



Effect of High Temperature Stress at Anthesis on Grain Yield and Biomass of Field-grown Crops of Wheat

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Spring wheat (*Triticum aestivum* L., 'Chablis') was grown under field conditions from sowing until harvest maturity, except for a 12-d period [70–82 days after sowing (DAS) coinciding with anthesis] during which replicated crop areas were exposed to a range of temperatures within two pairs of polyethylene-covered temperature gradient tunnels. At 82 DAS, an increase in mean temperature from 16 to 25 °C during this treatment period had no effect on above-ground biomass, but increased ear dry weight from 223 to 327 g m⁻² and, at 83 DAS, reduced root biomass from 141 to 63 g m⁻². Mean temperature over the treatment period had no effect on either above-ground biomass or grain yield at maturity. However, the number of grains per ear at maturity declined with increasing maximum temperature recorded over the mid-anthesis period (76–79 DAS) and, more significantly, with maximum temperature 1 d after 50% anthesis (78 DAS). Grain yield and harvest index also declined sharply with maximum temperature at 78 DAS. Grain yield declined by 350 g m⁻² at harvest maturity with a 10 °C increase in maximum temperature at 78 DAS and was related to a 40% reduction in the number of grains per ear. Grain yield was also negatively related to thermal time accumulated above a base temperature of 31 °C (over 8 d of the treatment from 5 d before to 2 d after 50% anthesis). Thus, grain fertilization and grain set was most sensitive to the maximum temperature at mid-anthesis. These results confirm that wheat yields would be reduced considerably if, as modellers suggest, high temperature extremes become more frequent as a result of increased variability in temperature associated with climate change.

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Key words: *Triticum aestivum*, spring wheat, temperature, grain number, grain yield, root growth.

INTRODUCTION

It is predicted that increases in 'greenhouse gas' concentrations will result in a rise in mean temperatures of about 2 °C by the middle of the next century (Kattenberg *et al.*, 1995). Although yields of temperate crops increase with enhanced CO₂ concentrations, this may be offset by the negative effects of warmer temperatures in determinate crops (Mitchell *et al.*, 1993; Moot *et al.*, 1996; Wheeler *et al.*, 1996a, b; Batts *et al.*, 1997, 1998).

The duration of grain filling in cereals is determined principally by temperature (Sofield *et al.*, 1977; Slafer and Rawson, 1994; Wheeler *et al.*, 1996b). In wheat, high temperatures (> 31 °C) after anthesis can decrease the rate of grain-filling (Al-Khatib and Paulsen, 1984; Randall and Moss, 1990; Stone *et al.*, 1995; Wardlaw and Moncur 1995), whilst high temperatures imposed before anthesis can also decrease yield (Wardlaw *et al.*, 1989; Tashiro and Wardlaw, 1990; Hunt *et al.*, 1991). In winter wheat, high temperature episodes occurring near to anthesis can reduce the number of grains per ear and the subsequent rate of increase in harvest index, resulting in smaller grain yields (Wheeler *et al.*, 1996b).

The effect of short periods of exposure to high temperatures (> 31 °C) on wheat grain yields are thought to be equivalent to a 2–3 °C warming in the seasonal mean temperature (Wheeler *et al.*, 1996b). Also, up to a 23% reduction in grain yield has been reported from as little as 4 d exposure to very high temperatures (Randall and Moss, 1990; Hawker and Jenner, 1993; Stone and Nicolas, 1994). Periods at such high temperature occur frequently during grain filling in both Mediterranean and continental climates, and such extremes may be more frequent throughout Europe in future climates of warmer mean temperatures (Barrow and Hulme, 1996).

Since high temperature episodes appear to be more severe around anthesis these may affect the pollination process. Grain set is reduced by temperatures warmer than 30 °C during the period from the onset of meiosis in the male generative tissue to the completion of anthesis (Smika and Shawcroft, 1980). The production and transfer of viable pollen grains to the stigma, germination of the pollen grains and growth of the pollen tubes down the style, and fertilization and development of the zygote are necessary for successful seed set. Although all these phases are temperature sensitive, some are more sensitive than others and high temperatures can cause both male and female sterility in wheat (Saini and Aspinall, 1982).

The response of roots to high temperature may also be important since transpiration cooling, which can limit the

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effects of thermal stress, depends on evaporation and the supply of water to the leaf from the soil. Any effects of thermal stress on the morphology and physiology of the root system may influence water movement through the plant (Mahan, McMichael and Wanjura, 1995). Moreover, roots are an important sink for assimilates in wheat. Since remobilization of assimilates occurs after anthesis, assimilates from roots may supplement primary sources from the leaf and stem (Cook and Evans, 1978; Hay and Walker, 1989). Research has focused on the development of root biomass in field or pot-grown plants of winter wheat exposed to higher seasonal mean temperatures from sowing (Mitchell *et al.*, 1993; Batts *et al.*, 1998). However, root length density tends to decline from anthesis onwards due to senescence (Belford and Henderson, 1985) and the response of roots of a field-grown spring wheat crop exposed to high temperature episodes close to anthesis is not known.

Here we examine whether exposure of field-grown crops of spring wheat to high temperatures for a 12 d period, beginning close to the start of anthesis, affected: (1) above- and below-ground biomass immediately after the treatment; and (2) above-ground biomass, grain yield, and components of yield at harvest maturity.

MATERIALS AND METHODS

Crop growing conditions

Spring wheat (*Triticum aestivum* L. 'Chablis', PBI, Cambridge) was sown by hand on 18 Apr. 1996, in rows 0.12 m apart, into a sandy loam overlying London Clay at The University of Reading School of Plant Sciences field unit (51° 27' N, 0° 56' W). Four 20 × 2 m areas were sown. Mean seedling emergence was 376 plants m⁻². Each 20 × 2 m area was divided into six plots each 3 m long; the discards within each plot were 0.5 m long at each end with one plant row discard at each side. There was an additional discard of 1.0 m at both ends of each area.

The wheat crop was grown in ambient conditions until 70 d after sowing (DAS) immediately before the anticipated date of anthesis. At this time, two replicate 3 m wide × 25 m long temperature gradient tunnel systems (Hadley *et al.*, 1995), clad in polyethylene and double-walled, were erected over pairs of crop areas. Temperature gradient tunnels covered the crop from 27 June to the morning of 9 July (70–82 DAS); all plots had reached full anthesis by 9 July. A temperature gradient was imposed from one end of a crop area, along the length of the first tunnel and continued down the second tunnel so that, although all plots were subjected to the normal diurnal variation in temperature, mean temperature increased progressively along the crop areas. This method of modifying the environment in which field crops are grown within temperature-gradient tunnels using a split-heat pump system has been described in detail by Hadley *et al.* (1995). Note that in this application, the heat exchangers were operated in heating (rather than cooling) mode. As a consequence of this, and the fact that the refrigeration equipment is regularly defrosted by reversing the temperature gradient briefly (Hadley *et al.*, 1995), the mean temperature in the coolest plot was about

2 °C warmer than ambient during the 12 d treatment period. Whereas controlled-environment investigations often maintain temperature constant during the day, these field-grown crops were subjected to both short-term variation in temperature, for example as occurs in mid-summer as direct solar radiation is temporarily interrupted by clouds, and to diurnal variation in temperature.

Air temperature was monitored at seven locations in each tunnel using screened, aspirated copper-constantan thermocouples installed below in-crop fans used to circulate air within the tunnels (Hadley *et al.*, 1995). Soil temperature at a depth of 50 mm was monitored at 5 m intervals along each tunnel using copper-constantan thermocouples. Kipp solari-meters were used to measure the radiation transmission through the polyethylene walls, which averaged 65% of incident radiation. Temperature and radiation were recorded every 10 sec and the 10 min means were stored using a data logger (CR10, Campbell Scientific Ltd., Shepshed, UK). Carbon dioxide was injected into each tunnel through perforated polyethylene pipes along the length of the tunnel in order to eliminate any CO₂ deficits along the tunnels. Carbon dioxide concentration was controlled using a solenoid valve connected to an IRGA controller (EGM-1 PP Systems, Hitchin, UK). The average daily mean CO₂ concentration in each pair of tunnels was thereby maintained close to their set points of 350 µmol mol⁻¹ along the length of the tunnels. The polyethylene covers were removed from all plots on 9 July in order that subsequent grain development occurred under ambient field conditions. Thus, ambient conditions were provided to all crop areas throughout the period from sowing to harvest maturity except for the 12 d period from 70–82 DAS.

Normal crop husbandry practices were followed in order to ensure a non-limiting nutrient and water supply and to minimize pest and disease incidence. Soil analyses indicated the following: N = 0.2%; P = 95.9 µg g⁻¹ and K = 342.2 µg g⁻¹; pH = 6.6. Consequently, 120 kg N ha⁻¹ was applied at sowing and 30 kg N ha⁻¹ at the three-leaf stage as ammonium nitrate. The following herbicides, fungicides and pesticides were applied: a pre-emergence herbicide (Tribunil at 2.25 kg ha⁻¹, MAFF No. 02169) on 19 March; a fungicide spray (Sportak Delta 460 at 1.25 l ha⁻¹, Schering EC05107) on 6 June and 11 July; a fungicide fumigant (Fungaflor, Imazalil MAFF No. 03599) on 2 July; a pesticide fumigant (Fumite 7000 Pirimiphos Methyl) on 1 July; and a pesticide spray (Malathion 60 at 2.1 l ha⁻¹, MAFF 05714) on 18 July and 5 August. The crops were irrigated through a network of porous pipes (20 mm bore, Entek, Iceland) laid along each area on the soil surface until 23 July (after the start of grain filling). Irrigation was supplied in order to maintain the soil near field capacity.

Crop development

The time of the double ridges stage was determined by dissection, under a stereomicroscope, of five main stem plant samples taken from each crop area at 3 d intervals. Double ridge was assumed to have occurred when four of the five plants reached this developmental stage. The time

by which half the plants were at anthesis (termed 50% anthesis; Porter *et al.*, 1987) was recorded in each plot. Harvest maturity was defined as that stage when grain moisture content declined naturally to 15–18%.

Measurements of shoots and roots

A 0.18 m² and 0.25 m² area of above-ground material was harvested within each plot before and after the 12 d temperature treatment, respectively, and separated into leaves and stems (before treatment) or leaves, stems and ears (after treatment). At crop maturity, a 1.25 m² area of above-ground material in each plot was harvested and separated into straw, chaff and ear fractions. The ears were counted and grains removed by threshing. The fresh weight of chaff and straw was determined immediately. Dry mass was determined after drying in a forced-air oven at 80 °C for at least 72 h. The grains were counted and the moisture content of two replicates of 3 g subsamples from each of the sub-plots was determined by drying at 130 °C for 2 h in accordance with the rules of the International Seed Testing Association (1993*a, b*). The total dry mass of the grains was calculated from the fresh mass of the whole sample and the grain moisture content.

Root biomass was determined from soil cores, taken using an auger to a depth of 40 cm in one pair of tunnels, on and between the rows 2 d before the treatment and 1 d after the treatment ended. Roots were dried at 80 °C for 48 h in order to determine their mass (g m⁻²); results are presented for cores taken on the row.

Statistical analyses

The effect of temperature applied for a 12 d period around anthesis on above- and below-ground biomass, grain yield, and components of yield was investigated by regression analysis using mean temperature, maximum temperature, or the thermal time [accumulated above a base temperature of 31 °C (Wheeler *et al.*, 1996*b*) during 8 d of the treatment period] as independent variables.

RESULTS

Ambient mean daily air temperature and solar radiation from sowing to harvest maturity and crop developmental stages are shown in Fig. 1. Ambient soil temperature followed air temperature closely (data not shown). Mean air temperature during the 12 d temperature treatment increased linearly with distance along the four tunnels, except for some non-linearity towards the warmer ends of Tunnels 2 and 4 (Fig. 2); ambient mean air temperature during the 12 d period was 14.0 °C. The trends for mean soil temperature along the tunnels were broadly similar to those for air temperature up to a mean air temperature of 19 °C, but above this value soil was cooler than air (Fig. 2). Anthesis began on the third day (72 DAS), 50% anthesis occurred in all but five plots on the eighth day (77 DAS), and crops in

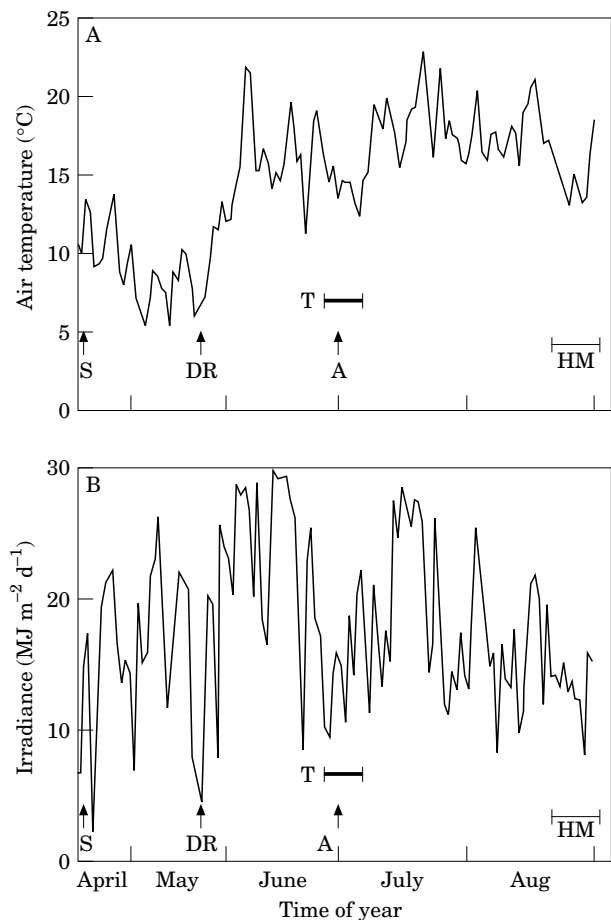


FIG. 1. Daily mean air temperatures (A), and mean daily incident total solar radiation (B) from sowing (S, 18 April) to harvest maturity recorded outside the temperature gradient tunnels. Crop developmental stages shown are: double ridges (DR); early anthesis (A); and harvest maturity (HM). The period of the 12 d temperature treatment is also shown (T).

almost all plots reached full anthesis by the eleventh day (80 DAS) of the 12 d treatment period.

Before the temperature gradient was imposed, no systematic differences in total above-ground biomass ($P > 0.05$) were detected among plots (Fig. 3A). Above-ground biomass immediately after the 12 d treatment period was not affected by mean temperature ($P > 0.05$), but had increased by 24% over the 12 d period from 886 to 1102 g m⁻² (Fig. 3A). The 12 d temperature treatment ended before grains began to accumulate dry matter, i.e. before the end of the lag phase which precedes grain filling. Nevertheless, differences in the mass of developing ears were detected: ear dry mass immediately after treatment increased linearly with mean temperature ($P < 0.001$; Fig. 3A). Similarly, although no difference in total root biomass among plots was detected before treatments began (average = 139 g m⁻²), 1 d after the treatment period ended a significant negative linear relation between root biomass and mean temperature was detected ($P < 0.001$; Fig. 3B).

Harvest maturity spanned 2 weeks with crops in the plots exposed to higher mean temperatures over the treatment

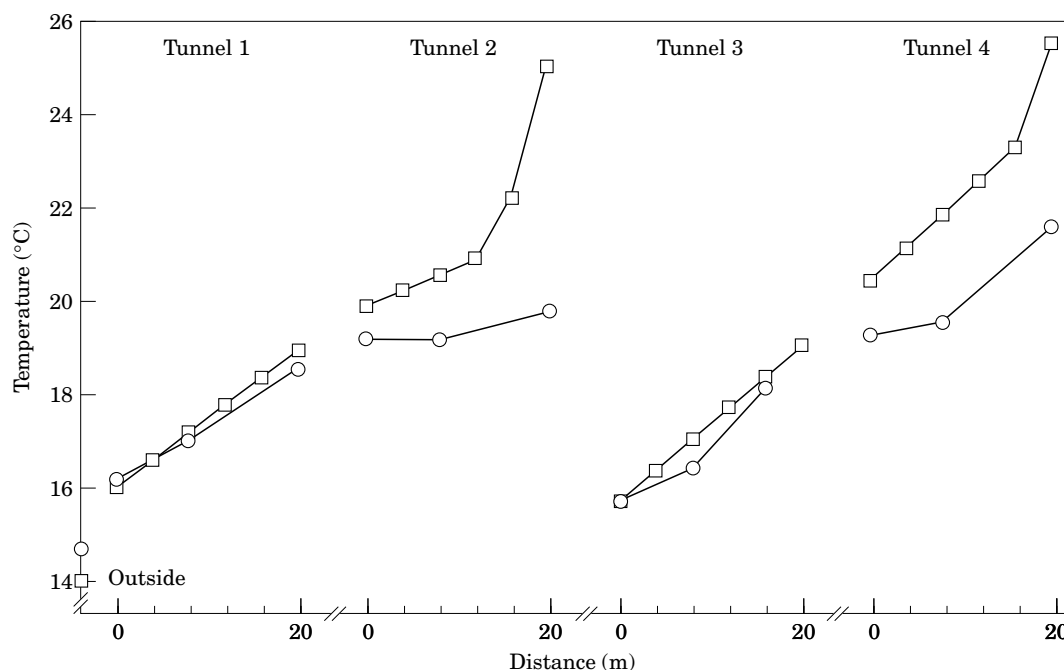


FIG. 2. Relationship between mean air temperature (□) and mean soil temperature at 50 mm depth (○) during the 12 d temperature treatment for each plot and distance along each of the four temperature gradient tunnels.

period maturing earlier (Table 1). However, no relationship between grain yield and development duration was observed ($P > 0.05$). In addition, at harvest maturity, no significant relationship between either above-ground biomass or grain yield per unit area and mean temperature during the 12 d treatment was detected ($P > 0.05$; Fig. 4). Nevertheless, grain yield varied more than two-fold among extreme plots.

In order to investigate further this variation in grain yield, the relations between the number of grains per ear at harvest maturity and the maximum temperature for each of the 12 d of temperature treatment were examined in turn (Fig. 5A–L). Because of variation in ambient temperature and incident solar radiation, the maximum temperatures to which the crop in each plot was exposed to varied from day to day during the treatment. The number of grains per ear was positively correlated with the maximum temperature experienced on days 1 and 2 (Fig. 5A and B), but these temperatures were comparatively cool. No significant response of grains per ear to the maximum temperature on either day 3 or 4 was detected (Fig. 5C and D), while the response on day 5 was negative (Fig. 5E) whereas that on day 6 was positive (Fig. 5F). In contrast, from day 7 to day 10, corresponding to mid-late anthesis, there were clear, consistent, and significant ($P < 0.01$) negative responses of the number of grains per ear to maximum temperature (Fig. 5G–J); the closest relationship was for the maximum temperature experienced on day 9. Grain numbers declined from approx. 26 per ear at cooler maximum temperatures of 28 °C to approx. 15 per ear at 38 °C on day 9, 1 d after 50 % anthesis (Fig. 5I). After this 4 d period (i.e. days 7 to 10), no effect of maximum temperature on the number of grains per ear was detected ($P > 0.05$; Fig. 5K and L).

Consequently the observations of grain yield, biomass, etc. at harvest maturity were regressed against the maximum

temperature experienced on day 9 of treatment. Significant negative linear relationships between grain dry mass per unit area and maximum temperature on day 9 ($P < 0.001$; Fig. 6A) and harvest index and maximum temperature on day 9 ($P < 0.01$; Fig. 6B) were detected. In contrast, no significant relationships were detected ($P > 0.05$) between the number of ears per unit area (mean \pm s.e.: $825 \pm 18 \text{ m}^{-2}$), straw dry mass ($1154 \pm 30 \text{ g m}^{-2}$) per unit area, or total above-ground biomass per unit area ($1837 \pm 40 \text{ g m}^{-2}$), and the maximum temperature on day 9.

At harvest maturity, there was a close, positive linear relationship between mean grain dry mass m^{-2} and the number of grains m^{-2} ($P < 0.001$; Fig. 7), whereas no significant relationship was detected ($P > 0.05$) between mean total grain dry mass m^{-2} and individual grain dry mass ($684 \pm 33 \text{ g m}^{-2}$). Individual grain dry mass varied only between extremes of 35.4 and 42.7 mg among the plots ($39.6 \pm 0.33 \text{ mg}$).

In order to determine whether cumulative exposure to high temperatures at anthesis reduced grain yield per unit area, the temperature stress during anthesis was calculated as the thermal time accumulated, over 10 min intervals, above a base temperature of 31 °C between days 3 and 10 of treatment (i.e. from early to almost full anthesis). There was a significant negative linear relationship ($P < 0.001$) between grain dry mass per unit area and the thermal time (Fig. 8).

DISCUSSION

This field study gives new information on the response of wheat root mass and grain yield to high temperature episodes occurring close to anthesis. Mean temperature during the 12 d temperature treatment affected ear dry mass (Fig. 3A), presumably by altering developmental progress,

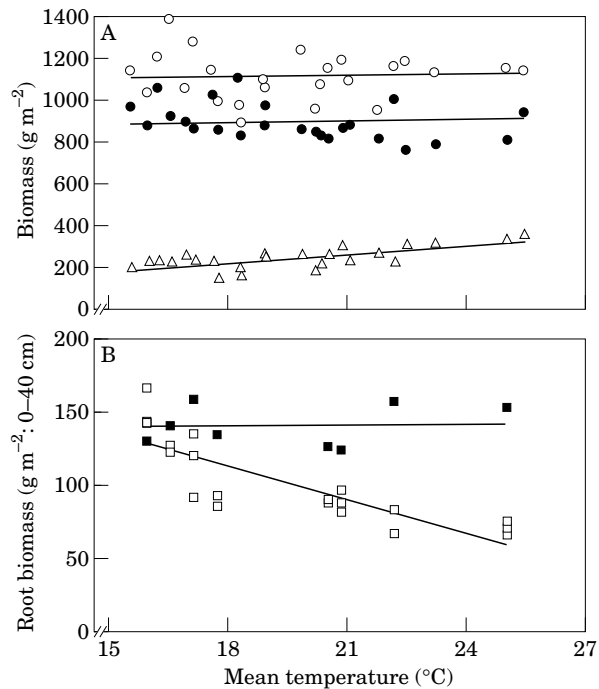


FIG. 3. Relationships between above-ground biomass (●, ○) ear dry mass (△) and mean temperature over the 12 d treatment (A); and total root biomass (■, □) at a depth of 0–40 cm and mean temperature over the 12 d treatment (B). Solid and open symbols represent results immediately before and after the treatment, respectively. Horizontal lines shown here and in subsequent figures indicate no significant relationship ($P > 0.05$). Fitted lines are: A, mean above-ground biomass before treatment, $y = 886.2$ (s.e. = 18.9), and after treatment, $y = 1101.9$ (s.e. = 22.9); ear dry mass after treatment, $y = 17.55$ (s.e. = 56.8) + 10.89 (s.e. = 2.9) x , ($r^2 = 0.40$; 22 d.f.); B, root biomass before treatment, $y = 138.8$ (s.e. = 4.9), and after treatment, $y = 254.5$ (s.e. = 22.3) – 7.9 (s.e. = 1.1) x ($r^2 = 0.71$, 20 d.f.). For roots after treatment, each replicate is presented.

TABLE 1. Dates of anthesis and harvest maturity of experimental treatments

Development stage	Mean date (DAS)	Range of dates (DAS)
Sowing	18 Apr. 1996	—*
Double ridge	19 May 1996 (31)	—*
50 % anthesis†	4 Jul. 1996 (77)	3–5 Jul. 1996 (76–78)
100 % anthesis	8 Jul. 1996 (81)	7–9 Jul. 1996 (80–82)
Harvest maturity‡	24 Aug. 1996 (128)	19 Aug.–1 Sept. 1996 (123–136)

DAS, Days after sowing.

* Development stage on same day.

† As defined by Porter *et al.* (1987).

‡ 15–18 % moisture content.

and root biomass down to 40 cm of soil depth (Fig. 3B) at the end of anthesis. However, no other effects of mean temperature during this period on yield or yield components were detected either at the end of anthesis or at harvest maturity.

The loss of biomass of roots at a mean temperature of 26 °C was three-fold greater than at 17 °C (Fig. 3B). Wheeler *et al.* (1997) found that the root:total biomass ratio

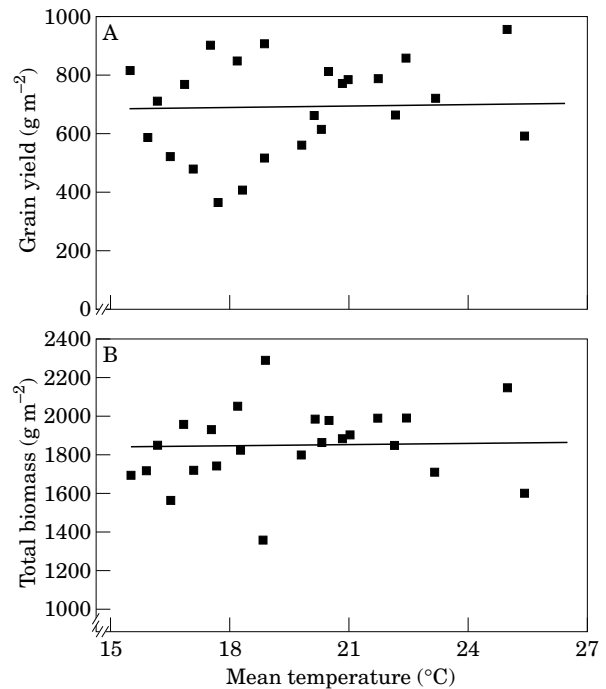


FIG. 4. Effect of mean temperature during the 12 d treatment on grain yield (A) and total biomass (B) at harvest maturity. Mean lines for A: $y = 1837$ (s.e. = 39.98) and B: $y = 684.1$ (s.e. = 32.7).

declined more rapidly after flowering in a high-temperature sensitive, compared to a high-temperature tolerant genotype of groundnut (*Arachis hypogaea* L.) exposed to high temperatures for 6 d, but a causal link between the partitioning of biomass to roots and to seed was unclear. Also, in both pot-grown plants of wheat (Mitchell *et al.*, 1993) and field-grown crops of wheat (Batts *et al.*, 1998), the decline in root biomass at anthesis was greater following exposure to warmer seasonal mean temperatures from sowing.

Wheat root biomass tends to decline around the time of anthesis (Belford and Henderson, 1985) which coincides with the remobilization of assimilates from various vegetative plant parts and translocation to the developing grain (Hay and Walker, 1989). The greater decline in root biomass at warmer temperatures observed in our study could be due to several factors: more rapid senescence, increased respiration or saprophytic decay, or perhaps greater repartitioning of carbon to the developing ear at the hotter as compared with the cooler temperatures (Fig. 3A). The latter suggestion is supported by the numerical similarity of the positive and negative gradients for ear dry weight and root biomass, respectively, in response to mean temperature (Fig. 3). Wardlaw, Solfield and Cartwright (1980) found in pot-grown wheat exposed to higher temperatures from anthesis that a greater movement of ^{14}C -labelled photosynthate from the flag leaf to the ear was due to a change in the pattern of distribution, with less going to roots. However, the authors found no parallel increase in the rate of ear dry matter accumulation and suggested any increase in dry matter may have been balanced by increased respiratory losses. Given that differences in temperature over a

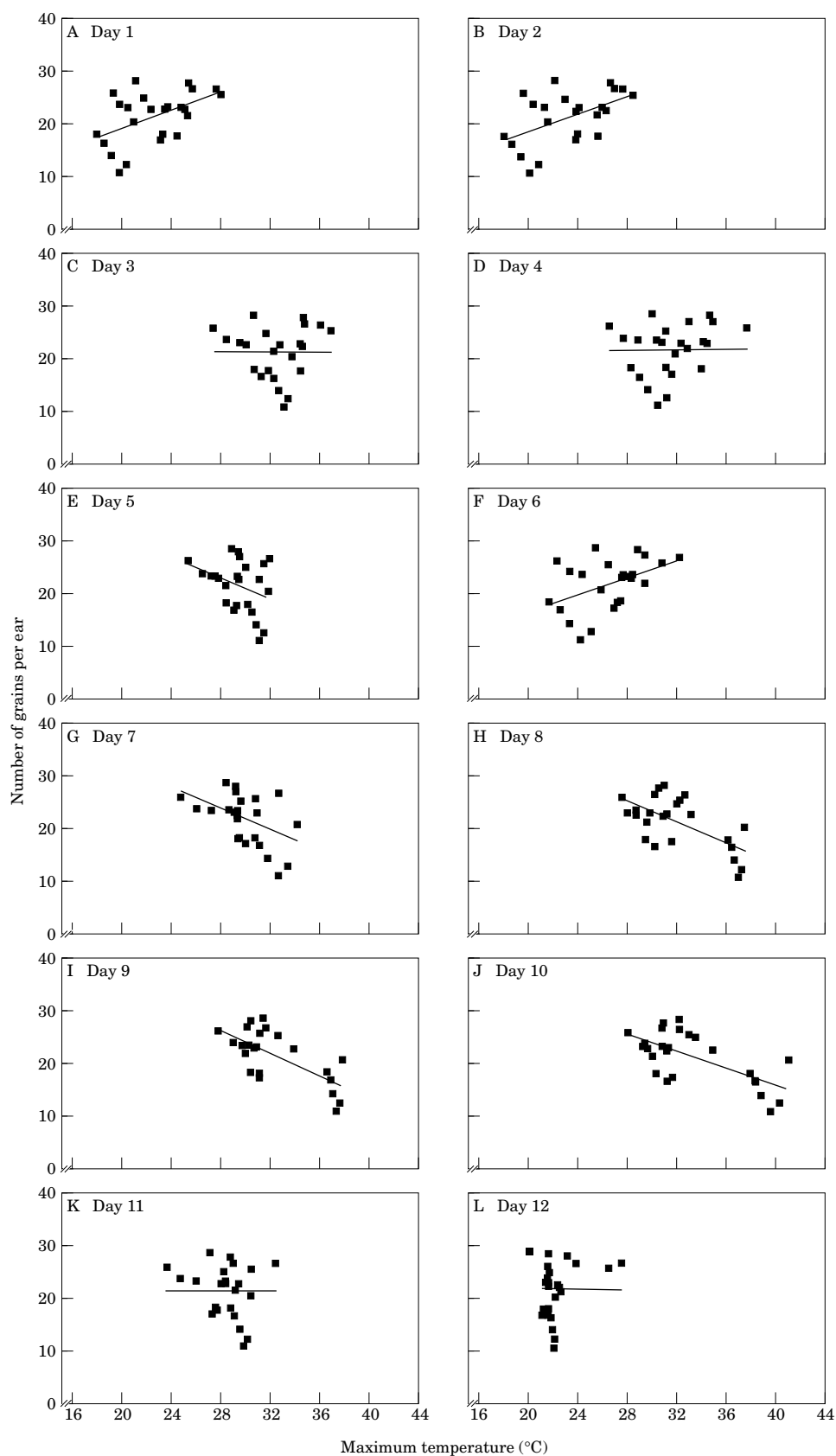


FIG. 5. For legend see facing page.

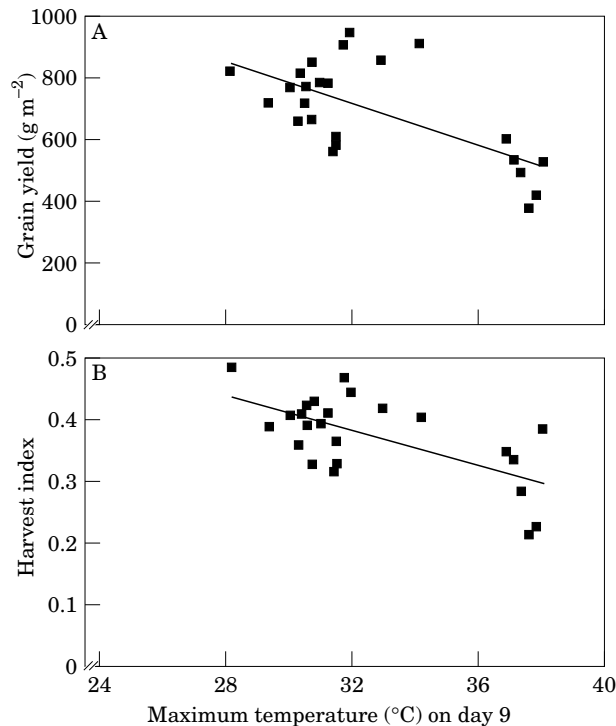


FIG. 6. Relationship between grain dry mass (A) and harvest index at harvest maturity (B) and the maximum temperature on day 9 of the 12 d temperature treatment. The regression lines shown are: A, $y = 1808.3$ (s.e. = 274.4) $- 34.47$ (s.e. = 8.38) x , ($r^2 = 0.44$; 22 d.f.); B, $y = 0.838$ (s.e. = 0.118) $- 0.0143$ (s.e. = 0.004) x , ($r^2 = 0.42$; 22 d.f.).

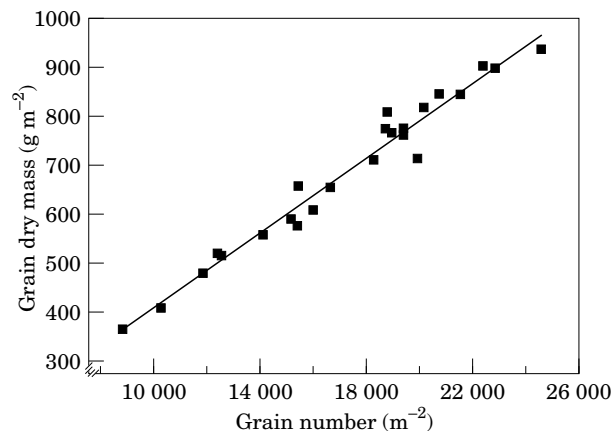


FIG. 7. Relationship between grain dry mass per unit area and the number of grains per unit area. The regression line shown is: $y = 24.76$ (s.e. = 25.79) $+ 0.038$ (s.e. = 0.001) x , ($r^2 = 0.97$; 22 d.f.).

comparatively short period can affect the reduction in root biomass so substantially, this is an area which should be investigated further especially since higher root temperatures

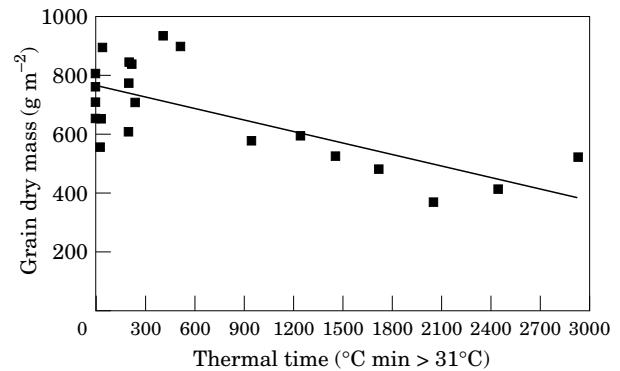


FIG. 8. Relationship between grain dry mass at harvest maturity and thermal time (accumulated, in 10 min intervals, above a base temperature of 31 °C between days 3 and 10 of the 12 d temperature treatment). The regression line shown is: $y = 769.65$ (s.e. = 28.49) $- 0.134$ (s.e. = 0.03) x , ($r^2 = 0.53$; 22 d.f.).

in wheat have been shown to retard shoot and kernel growth (Wardlaw and Moncur, 1995; Kuroyanagi and Paulsen, 1988).

Whereas there was no relationship between grain yield and mean temperature (Fig. 4A) and above-ground biomass and mean temperature (Fig. 4B) at maturity, a further examination showed a negative linear relationship between grain number and maximum temperatures (Fig. 5) and grain yield and maximum temperatures around mid-late anthesis (Fig. 6A). Thus, there was no simple association between the effects of mean temperature and maximum temperature. The results, therefore, show the dramatic effect of brief exposure to high temperature during anthesis, and that plants at mid-anthesis are particularly sensitive to high temperature stress (Fig. 5). This decline in grain numbers per ear (of approx. 40%) from the coolest to the warmest maximum temperature was associated with a decrease in grain yield from 850 g m⁻² to 500 g m⁻² (Fig. 6A) and a decline in harvest index from 0.43 to 0.30 (Fig. 6B), but was not related to individual grain weight. Grain abortion due to high temperature was also found by Saini and Aspinall (1982), Thorne and Wood (1987), Tashiro and Wardlaw (1990), Mitchell *et al.* (1993) and Wheeler *et al.* (1996b). Some parthenocarpic grains were observed in the high maximum temperature treatments in the present study (data not shown). Mitchell *et al.* (1993) attributed a high proportion of sterile grains to a maximum temperature of 27 °C whilst Wheeler *et al.* (1996a) indicated that this was due to temperatures in excess of 31 °C, at 50% anthesis. Saini and Aspinall (1982) showed that low grain fertility was induced by exposure to high temperature for as little as 1 d during critical periods between booting and anthesis, which corresponds to our conclusion from Fig. 5.

The presentation of results in Figure 5 implies that a single high-temperature episode to plants at anthesis caused

FIG. 5. Relationship between number of grains per ear at harvest maturity and maximum temperature on each of days 1–12 (A–L) of the temperature-treatment period. Fitted regression lines are: A, $y = 2.56$ (s.e. = 7.21) $+ 0.82$ (s.e. = 0.32) x , ($r^2 = 0.23$; 22 d.f.); B, $y = 1.88$ (s.e. = 6.98) $+ 0.82$ (s.e. = 0.30) x , ($r^2 = 0.26$; 22 d.f.); E, $y = 49.23$ (s.e. = 16.42) $- 0.96$ (s.e. = 0.56) x , ($r^2 = 0.12$; 22 d.f.); F, $y = 0.22$ (s.e. = 8.91) $+ 0.79$ (s.e. = 0.33) x , ($r^2 = 0.20$; 22 d.f.); G, $y = 56.01$ (s.e. = 12.33) $- 1.16$ (s.e. = 0.41) x , ($r^2 = 0.27$; 22 d.f.); H, $y = 52.81$ (s.e. = 8.18) $- 0.98$ (s.e. = 0.25) x , ($r^2 = 0.41$; 22 d.f.); I, $y = 57.16$ (s.e. = 7.94) $- 1.10$ (s.e. = 0.24) x , ($r^2 = 0.49$; 22 d.f.); J, $y = 46.16$ (s.e. = 6.27) $- 0.75$ (s.e. = 0.19) x , ($r^2 = 0.42$; 22 d.f.). In C, D, K and L, the mean value is shown: $y = 21.16$ (s.e. = 0.99) grains per ear.

the variation in the number of grains per ear and thus, given a constant number of ears per unit area (825 m^{-2}), in grain yield per unit area (Fig. 7). Since thermal amplitude varies daily in field environments, a more useful quantification of the effect of high temperature episodes may be provided through the calculation of 'stress' thermal time. In the present study, the integration of high temperatures (i.e. accumulated thermal time above 31°C over 8 d of the treatment during anthesis) was related to a 50% reduction in grain yield (Fig. 8). Thus, an alternative explanation is that cumulative exposure to high temperatures at anthesis reduces grain number and thus grain yield. This thermal time stress relation is of considerable potential in modelling impacts of warmer air temperatures on yields of field-grown wheat.

Wiley and Dent (1969) suggested that grain yield is not limited by assimilate supply nor by the storage capacity of the ear alone, but by both. Wheeler *et al.* (1996b) showed in winter wheat 'Hereward' that when high temperatures at anthesis reduced grain numbers per ear below a threshold (the critical grain number), grain yield was reduced as a result of sink limitations. That critical value was about $20000 \text{ grains m}^{-2}$ (Wheeler *et al.*, 1996b) and is broadly similar to the current results for spring wheat in which grain yield declined with reduction in grain number m^{-2} below about $22000\text{--}25000$ with variation in grain number explaining 97% of the variation in final grain yield (Fig. 7). Thus, similarly in this study with spring wheat, the majority of the reduction in grain yield can be attributed to sink limitation given the similarities of the declines in grain number, grain yield and harvest index with an increase in the maximum temperature (Figs 5I, 6A and B) and the fact that individual grain mass did not compensate for the reduced number of grains per unit area.

In conclusion, warmer maximum temperatures over 4 consecutive days close to anthesis directly reduced grain number and, as a consequence, grain yield at harvest maturity, while higher mean temperatures reduced root biomass immediately after anthesis. If climates become both warmer and more variable, the occurrence of high temperature during anthesis could reduce wheat grain yields substantially. Deleterious effects of higher temperatures on root growth could pose a further threat to crop production if high temperatures are also associated with periods of drought in future climates.

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