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The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO_2

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Abstract

Winter wheat (*Triticum aestivum* L. cv. Hereward) was grown in the field inside polyethylene-covered tunnels at a range of temperatures at either 380 or 684 μmol mol^{-1} CO_2. Serial harvests were taken from anthesis until harvest maturity. Grain yield was reduced by warmer temperatures, but increased by CO_2 enrichment at all temperatures. During grain-filling, individual grain dry weight was a linear function of time from anthesis until mass maturity (attainment of maximum grain dry weight) within each plot. The rate of progress to mass maturity (the reciprocal of time to mass maturity) was a positive linear function of mean temperature, but was not affected by CO_2 concentration. The rate of increase in grain dry weight per ear was 2.0 mg d^{-1} greater per 1 °C rise, and was 8.0 mg d^{-1} greater at 684 compared with 380 μmol mol^{-1} CO_2 at a given temperature. The rate of increase in harvest index was 1.0% d^{-1} in most plots at 380 μmol mol^{-1} CO_2 and in open field plots, compared with 1.18% d^{-1} in all plots at 684 μmol mol^{-1} CO_2. Thus, the increased rate of grain growth observed at an elevated CO_2 concentration could be attributed partly to a change in the partitioning of assimilates to the grain. In contrast, the primary effect of warmer temperatures was to shorten the duration of grain-filling. The rate of grain growth at a given temperature and the rate of increase in harvest index were only independent of the number of grains per ear above a critical grain number of 23–24 grains per ear (~20 000 grains m^{-2}).

Key words: Winter wheat, grain growth, temperature, CO_2, harvest index, critical grain number.

Introduction

Grain growth in wheat (*Triticum aestivum* L.) comprises three phases, each of which is influenced by environment. Little increase in grain dry weight occurs during an initial lag phase, which lasts about 4–6 d at 18 °C (Hunt *et al.*, 1991), immediately after anthesis. Grain dry weight then increases rapidly during the grain-filling period until a maximum dry weight is attained, after which it remains approximately stable while the grain dries. The end of the grain-filling period has been termed mass maturity (Ellis and Pieta-Filho, 1992). Grain dry weight increases as a linear function of time during the grain-filling phase (Gallagher *et al.*, 1976; Biscoe and Gallagher, 1977; Brocklehurst, 1977; Jenner, 1991). Thus, grain dry weight can be quantified as the product of the duration and rate of grain-filling (Gallagher *et al.*, 1976) and the effect of the environment on each of these components may then be determined.

The duration of grain-filling is determined principally by temperature (Sofield *et al.*, 1977; Slafer and Rawson, 1994) and is shorter at warmer temperatures (Sofield *et al.*, 1977; Wardlaw *et al.*, 1980; Al-Khatib and Paulsen, 1984; Hunt *et al.*, 1991; Jenner, 1991). The rate of progress to mass maturity (the reciprocal of the time from anthesis, or the start of grain-filling, to mass maturity) is a positive linear function of temperature (Slafer

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and Rawson, 1994). Thus, in accordance with the concept of thermal time (Monteith, 1977), the duration of grain-filling (t_{gf}) is given by:

$$t_{gf} = \theta/(\bar{T} - T_b) \text{ where } T_b < \bar{T} < T_o \quad (1)$$

in which $\bar{T}$ is mean temperature, θ is the thermal time from the start of grain-filling (or anthesis) to mass maturity above a base temperature T_b, and T_o is an optimum temperature. Estimates of T_b for the rate of progress to mass maturity in wheat vary from 4.7 °C (Hunt *et al.*, 1991) to 8.9 °C (Angus *et al.*, 1981) at least, and differ among cultivars (Loss *et al.*, 1989; Darroch and Baker, 1995).

The rate of increase in grain dry weight is principally determined by temperature, but effects of differences in irradiance have also been found (Sofield *et al.*, 1977). Grain growth rate is increased at warmer temperatures (Sofield *et al.*, 1977; Angus *et al.*, 1981; Hunt *et al.*, 1991; Jenner, 1991). However, warmer temperatures can result in smaller grain weights at harvest maturity because the increase in growth rate at warmer temperatures may be more than offset by the negative effects of shorter grain-filling durations (Sofield *et al.*, 1977; Al-Khatib and Paulsen, 1984). Differences among varieties in the response of grain dry weight to high temperatures are thought to occur because more temperature-tolerant varieties maintain higher rates of grain growth, rather than longer durations of grain filling, compared with more temperature-sensitive varieties, at high temperatures (Wardlaw and Moncur, 1995).

Continued anthropogenic increases in atmospheric carbon dioxide (CO_2) concentrations are expected to increase the yields of temperate crops (Kimball, 1983; Idso and Idso, 1994), largely through increased rates of photosynthesis and reduced transpiration rates (Pearcy and Björkman, 1983; Bowes, 1993). It is not clear whether or not increased yields at elevated CO_2 concentrations are solely a result of larger crop biomass, or are partly due to a change in dry matter partitioning to the harvested component (harvest index; Donald and Hamblin, 1976) at elevated CO_2 (Lawlor and Mitchell, 1991). However, increases in the concentrations of 'greenhouse' gases may also result in warmer temperatures (Houghton *et al.*, 1992). Thus, it is important to consider both elevated CO_2 concentrations and differences in temperature in order to assess the possible effects of climate change on the grain growth of wheat.

To study the effects of CO_2, temperature and their interaction, crops have been grown in the field within temperature gradient tunnels maintained at either normal atmospheric or an elevated CO_2 concentration (Wheeler *et al.*, 1994, 1995, 1996; Hadley *et al.*, 1995; Batts *et al.*, 1996). Field experiments using this approach have shown that the effect of doubling CO_2 concentration from current values on the grain yield of winter wheat may vary with temperature (Wheeler *et al.*, 1996). Here, we seek to determine how such effects of CO_2 on yield may arise by defining the effects of CO_2 concentration on the response of grain-filling duration (equation 1) and grain growth rate to differences in temperature, and on the harvest index of winter wheat under field conditions.

Materials and methods

Crop husbandry

Seeds of winter wheat (cv. Hereward) were sown on 24 November 1992 in field plots within four polyethylene-covered temperature gradient tunnels at a population of 275–300 plants m^{-2}, and grown until harvest maturity. Details of tunnel construction, equipment and environmental monitoring are given in Hadley *et al.* (1995), and a description of crop husbandry is given in Batts *et al.* (1996). One pair of tunnels was maintained at a seasonal average of 380 μmol mol^{-1} CO_2, and the other at 684 μmol mol^{-1} CO_2 from seedling emergence to final harvest. These treatments are subsequently referred to as 'normal' and 'elevated' CO_2 concentrations, respectively. Within each tunnel a temperature gradient (from about 1–2 °C below to about 2–3 °C above ambient) was superimposed on the normal diurnal and seasonal patterns, such that the average difference in daily mean temperature between the plots at the coolest and warmest ends of the gradients was about 3 °C between sowing and harvest maturity. Mean transmission of solar radiation from sowing to harvest maturity was about 65% (Hadley *et al.*, 1995). All plots were irrigated until after the start of grain-filling. For the experiment described here, samples were taken from within each of six 2 × 3 m plots arranged along one tunnel at each CO_2 concentration and from two additional plots grown at the same population density outside the tunnels.

Plant sampling

The day by which half the plants reached 50% anthesis (Porter *et al.*, 1987) was recorded in each of the 14 plots. Starting from between 5 and 11 d after 50% anthesis, eight or nine destructive harvests of all above-ground material in two 0.3 m rows (about 20 plants) were taken twice a week from the two warmest plots in each tunnel; every 5 d from the two intermediate plots; and once a week from the two coolest and two outside plots. The plants and ears were counted and plants separated into ears and straw. Grains were removed by hand. The fresh weight of chaff and straw was determined immediately and the dry weight determined after drying in a forced-air oven at 80 °C for 96 h. The grain was separated into normal and small (i.e. undeveloped) grain fractions and the number and fresh weight of each fraction determined. The moisture content of two replicates of 3 g of normal grains was determined by drying at 130 °C for 2 h (ISTA, 1993*a*, *b*). The dry weight of the normal grain fraction was calculated from the fresh weight and moisture content. The dry weight of the small grain fraction was determined after drying the whole sample at 80 °C for 96 h.

Statistical analyses

The mean number of normal grains per ear was calculated over all harvests and analyses of grain growth restricted to these grains. To determine mass maturity, a broken-stick relationship between individual grain dry weight and time from 50% anthesis was fitted for each plot; this comprised an initial positive linear relationship and a subsequent phase of constant dry weight fitted by an iterative regression analysis procedure, mass maturity being the time when the two lines intersected (Pieta-Filho and Ellis, 1991). The effect of temperature and CO_2 concentration on the rate of progress to mass maturity was determined by comparing regressions between the reciprocal of time from 50% anthesis to mass maturity and mean temperature for this period for each CO_2 concentration. The mean rate of grain growth per ear was estimated from slopes of linear relationships between grain dry weight per ear and time from 50% anthesis until mass maturity, as defined above, for each plot. The effect of mean temperature during grain-filling (i.e. from the time of the first sample until mass maturity) and CO_2 on the mean rate of grain growth was determined by comparing regressions between the rate of increase in grain weight per ear and temperature. These regressions were weighted by the reciprocal of the variance of each estimate in order to account for variation in the precision of these estimates of grain growth rate. Differences in the rate of increase in harvest index (the ratio of normal grain dry weight to total above-ground dry weight) among different groups of plots (divided, for example, into each CO_2 concentration) were tested by comparing the slope of groups of regressions of harvest index on time from 50% anthesis and assessing the significance of both within and among group differences. Seven observations (open diamonds in Fig. 5) were omitted from the latter analysis because, despite sensible grain weights, the harvest indices were atypically high or low.

Results

The dry weight of normal grains per ear at the last harvest (48–60 d after anthesis) was a negative linear function of mean temperature from 50% anthesis in both CO_2 treatments ($P<0.001$ for each). Enrichment with CO_2 increased grain weight per ear at all temperatures ($P<0.001$), with no interaction between CO_2 and temperature ($P>0.1$; Fig. 1a). The number of normal grains per ear (averaged over all harvests) was not greatly affected by temperature at elevated CO_2, but progressively declined (from 30.2 to 8.8 grains per ear) with warmer temperatures at normal CO_2 (Fig. 1b).

The dry weight of individual normal grains increased as linear functions of time between 5 and 11 d after anthesis until mass maturity in all 14 plots and remained constant thereafter. Examples from the warmest, coolest and outside plots are shown in Fig. 2. These results confirm that the first observations were within the grain-filling phase rather than the lag phase as these observations were adequately described by the linear function for each plot (Fig. 2). Times from 50% anthesis to mass maturity (t_{gf}, equation 1) ranged from 29 d at a mean temperature of 18.8 °C at normal CO_2 (Fig. 2d) to 50 d at 13.9 °C and elevated CO_2 (Fig. 2c). The rate of progress to mass maturity ($1/t_{gf}$) was a positive linear function of mean temperature (Fig. 3). Separate regressions for each CO_2 treatment and for the outside plots were not a significant improvement on a single relationship ($P>0.1$). Thus, a common function described all 14 observations with estimates of T_b and θ (equation 1) of 3.5 °C (95% $CI=-1.0$, 8.0) and 502 °Cd (95% $CI=370$, 776), respectively (Fig. 3).

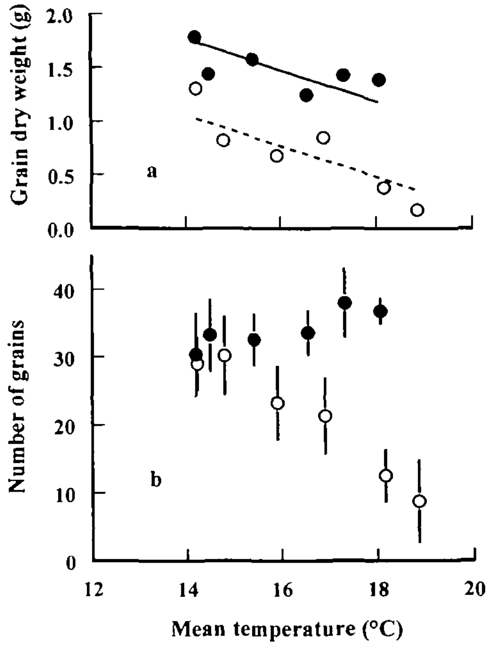

Fig. 1. Total grain dry weight per ear at harvest maturity (a) and number of normal grains per ear averaged between anthesis and harvest maturity (b) at either 380 (O) or 684 (●) μmol mol^{-1} CO_2. The fitted functions in (a) are of the form $y=\beta_0+\beta_1x$ in which β_0 is 3.098 (SE= 0.605) and β_1 is −0.145 (SE=0.036) at 380 μmol mol^{-1} CO_2, and the displacement of β_0 at 684 μmol mol^{-1} CO_2 is 0.711 (SE=0.115, r^2= 0.875, 9 df). Vertical bars in (b) represent the mean ± 1 SE of eight or nine observations.

Mean grain growth rate per ear increased as a positive linear function of temperature for all observations at elevated CO_2 and for observations at the three coolest temperatures at normal CO_2 (Fig. 4). Comparison of weighted regressions for each of these CO_2 treatments showed that CO_2 enrichment increased the intercept of this function ($P<0.001$) but did not affect the slope ($P>0.25$; Fig. 4). Thus, the rate of increase in grain dry weight per ear was 2.0 mg d^{-1} greater per 1 °C rise, and at a given temperature was 8.0 mg d^{-1} greater at elevated compared with normal CO_2. Fitting linear functions with different slopes for each CO_2 concentration but with a common T_b (of −5 °C) was also a significant improvement ($P<0.001$) over a single relationship for all these data, but the fitted lines were not visibly different to those from the previous analysis. Grain growth rate declined rapidly with increase in temperature above 16 °C at normal CO_2 (Fig. 4).

A linear relationship between harvest index and time from 50% anthesis before mass maturity was found in each of the 14 plots. The slope of the individual functions for each of the two outside plots and the coolest plots at normal CO_2 (solid lines, Fig. 5a, b, l–n) were not significantly different ($P<0.25$) from a common slope of 1.0% d^{-1} (SE=0.047). Similarly, the slope of the relationship

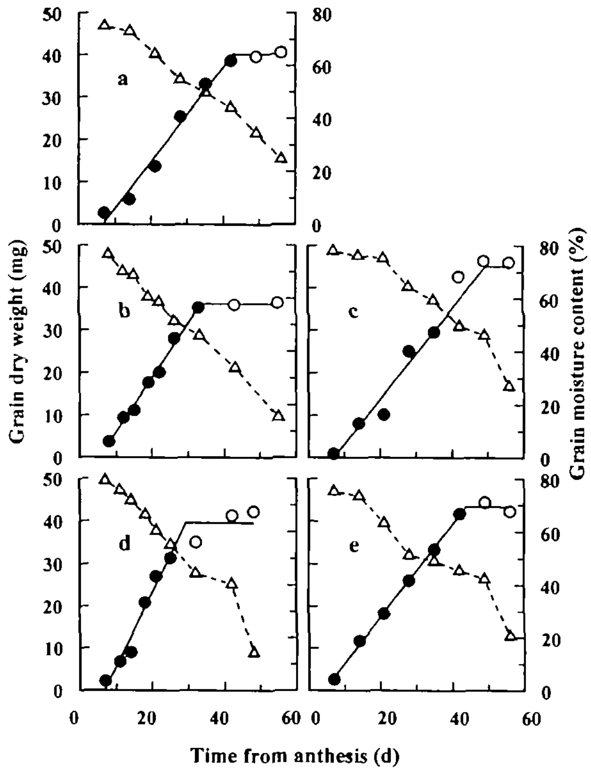

Fig. 2. Relationship between mean grain dry weight (●, ○, —) and grain moisture content (△, ---) and time from 50% anthesis at either 380 (d, e) or 684 (b, c) μmol mol^{-1} CO_2 or outside the tunnels (a). The functions are fitted to mean grain dry weight either before (●) or after (○) the time of mass maturity. Mean temperature from anthesis to mass maturity, rate of grain-filling and grain weight at mass maturity in each plot are: (a) 16.3 °C, 1.12 mg d^{-1}, 40.2 mg; (b) 18.3 °C, 1.29 mg d^{-1}, 36.2 mg, (c) 13.9 °C, 1.06 mg d^{-1}, 45.1 mg; (d) 18.8 °C, 1.77 mg d^{-1}, 39.5 mg; (e) 14.3 °C, 1.10 mg d^{-1}, 43.4 mg.

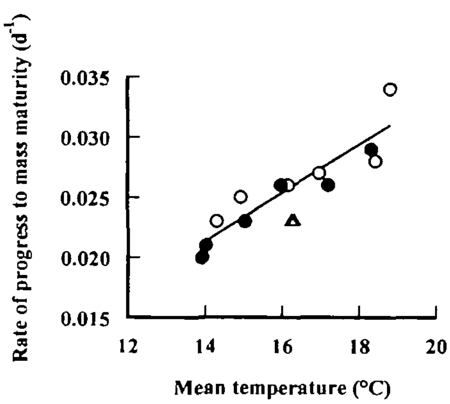

Fig. 3. Relationship between the rate of progress to mass maturity and mean temperature from 50% anthesis to mass maturity at either 380 (○) or 684 (●) μmol mol^{-1} CO_2 or outside the tunnels (△). The fitted function shown is in accordance with equation (1) with values of T_b and θ of 3.5 °C and 502 °Cd, respectively (r^2=0.760, 12 df).

between harvest index and time did not differ among the six plots at elevated CO_2 (P>0.25) and was 1.18% d^{-1} (SE=0.042) (dashed lines, Fig. 5c–h). However, these two pooled slope estimates were significantly different

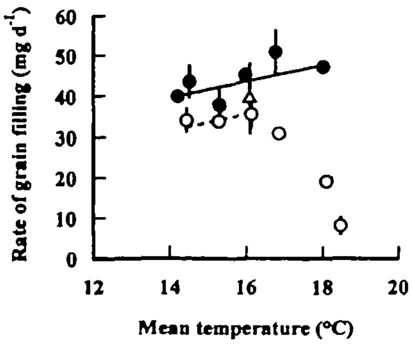

Fig. 4. Relationship between the rate of grain-filling per ear and mean temperature during grain-filling at either 380 (○) or 684 (●) μmol mol^{-1} CO_2 or outside the tunnels (△). The fitted functions shown are of the form $y=\beta_0+\beta_1 x$ in which β_0 is 11.22 (SE=4.13) and β_1 is 2.02 (SE=0.28) at 684 μmol mol^{-1} CO_2 and the displacement of β_0 for the observations at the three coolest temperatures at 380 μmol mol^{-1} CO_2 is −7.97 (SE=1.06; r^2=0.939, 6 df). The vertical bars represent the mean ± 1 SE of between four and seven observations.

from each other (P<0.01, compare the solid and dashed lines, Fig. 5c–h), such that the rate of change in harvest index at elevated CO_2 was 18% greater than for the outside plots and the three coolest plots at normal CO_2. The rate of change in harvest index declined progressively with temperature in the three warmest plots at normal CO_2.

The effects of temperature and grain number on grain growth rate were examined separately by determining the relationship between grain number per ear and the difference between grain growth rate at elevated CO_2 (provided by the fitted function shown in Fig. 4) to that observed at normal CO_2 (Fig. 6a). This relationship could be divided into two parts: the difference in grain growth rate was constant for the three plots with the most grains per ear, but the difference in growth rate was a negative function of grain number for the remaining three observations. These two functions crossed at 24 grains per ear (Fig. 6a). Similarly, the rate of increase in harvest index is shown as a function of the number of grains per ear in Fig. 6b. Again, the fitted relationships shown for the elevated CO_2 plots and for the outside and three coolest plots at normal CO_2 are from previous analyses (Fig. 5), but for the three observations with fewer grain numbers the function was fitted using these observations and constrained through the origin. The two functions for observations at normal CO_2 within and outside the tunnels crossed at 23 grains per ear (Fig. 6b).

Discussion

Enrichment to 684 μmol mol^{-1} CO_2 increased overall grain yield per ear at all temperatures. The average effect of elevated CO_2 on grain yield was similar to the 15–55% rise observed in previous studies of wheat yield in response to a doubling of CO_2 (Sionit *et al.*, 1981; Teramura *et al.*,

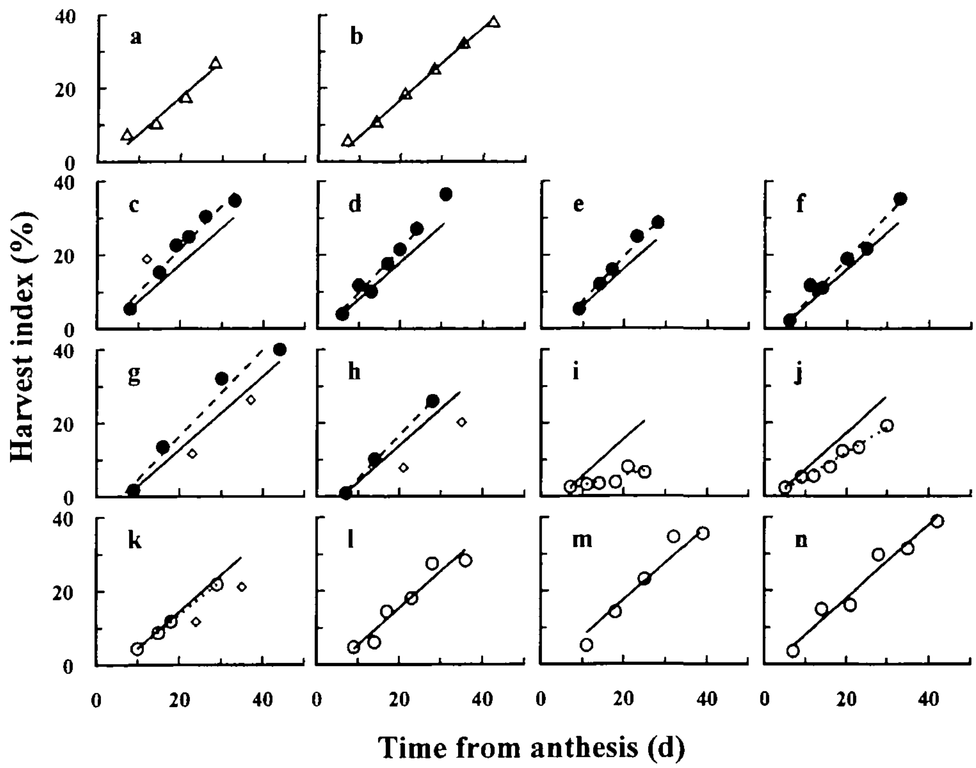

Fig. 5. Relationship between harvest index and time from anthesis at either 684 (c–h; ●) or 380 (i–n; ○) μmol mol^{-1} CO_2 or outside the tunnels (a, b; △). Within each CO_2 concentration, plots are arranged from the warmest (c, i) to the coolest (h, n) plot in each tunnel. The solid and dashed lines have slopes of 1.00% d^{-1} (SE =0.047) and 1.18% d^{-1} (SE=0.042), respectively. The dotted lines in j–l have slopes of 0.27 (SE=0.09), 0.68 (SE =0.05) and 0.92% d^{-1} (SE=0.01), respectively. The open diamonds denote outlying observations not included in the analyses.

1990; Mitchell *et al.*, 1993) except at the warmest mean temperatures where the effect of elevated CO_2 was greater than these estimates. This was because of the high frequency of small undeveloped grains (similar to the 'sterile' grains described by Tashiro and Wardlaw, 1990) at the warmest temperatures at normal CO_2 which were associated with high temperatures (>31 °C) in a 5 d period ending at anthesis (Wheeler *et al.*, 1996). The decline in grain number at normal CO_2 was also associated with an increase in the individual grain dry weight of the remaining normal grains. Although the effect of increased temperature and CO_2 concentration throughout crop growth on grain yield reflects the influence of the environment both before and after anthesis, we concentrate here solely on the effects of CO_2 and temperature during grain-filling; that is, on the duration and rate of grain-filling, and the increase in harvest index.

The positive linear relationship between the rate of progress to mass maturity and mean temperature is in accordance with previous studies (Slafer and Rawson, 1994). Thus, the duration of grain-filling over this temperature range can be described simply by two parameters; T_b and θ in equation (1). The estimates of T_b and θ (3.5 °C and 502 °Cd, respectively) differ from those of earlier experimental studies (8.9 °C, 416 °Cd from Angus *et al.*, 1981; 0 °C, 476 °Cd from Hunt *et al.*, 1991) and from those used in a wheat crop simulation model (9 °C, 295 °Cd to mass maturity, in ARCWHEAT; Weir *et al.*, 1984). Comparisons between these estimates are complicated by the differences in the precise durations modelled, any differences between spikelet and air temperatures (Pararajasingham and Hunt, 1991), the cultivars studied, and because thermal time above different base temperatures can not be compared directly. Also, the confidence limits of estimates of T_b and θ derived from field-based studies at a range of mean temperatures which are not close to T_b are usually large. Nevertheless, limited comparisons of the predicted durations at specified temperatures can be made. For example, the predicted durations from anthesis to mass maturity at 14, 16 and 19 °C using the values of T_b and θ for cv. Hereward found in the current experiment are 48, 40 and 32 d, respectively. The predicted durations at these temperatures for cv. Hustler are 59, 42 and 33 d, respectively, with the values of T_b and θ used in ARCWHEAT (Weir *et al.*, 1984).

Once these effects of temperature on the duration of grain-filling were accounted for, neither elevated CO_2 nor reduced incident radiation (due to the tunnel plastic) affected the duration of grain-filling. Similarly, Sofield *et al.* (1977) did not find any effect of irradiance on grain-filling duration, and Rawson (1992), Mitchell *et al.* (1993), and Batts *et al.* (1996) reported little or no effect

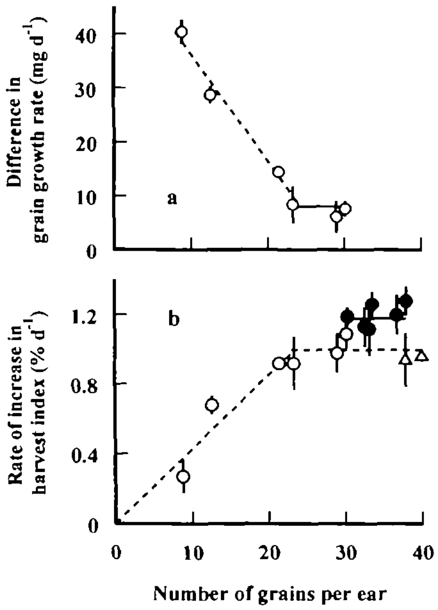

Fig. 6. Relationship between the difference in the rate of grain-filling per ear at 684 μmol mol^{-1} CO_2 to that at 380 μmol mol^{-1} CO_2 (a), and rate of increase in harvest index (b) and the number of grains per ear at either 380 (○) or 684 (●) μmol mol^{-1} CO_2 or outside the tunnels (△). The solid line shown in (a) is calculated from the two fitted lines shown in Fig. 4. The dashed line in (a) is derived from the three observations below 22 grains per ear and the solid line in Fig. 4. The solid line shown in (b) is the slope of the dashed regression line shown in Fig. 5c–h. The broken lines in (b) are the slope common to the regression lines shown in Fig. 5a, b, l–n for observations above 23 grains per ear, or fitted directly to the three observations below 23 grains per ear.

of elevated CO_2 on the duration of several other developmental stages in wheat. Hence, the duration of grain-filling in this wheat cultivar is a simple function of temperature (when mean temperature <19 °C) at both CO_2 concentrations.

The rate of grain growth per ear was generally higher at warmer temperatures, as reported previously (Sofield *et al.*, 1977; Angus *et al.*, 1981; Hunt *et al.*, 1991; Jenner, 1991; Wardlaw and Moncur, 1995). Unlike the rate of progress to mass maturity, the rate of grain growth per ear was greater at elevated compared with normal CO_2; an increase of between 21–24% for a doubling of CO_2. Total biomass was also greater (by 6–31%) for crops grown at elevated CO_2 than at normal CO_2 (Wheeler *et al.*, 1996). Therefore, the greater grain growth rate observed at this elevated CO_2 concentration could have been solely due to the greater total biomass at elevated CO_2, or to both a greater total biomass and an increase in harvest index at elevated compared with normal CO_2.

The linear increase in harvest index with time found for all plots was also reported by Moot *et al.* (1996). Moreover, the slope common to these functions at cooler temperatures at 380 μmol mol^{-1} CO_2 and outside the tunnels (1.00% d^{-1}) was within the range of values found for wheat grown under normal fertility conditions (0.9–1.19% d^{-1}; Moot *et al.*, 1996). Moot *et al.* (1996) proposed that estimates of the rate of increase in harvest index may be conservative over a range of environments, so that the yield of wheat crops is simply a function of the duration of reproductive growth and the total crop biomass. The present results support this generalization of about a 1% d^{-1} increase in harvest index for winter wheat crops, but also provide some indications of environments in which this generalization does not apply.

The 18% greater rate of increase in harvest index at elevated compared with normal CO_2 at cooler temperatures, and the even greater response at warmer temperatures, suggests that CO_2 enrichment directly affected the pattern of dry matter partitioning to the grain in these crops. This was not because of an increase in the number of grain-filling sites because an average of 825 ears m^{-2} were found at all temperatures in all these plots (Wheeler *et al.*, 1996), and the number of grains per ear was similar at both CO_2 concentrations at cooler temperatures (Fig. 1b). As CO_2 enrichment did not affect the duration of grain-filling, the greater rate of increase in harvest index at elevated compared with normal CO_2 should result in higher estimates of final harvest index at elevated CO_2. However, no difference in the harvest index of wheat due to CO_2 enrichment could be detected using observations from the samples at harvest maturity alone (data not shown), and none was reported by Mitchell *et al.* (1993) and Gifford and Morison (1993). Nevertheless, in the current analysis, not only were any differences (due to temperature) in the duration of grain growth (hence harvest index) between treatments accounted for, but the use of many observations during reproductive growth increased the precision of the test of any CO_2 effect on harvest index.

Observations of a linear increase in grain dry weight at a time when crop growth rate, and ear and flag leaf photosynthesis are declining have led to conclusions that the grain growth of wheat is not limited by assimilate supply (Biscoe and Gallagher, 1977; Sofield *et al.*, 1977). However, Willey and Dent (1969) considered that grain yield is not limited by assimilate supply nor the storage capacity of the ear alone, but by both. They concluded that it is 'impossible to say ... under what conditions the relative importance of ear capacity and carbohydrate supply may change'. The analyses presented here (Fig. 6) offers a criterion to discriminate between these two situations: the critical grain number. Below the critical grain number, grain yield appears limited by the capacity of the ear to provide sufficient reproductive sinks and final grain yield will be dominated by the effects of the environment on the number of these sinks (in the current experiment, high temperatures before anthesis). Above the critical grain number, changes in ear capacity (i.e. numbers of grains) are balanced by assimilate supply to permit a conservative rate of increase in harvest index (at a given CO_2 concentration) to be maintained, and a linear increase in grain dry weight with time during most of grain-filling. In our experiments the critical grain number was estimated to be 23–24 grains per ear (or, at the ear population of 825 ears m^{-2}, about 20 000 grains m^{-2}), but this estimate may be expected to vary with factors such as nitrogen supply, drought and genotype.

In conclusion, a doubling of CO_2 concentration increased the rate of increase in grain weight but did not affect the duration of grain-filling in wheat. Grain-filling duration was solely determined by temperature. Increased partitioning of dry matter to grain at elevated CO_2 accounted for part of the higher grain yield at elevated compared with normal CO_2. Nevertheless, the effects of elevated CO_2 and warmer temperatures were not simply additive but were subject to interaction. The effects of such an interaction are likely to be greatest in environments in which the critical grain number is transgressed as a result of extreme climatic episodes.

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