al., 1995).
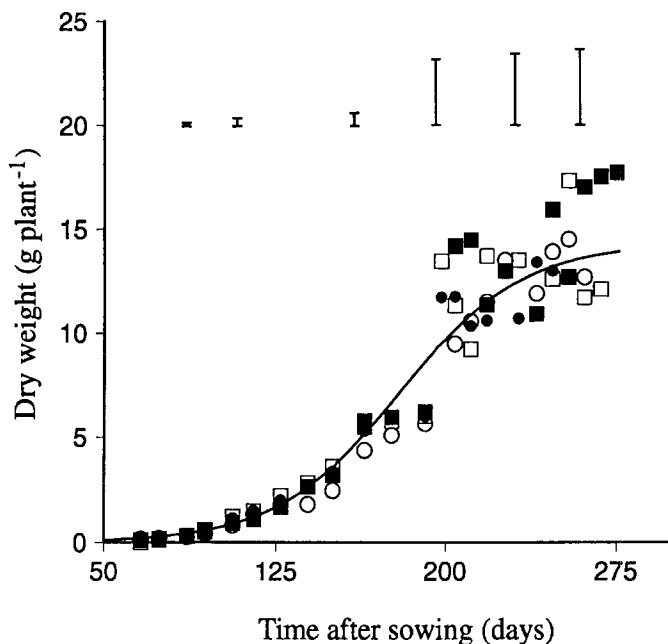
Figure 3. Dry weight against time after sowing for plants grown in four controlled environments (CE1 □, CE2 ●, CE3 ○, CE4 ■), and the fitted logistic curve for CE1 (—). Treatments details were given in Figure 1. Vertical lines represent standard errors of the mean across cultivars.

Temperature also affected the growth and yield of the plants. The maximum growth rate occurred earlier in CE2, and yields of grain and TDM were lower than in other treatments (Tables II and V). A similar magnitude of difference was found from simulation analyses for *cv* Avalon (Table I) and winter wheat crops in the U.K. generally (Semenov et al., 1993; Semenov and Porter, 1995). The decreased yields from CE2 were probably caused by the shorter crop growth duration (Table II), resulting in less absorbed PAR in CE2, particularly during grain-fill (Gallagher and Biscoe, 1978; Amir and Sinclair, 1991), and an increase in maintenance respiration rate (McCree and Amthor, 1982). The 10% reduction in grain yield for CE3 may have been caused by the extended lag phase reducing the period of grain-filling (Table II), although no differences in the rate of change of harvest index were detected for this treatment (Moot et al., 1996).

The major influence of the increased diurnal temperature variation in CE3 was a 27% reduction in the maximum leaf area relative to the control (Table VI, Figure 4). Leaf extension rates are linearly related to temperature, although the base temperature at which growth starts may vary (Gallagher and Biscoe, 1979; Gallagher et al., 1979). Low night, rather than high day, temperatures were implicated as the cause of differences in leaf area. The leaf area expansion for CE2 followed the same general pattern with a temporal displacement compared to CE1 (Figure 4), indicating that elevated day and night temperatures affected the rate, but not the
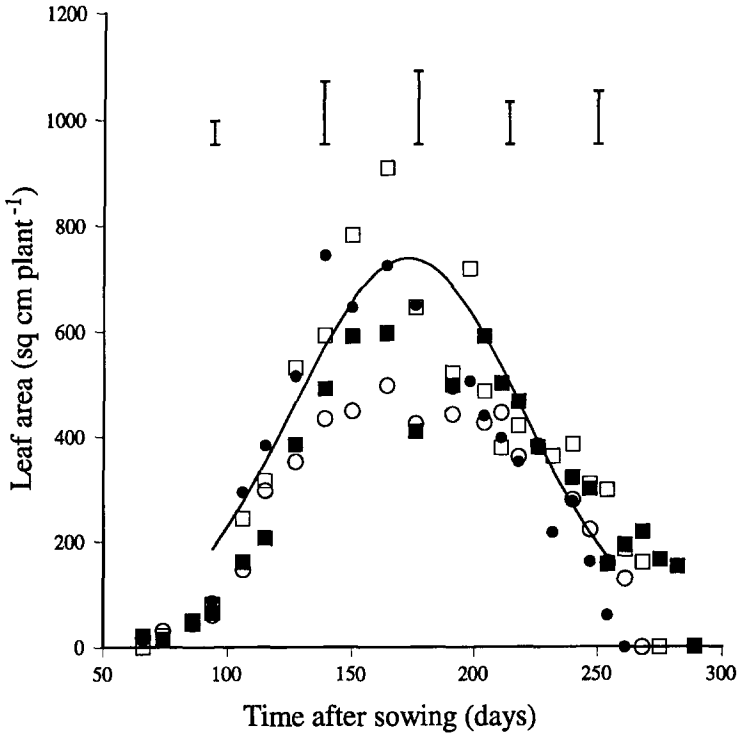
Figure 4. Leaf area against time after sowing for plants grown in four controlled environments (CE1 □, CE2 ●, CE3 ○, CE4 ■), and the fitted Gaussian curve for CE1 (—). Treatments details were given in Figure 1. Vertical lines represent standard errors of the mean across cultivars.

final magnitude, of expansion. During the period of rapid leaf expansion, 100–180 days after sowing (Figure 4), day temperatures in CE3 were between those in CE1 and CE2 (Figure 1). This implies the difference in day temperatures was not responsible for the reduced leaf area in CE3 (Figure 4). In contrast, the night temperature was lowest and maintained at 4–5 °C for CE3, but for CE1 it increased from 6 °C to 12.5 °C (Figure 1), and this period corresponded to the appearance of differences in leaf area (Figure 4).

Contrary to previous reports, there was no evidence of accelerated plant development (Goudriaan and the Ruiter, 1983) or leaf emergence (Schonfield et al., 1989) from elevated levels of CO_2. Indeed anthesis and, subsequently, maturity were delayed by 4 days in CE4 (Table II), and leaf emergence rates were also similar to those in CE1 (Table III). Lawlor and Mitchell (1991) postulated that small differences in development are due to indirect effects, such as altering the difference between plant and air temperatures, rather than via the direct effects of CO_2. Analyses of dry-matter production also showed no significant differences between control and elevated CO_2 treatments, although grain yield and TDM increased by 7 and 14% respectively, in CE4 (Tables II and V). A feature of the elevated CO_2

Table VI

Estimates of maximum leaf area (Max), days after sowing (DAS) to the maximum (Mean), and rate of change (Rate), derived from Gaussian curves fitted to leaf area over time. Results are for wheat plants of three cultivars grown in controlled environments (CE1–CE4). Environmental details were given in Figure 1. Note: (1) Results are for environments over cultivars and cultivars over environments. (2) s.e.d. is the standard error of the difference. (3) Values within columns with a letter subscript in common are not significantly different by least significant difference tests ($\alpha = 0.05$, 9 df)

	Max (cm² plant⁻¹)	Mean (DAS)	Rate (cm² plant⁻¹ d⁻¹)
Environment			
CE1	740_a	173_b	6.6_a
CE2	719_a	165_c	7.2_a
CE3	538_b	177_{ab}	4.7_b
CE4	585_b	182_a	4.8_b
Cultivars			
Cappelle-Desprez	608	173_{ab}	5.8
Little Joss	627	172_b	5.6
Prince Albert	699	178_a	6.3
Holdfast	649	174_{ab}	5.7
s.e.d.	55.0	2.32	0.64

treatment was the maintenance of approximately 200 sq cm per plant of green leaf area after the end of grain-filling (251 days after sowing). Although grain growth was no longer a sink for assimilate, the post-maturity increase in dry weight (Figure 3), suggests plants continued to photosynthesize and store carbohydrates. The continued accumulation of carbohydrates may have been responsible for a flush of small immature tillers which was observed about 20 days after grain growth had stopped. This phenomenon has also been observed in field studies, where the continued supply of CO_3 and water induced a flush of tillering in winter wheat after the end of grain-filling (R. H. Ellis, personal communication).

Increases in dry matter of over 30% are commonly simulated (Table I: Semenov et al., 1993) and reported under elevated CO_2 conditions (Cure and Acock, 1986), even in low light conditions (Gifford, 1977), due to additional tiller survival (Havelka et al., 1984). However, for the 'old' varieties used in this study, which have a high propensity to tiller (Figure 2), final tiller number was not increased by elevated CO_2 (Table IV), and the maximum leaf area was reduced by 21% (Table VI). Neales and Nicholls (1978) also reported a decrease in leaf area under elevated CO_2, associated with an increased specific leaf weight.

The comparatively small influence of elevated CO_2 on the yields of plants in the present study indicates CO_2 was not the main limiting factor in this environment.

Restricted root growth, reducing the sink capacity for photosynthates (Arp, 1991), and nutrient deficiency (Cure and Acock, 1986) may restrict plant responses to CO_2 in controlled environments compared to field studies (Lawlor and Mitchell, 1991). In part, these factors may explain the highly variable yield and TDM responses previously reported from controlled environment studies (Cure and Acock, 1986). Thus, controlled environment chambers seem less preferable than open-field studies for quantifying the seasonal effects of elevated CO_2.

The results showed that development was predominantly affected by temperature. There was no indication that this relationship was modified by the pattern of thermal time accumulation or by doubling the ambient CO_2 level. However, the growth processes, such as dry matter accumulation, leaf area and grain yield were affected by treatments. In particular, TDM and grain yield were lowest for the elevated mean temperature treatment, which was in agreement with our previous simulation studies, and leaf area was reduced by both an increase in diurnal temperature variation and a doubling of ambient CO_2.

Finally, we think that two important questions for the future, and particularly in the context of climate change studies, are: 'What is the relationship between environmental variability and any consequential plant-to-plant variability and are there temporal scales of variability (e.g., hourly, daily, seasonally) which do not affect plant growth?'. Secondly, much physiological experimentation is geared to elucidating how differences in growing conditions lead to differences in growth. However, 'What mechanisms lie behind the relatively conservative responses (e.g., leaf number and relative growth rate in this experiment; harvest index, Moot et al., 1996) of plants to wide fluctuations in their growing conditions?'.

Acknowledgments

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