Global Change Biology (1997) 3, 269–278

PURCHASED FOR USDA
FOR OFFICIAL USE ONLY

Yield of wheat across a subambient carbon dioxide gradient

HERMAN S. MAYEUX,* HYRUM B. JOHNSON,* H. WAYNE POLLEY* and STEPHEN R. MALONE[1]

*Grassland, Soil and Water Research Laboratory, U.S. Department of Agriculture, Agricultural Research Service, 808 E. Blackland Road, Temple, TX 76502, USA, [1]Department of Biology, University of West Alabama, Livingston, AL 35470, USA.

Abstract

Yields and yield components of two cultivars of day-neutral spring wheat (*Triticum aestivum* L.) were assessed along a gradient of daytime carbon dioxide (CO_2) concentrations from about 200 to near 350 μmol CO_2 (mol air)$^{-1}$ in a 38 m-long controlled environment chamber. The range in CO_2 concentration studied approximates that of Earth's atmosphere since the last ice age. This 75% rise in CO_2 concentration increased grain yields more than 200% under well-watered conditions and by 80–150% when wheat was grown without additions of water during the last half of the 100-day growing season. The 27% increase in CO_2 from the pre-industrial level of 150 years ago (275 μmol mol^{-1}) to near the current concentration (350 μmol mol^{-1}) increased grain yields of 'Yaqui 54' and 'Seri M82' spring wheats by 55% and 53%, respectively, under well-watered conditions. Yield increased because of greater numbers of grains per spike, rather than heavier grains or numbers of spikes per plant. Water use increased little with CO_2 concentration, resulting in improved water use efficiency as CO_2 rose. Data suggest that rising CO_2 concentration contributed to the substantial increase in average wheat yields in the U.S. during recent decades.

Keywords: drought, historical increase in yield, Seri M82, water use efficiency, Yaqui 54, yield components

Received 20 June 1996; revision accepted 30 September 1996

Introduction

Atmospheric carbon dioxide (CO_2) concentration rose from below 200 μmol mol^{-1} during the last Glacial period 30–15 ky BP (Delmas *et al.* 1980; Neftel *et al.* 1988) to about 275 μmol mol^{-1} between 15 and 12 ky BP (Neftel *et al.* 1988). It has risen about 30%, to the current ≈ 360 μmol mol^{-1}, since the Industrial Revolution 200 years ago (Bascastow *et al.* 1985; Friedli *et al.* 1986; Keeling & Whorf 1994).

These changes in atmospheric CO_2 are small compared to those possible during the next century (Trabalka *et al.* 1985), but may have significantly influenced plant evolution (Ehleringer *et al.* 1991) and productivity (Johnson *et al.* 1993). Per unit increase in CO_2, growth of C3 plants is stimulated more over subambient than elevated concentrations (Baker *et al.* 1990; Allen *et al.* 1991). Seed yields of soybean [*Glycine max* (L.) Merr.] (Allen *et al.* 1991) and rice [*Oryza sativa* L.] (Baker *et al.* 1990), for example, were about 50% and 60% greater, respectively, when plants were grown at today's CO_2 concentration than the pre-industrial level. Yields were increased proportionally less, 20–50%, by elevating CO_2 by 330 μmol mol^{-1} above the current concentration. Similarly dramatic increases in growth have been reported for other C_3 species when CO_2 was increased over subambient concentrations (Polley *et al.* 1992; Dippery *et al.* 1995). By stimulating plant productivity, rising CO_2 may have made possible the widespread domestication of plants at the end of the Pleistocene (Sage 1995). The increase in CO_2 concentration during recent decades may have improved harvestable yields of some crops (Gifford 1979).

Growth is usually less responsive to atmospheric CO_2 when plants are limited by nutrients, light, or water (Strain 1992), although the relative response of growth to CO_2 may be maximal under these conditions. Wheat yield increases less at elevated CO_2 concentration, for example, when the availability of water (Gifford 1979; Sionit *et al.* 1980; Chaudhuri *et al.* 1990), nitrogen

Correspondence: Wayne Polley, fax +1/817-770-6561, e-mail polley@brcsun0.tamu.edu

OUR AREA CODE
IS NOW *254*
Please Correct Your Records

© 1997 Blackwell Science Ltd.

(Goudriaan & de Ruiter 1983), a mixture of nutrients (Sionit *et al.* 1981a), or light (Gifford 1977) are less than optimal than when these resources are abundant. Low resource levels probably limited the absolute increase in plant growth and harvestable yield as atmospheric CO_2 rose, but data at subambient concentrations are few (Gifford 1977).

We report yields of two daylength-neutral cultivars of spring wheat that were grown to maturity across a continuous daytime gradient in CO_2 concentration from near the Glacial level (200 μmol mol^{-1}) to near the current concentration (350 μmol mol^{-1}). Plants were grown with abundant and limited water to determine effects of water availability on the response of this important C_3 crop to past changes in CO_2 concentration. Low water availability is considered a major limitation on agricultural productivity (Loomis 1983). Data are used to address the possible contribution of rising CO_2 concentration to the historical increase in wheat yield in the U.S.

Materials and methods

Controlled environment chamber

Wheat was grown in an elongated chamber in which plants were exposed during daylight to a continuous gradient in CO_2 concentration from near 200–350 μmol mol^{-1} (Mayeux *et al.* 1993). The 38 m-long chamber is located in a ventilated glasshouse and consists of five parallel, 7.6 m lengths of a 0.76 m-deep and 0.45 m-wide soil container. Aerial growth of plants was enclosed in a transparent and tunnel-shaped polyethylene cover that was attached to the top edges of the soil container. Polyethylene covers of adjacent lengths of the chamber were connected by ducts to form a continuous 38-m system. The plastic-lined soil container was partitioned into 0.6 m-long, water-tight compartments that were filled with fine sandy loam soil (Alfisol, Udic Paleustalfs; Huckabee *et al.* 1977). Soil pH was 7.1 and initial organic carbon content was 0.57%.

Photosynthesis by plants within the chamber progressively reduced the CO_2 concentration of chamber air from that in the glasshouse (about 350 μmol mol^{-1}) to 200 μmol mol^{-1} as air was moved by a blower from the air intake to the outlet of the system. The CO_2 concentration gradient was maintained during daylight each day (daylight period > 8 h on 75% of days) by automatically varying the rate of air flow through the chamber in response to changes in incident light. The CO_2 concentration was measured each minute with an infra-red gas analyser (Leybold-Heraeus, Hanau, Germany; Model BINOS 67) in air drawn from the chamber outlet and sequentially from five points spaced at 7.6 m- intervals along the chamber. Daytime CO_2 concentration declined linearly with distance along the chamber from (mean $\pm$ SE) 352 $\pm$ 2 μmol mol^{-1} at the entrance to 204 $\pm$ 1 μmol mol^{-1} at the outlet. Blower speed was increased at night to vent CO_2 generated by soil and plant respiration. The CO_2 concentration at night increased from a mean 365 μmol mol^{-1} at the air inlet of the chamber to 400 μmol mol^{-1} at the chamber outlet.

Photosynthetically active photon flux density (PPFD) was measured on the glasshouse roof with a quantum sensor (Li-Cor Inc., Nebraska, USA; Model LI-190SB) and above the polyethylene canopy with 1 m long line quantum sensors (LI-191SA). The PPFD incident on wheat in the chamber was calculated by multiplying quantum flux measured above the chamber by transmission of the polyethylene canopy (90%). The daily integral of PPFD incident on plants in the 38 m chamber averaged 60% of that outside the glasshouse. Attenuation of PPFD was greatest in early morning and late evening. PPFD incident on plants within the chamber approached 80% of that outdoors during midday. Daily total PPFD varied by 5% among the five 7.6 m chamber lengths. The line quantum sensor used does not employ a full cosine correction, and so underestimates diffuse radiation and light at low solar angles. Attenuation of PPFD by the glasshouse and polyethylene canopy therefore likely was lower than calculated.

Dry bulb and dew point temperatures of air were regulated at the beginning of each 7.6 m length of the chamber with chilled-water cooling coils and resistance heating elements to track temporal changes in these temperatures within the glasshouse. Regulation each 7.6 m along the chamber suppressed the temperature and humidity gradients that develop in a semi-closed system. Dry bulb and dew point temperatures of air at the beginning and end of each length of chamber were monitored with 25 μm diameter thermocouples and chilled-mirror hygrometers (General Eastern Instruments, Maine, USA; Model DEW-10), respectively. Vapor pressure deficit of air (VPD) at extremes of chamber lengths was calculated from these data.

The mean dry bulb temperature of conditioned air entering each 7.6 m length of chamber increased linearly from 18.5 °C at the beginning of the experiment to 28.0 °C at the end. The VPD of conditioned air increased linearly from 0.9 to 2.5 kPa over the same period. Mean night-time temperature was 17 °C. Drybulb temperature increased a mean 3.8 °C and air VPD increased a mean 0.1 kPa between points of regulation located each 7.6 m along the chamber. The repeated temperature and humidity gradients within each of the five chamber lengths did not appear to influence measured responses.

Culture and harvest

'Yaqui 54' and 'Seri M82', day-neutral cultivars of spring wheat, each were planted on 12 February 1991 in four

0.6 m-long soil compartments in each of the five 7.6 m lengths of chamber (total of 20 compartments per cultivar). The spring wheat cultivar 'Glennson' was seeded into 0.6-m compartments in the middle and at extremes of chamber lengths well before Yaqui 54 and Seri M82 were planted. Glennson wheat served as a photosynthetic 'sink' for CO_2 as air passed through the chamber, so that the desired CO_2 gradient from near 350–200 μmol mol^{-1} was established by 26 February, while seedlings of Seri M82 and Yaqui 54 were small.

Yaqui 54 is representative of 'traditional' tall cultivars, and was released about 40 years ago. Seri M82 is a semidwarf type more representative of modern spring wheats. Seedlings of the two cultivars were thinned on three occasions to a final density of 96 plants in each compartment on 17 April, the equivalent of 355 plants m^{-2}. No fertilizer was provided. The nitrogen concentration of flag leaves from plants thinned on 17 April was high and uniform across the CO_2 gradient, averaging 4.4% and 4.5% for Yaqui 54 and Seri M82, respectively, (Polley *et al.* 1993).

Soil water content was monitored weekly by neutron attenuation through the exterior plywood wall of each compartment with a surface moisture gauge (Troxler Electronics, North Carolina, USA; Model 3218). An empirically determined relationship between the volume of water lost per compartment and the decline in gauge reading from that at 'field capacity' was used to determine water deficit and to calculate water additions. Soil water in each compartment was restored to 'field capacity' weekly until 3 April. Additional water was withheld from half of the soil compartments with Yaqui 54 and Seri M82 in each 7.6 m chamber length for the final 50 days of the 100-day growing season (droughted treatment). Yaqui 54 was in the early boot stage when the different water treatments were imposed, but Seri M82 did not have flag leaves.

Numbers of vegetative tillers and spikes in each compartment were recorded on 22 May, after wheat matured. Spikes were harvested, oven-dried at 60 °C, and individually threshed by hand. Grains per spike were counted, and grain and chaff were weighed. Remaining above-ground tissues were separated into stems and leaves (sheaths and leaf blades), dried, and weighed. Area was measured before drying on a subsample of senescent and, when necessary, unfurled leaves from each compartment with a photoelectric leaf area meter. Leaf area per compartment was calculated by multiplying total leaf mass by specific leaf area of the subsample. Harvest index for each compartment was the ratio of grain mass to total above-ground biomass. Apparent water use efficiency (WUE) per compartment was calculated by dividing total above-ground biomass, including that removed when plants were thinned, by the volume of water lost during the experiment (evapotranspiration).

The mean daytime CO_2 concentration to which plants in each 0.6 m soil compartment were exposed was estimated from a linear regression of CO_2 concentration at the six locations routinely sampled on distance from the air intake of the chamber ($r^2 = 0.95$). Linear regressions were used to describe relationships between plant parameters and daytime CO_2 concentration. Higher order polynomial regressions and other non-linear relationships rarely provided a better fit to the data. For each plant parameter, separate linear regressions were fitted for each cultivar and water treatment. Regressions were compared with the F statistic (Weisberg 1980).

Results

Growth

Leaf area index (LAI) of Yaqui 54 and Seri M82 at maturity increased linearly from about 1.0 and 1.4–2.0 and 3.0, respectively, with the 75% increase in CO_2 concentration, regardless of watering regime (Fig. 1). Area was measured on senescent leaves, so LAI during grain fill likely was higher.

Above-ground biomass of well-watered Yaqui 54 and Seri M82 increased from about 230 and 310 g m^{-2} to an average of about 700 g m^{-2} over the 200–350 μmol mol^{-1} CO_2 gradient, a gain of 136–193% (Fig. 2). Withholding water during the last half of the growing season significantly ($P < 0.001$) reduced above-ground biomass of each cultivar. The increase in biomass per unit increase in CO_2 was halved by water stress in Seri M82, but did not differ significantly ($P > 0.75$) between watering treatments in Yaqui 54.

Plant height at harvest increased ($P < 0.001$) as CO_2 rose, but was little affected by water treatment (not shown). Mean height of well-watered Seri M82 increased from 0.45–0.57 m and that of Yaqui 54 rose from 0.48–0.66 m with the near 150 μmol mol^{-1} increase in CO_2 concentration.

Grain yield

Grain yield of well-watered plants of each cultivar more than tripled and yield of droughted Yaqui 54 increased about 150% with the near 150 μmol mol^{-1} increase in CO_2 concentration (Fig. 3). The linear relationship between grain yield and CO_2 was only marginally significant ($P = 0.07$) in droughted Seri M82, however. Grain yield was significantly ($P < 0.005$) higher in Seri M82 than Yaqui 54 under well-watered conditions, but the increase in yield per unit increase in CO_2 concentration

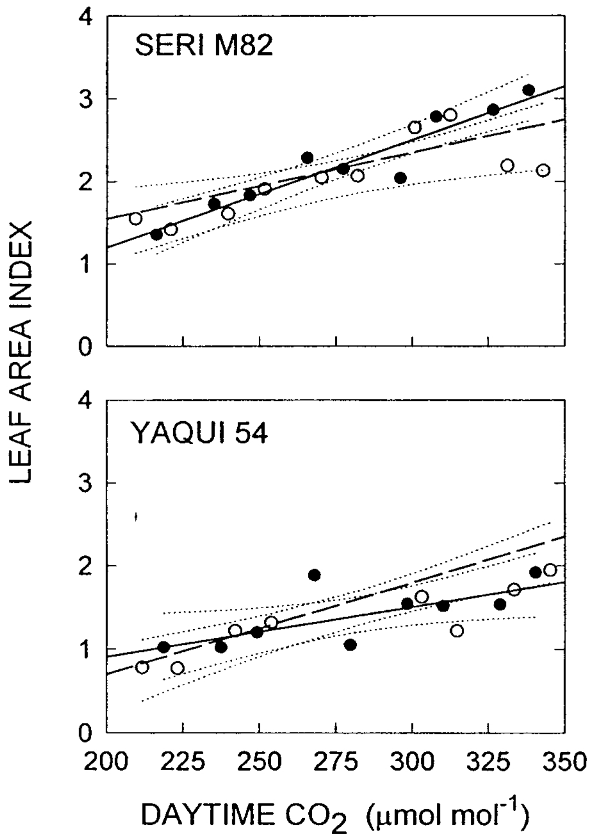

Fig. 1 Leaf area index (LAI) at maturity of well-watered (filled symbols) and droughted (open symbols) stands of two cultivars of spring wheat grown across a subambient CO_2 gradient. Solid lines are linear regressions of LAI of well-watered Seri M82 ($y = -1.4 + 0.013x$, $r^2 = 0.90$, $P < 0.001$) and Yaqui 54 ($y = -0.29 + 0.006x$, $r^2 = 0.50$, $P = 0.033$) on CO_2. Dashed lines are linear regressions of LAI of droughted Seri M82 ($y = -0.05 + 0.008x$, $r^2 = 0.60$, $P = 0.009$) and Yaqui 54 ($y = -1.5 + 0.011x$, $r^2 = 0.82$, $P = 0.008$) on CO_2. Dotted lines depict 95% confidence intervals for regression lines.

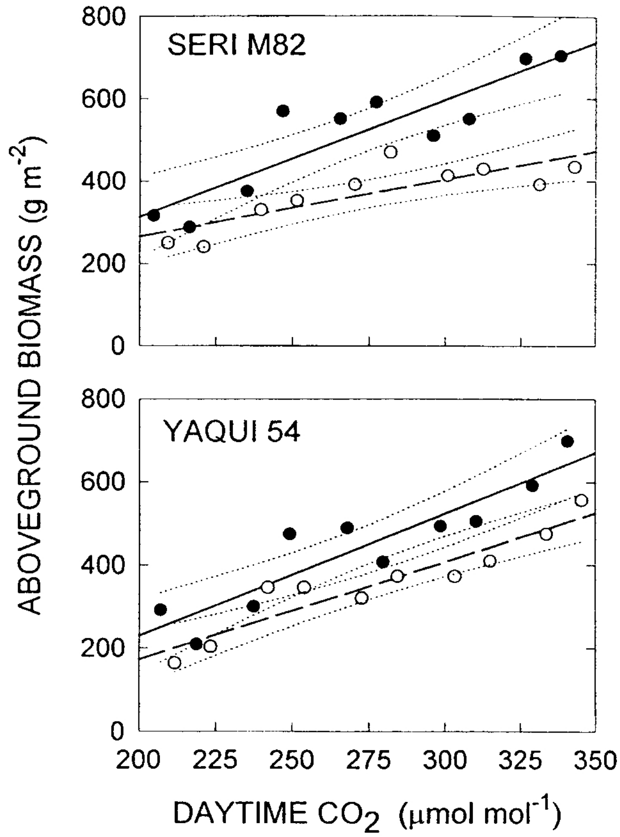

Fig. 2 Above-ground biomass at maturity of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. Solid lines are linear regressions of biomass of well-watered Seri M82 ($y = -254 + 2.83x$, $r^2 = 0.80$, $P < 0.001$) and Yaqui 54 ($y = -359 + 2.94x$, $r^2 = 0.84$, $P < 0.001$) on CO_2. Dashed lines are linear regressions of biomass of droughted Seri M82 ($y = -12 + 1.39x$, $r^2 = 0.68$, $P = 0.003$) and Yaqui 54 ($y = -298 + 2.35x$, $r^2 = 0.88$, $P < 0.001$) on CO_2. Dotted lines depict 95% confidence intervals for regression lines.

did not differ significantly ($P > 0.75$) between cultivars under either watering regime.

Grain yield increased proportionally more than did above-ground biomass in well-watered plants because of a 20–42% increase in harvest index over the full CO_2 gradient (Fig. 4). Harvest index changed little above about 250 µmol mol^{-1} in well-watered wheat, however, and was not significantly affected by CO_2 when water was withheld during the latter half of the growing season. Tiller density (no. m^{-2}) at harvest was not closely associated with CO_2 concentration ($r^2 = 0.07$–0.5) in either cultivar, and was not strongly depressed by withholding water (Fig. 5). Consequently, spike density did not change significantly with CO_2 concentration ($P = 0.13$–0.58). The mean mass of individual grains was also not strongly or consistently influenced by CO_2 (Fig. 6). Individual grain mass of well-watered plants was not affected by CO_2 in Seri M82 (mean = 34.9 ± 1.0 mg) and changed little in Yaqui 54 above about 250 µmol mol^{-1} CO_2. Mass per grain declined at higher CO_2 concentrations ($P = 0.02$) in Seri M82 and did not change significantly with CO_2 treatment ($P = 0.57$) in Yaqui 54 when water was withheld during grain fill.

By contrast, the number of grains per spike was highly sensitive to CO_2 concentration. Grains per spike more than doubled in Yaqui 54 and droughted Seri M82 and more than tripled in well-watered Seri M82 from 200 to 350 µmol mol^{-1} CO_2 (Fig. 7). Per unit rise in CO_2 concentration, grains/spike increased by a similar amount in three of the four cultivar and watering treatment combinations. The increase was greatest in well-watered Seri M82 ($P < 0.05$).

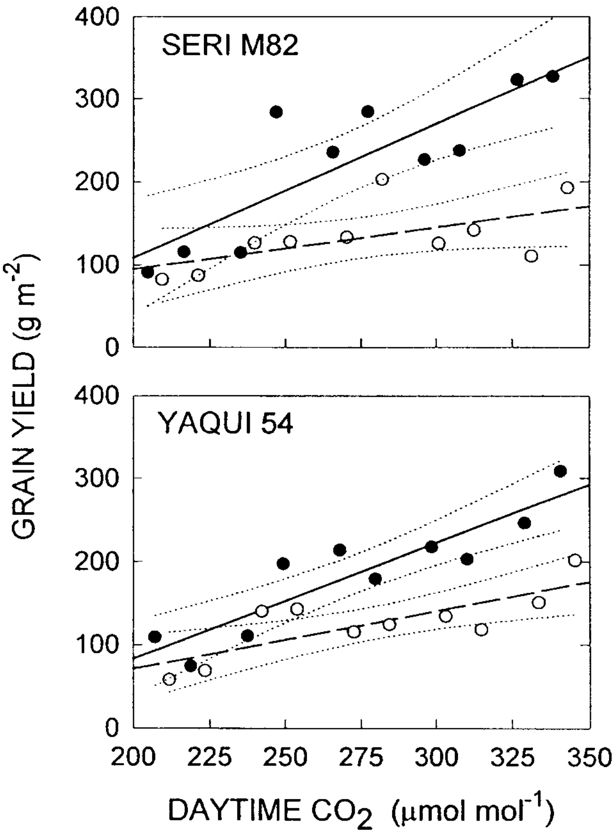

Fig. 3 Grain yield of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. Solid lines are linear regressions of grain yield of well-watered Seri M82 (y = –214 + 1.61x, r^2 = 0.71, P = 0.002) and Yaqui 54 (y = –196 + 1.40x, r^2 = 0.82, P < 0.001) on CO_2. Dashed lines are linear regressions of grain yield of droughted Seri M82 (y = –7.1 + 0.51x, r^2 = 0.35, P = 0.07) and Yaqui 54 (y = –69 + 0.70x, r^2 = 0.61, P = 0.007) on CO_2. Dotted lines depict 95% confidence intervals for regression lines.

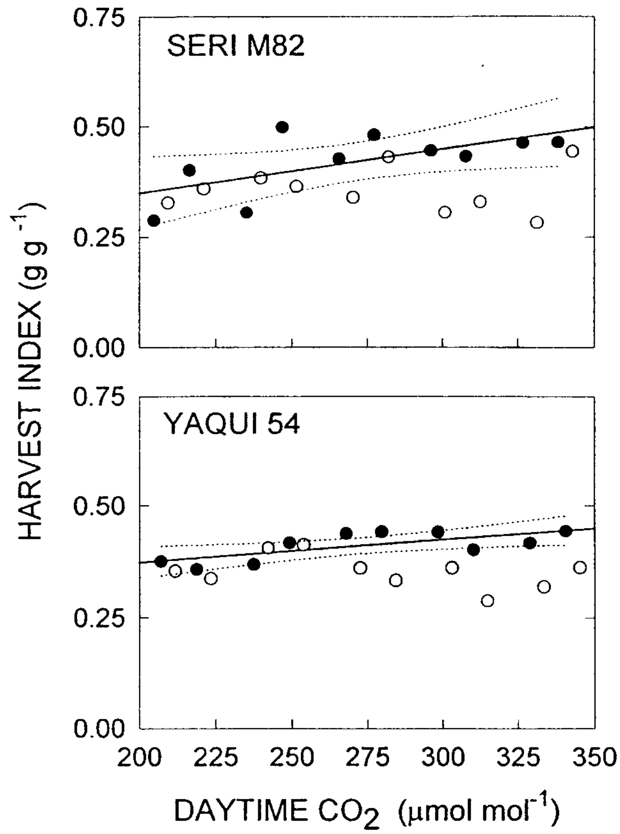

Fig. 4 Harvest index of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. Solid lines are linear regressions of the index for well-watered Seri M82 (y = 0.153 + 0.001x, r^2 = 0.41, P = 0.05) and Yaqui 54 (y = 0.27 + 0.0005x, r^2 = 0.51, P = 0.02) on CO_2. Dotted lines depict 95% confidence intervals for regression lines. Harvest index of droughted plants was not related to CO_2.

Evapotranspiration and water use efficiency

The large increases in biomass and leaf area as CO_2 rose were accompanied by smaller increases in evapotranspiration (data not shown). The total volume of water added to maintain soil in compartments with Seri M82 near field capacity ranged from 63.6 L at the lowest CO_2 level to 87.2 L at the highest concentration. Cumulative water additions to well-watered Yaqui 54 compartments increased 22%, from 65.4 to 80.0 L, at higher CO_2 concentration. Cumulative water additions to droughted Seri M82 did not differ with CO_2 treatment (mean = 51 L per compartment). The volume of water added to droughted Yaqui 54 increased linearly from 43.1–54.5 L with increasing CO_2.

CO_2-caused increases in WUE of above-ground biomass production of both cultivars were significant, although only marginally so in droughted Seri M82 (P = 0.10), and similar in magnitude (Fig. 8). WUE increased from less than 2 to about 3 g L^{-1} with increasing CO_2. WUE tended to be higher in droughted than well-watered plants because above-ground biomass declined less than did evapotranspiration when water was withheld.

The level of water stress that developed in droughted treatments over the 50 days of deprivation was not severe until near the end of the experiment, but evapotranspiration in droughted compartments declined to about 50% of that in continuously watered compartments. Evapotranspiration over the 44 days prior to 15 May averaged 24 L and 47 L in droughted and continuously watered compartments, respectively. Average volumetric water content on 15 May, 7 days before harvest, was 16.8% in the droughted soil compartments and 22.5% (the approximate field capacity) in the well-watered compartments.

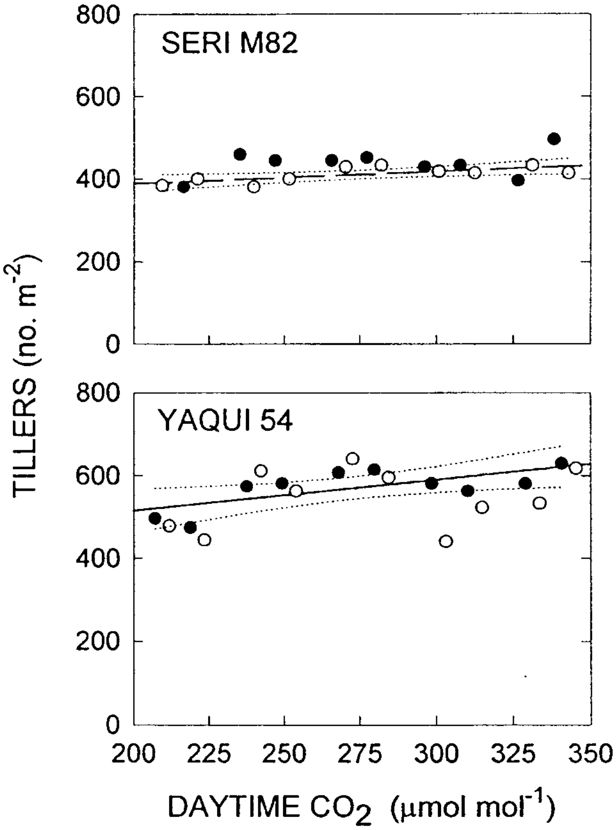

Fig. 5 Tiller density of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. The solid line is a linear regression of tillers m^{-1} of well-watered Yaqui 54 (y = 361 + 0.765x, r^2 = 0.50, P = 0.02) on CO_2. The dashed line is a linear regression of tillers m^{-1} of droughted Seri M82 (y = 331 + 0.291x, r^2 = 0.50, P = 0.02) on CO_2. Dotted lines depict 95% confidence intervals for regression lines. Tiller density in other treatments was not related to CO_2.

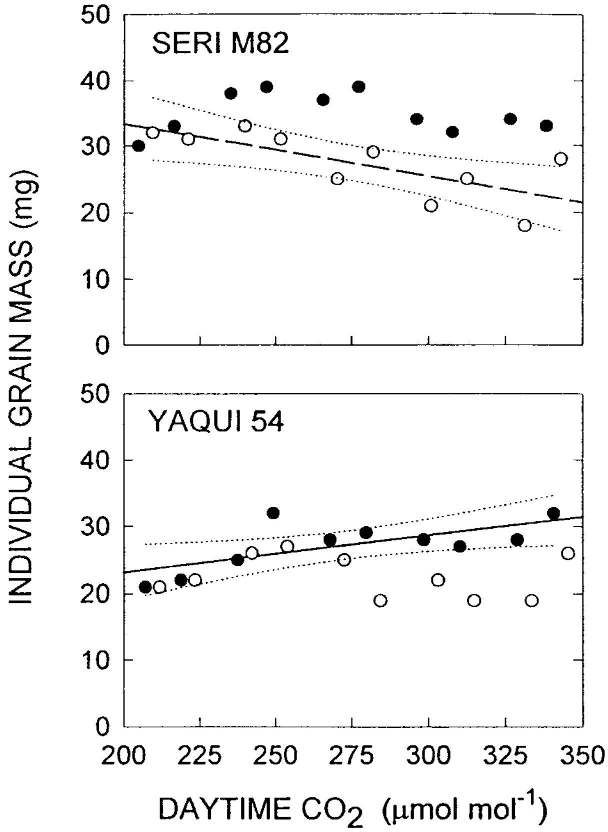

Fig. 6 Mass of individual grains of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. The solid line is a linear regression of grain mass of well-watered Yaqui 54 (y = 12.1 + 0.06x, r^2 = 0.48, P = 0.03) on CO_2. The dashed line is a linear regression of grain mass of droughted Seri M82 (y = 49.2–0.08x, r^2 = 0.53, P = 0.02) on CO_2. Dotted lines depict 95% confidence intervals for regression lines. Grain mass in other treatments was not related to CO_2.

Discussion

Grain yield

A 27% increase in CO_2 from the pre-industrial concentration (275 µmol mol^{-1}) to near the current level (350 µmol mol^{-1}) increased grain yields of Yaqui 54 and Seri M82 spring wheats more than 50% under well-watered conditions (Fig. 3). Grain yields of the two cultivars more than tripled when well-watered and increased 80% to 150% when droughted during the latter half of the growing season as CO_2 rose nearly 75% from slightly above 200 to about 350 µmol mol^{-1}. These proportional increases generally exceed the 80% increase in yield of spring wheat grown in pots over a comparable CO_2 range, 150–300 µmol mol^{-1} (Gifford 1977). They also exceed proportional increases in yield of usually 60% or less when wheat or other C_3 crops are exposed to elevated CO_2 concentrations (Kimball 1983; Cure & Acock 1986; Baker *et al.* 1990; Allen *et al.* 1991; Lawlor & Mitchell 1991; Kimball *et al.* 1995). Per unit increase in CO_2, however, the increases in yield that we observed are similar to those of spring wheat grown from about 350–600 µmol mol^{-1} CO_2 (Gifford 1979). Gifford (1979) observed that grain yield of spring wheat rose 0.5 and 1.3 g m^{-2} for each annual increment in the current rise in atmospheric CO_2 concentration, 1.2 µmol mol^{-1}, under water-stressed and well-watered conditions, respectively. Grain yield of Seri M82 and Yaqui 54 increased about 0.5 g m^{-2} per µmol mol^{-1} increase in subambient CO_2 under late-season drought, and 1.6 and 1.4 g m^{-2} per µmol mol^{-1} rise in CO_2 under well-watered conditions, respectively.

Yield components

Increases in grain yield of Seri M82 and Yaqui 54 wheat resulted almost entirely from greater numbers of grains

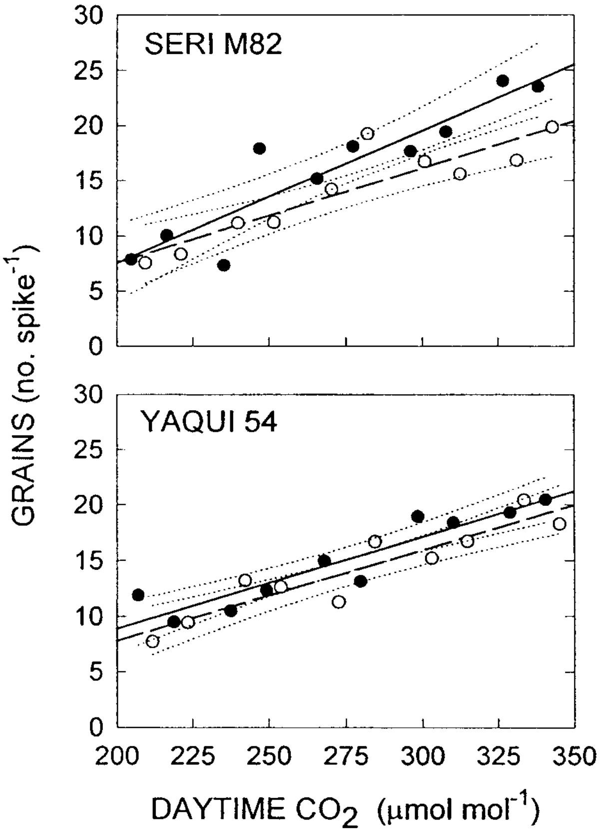

Fig. 7 Number of grains per spike of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. Solid lines are linear regressions of grains spike^{-1} of well-watered Seri M82 ($y = -16.5 + 0.120x$, $r^2 = 0.85$, $P < 0.001$) and Yaqui 54 ($y = -7.5 + 0.082x$, $r^2 = 0.87$, $P < 0.001$) on CO_2. Dashed lines are linear regressions of grains spike^{-1} of droughted Seri M82 ($y = -9.6 + 0.086x$, $r^2 = 0.82$, $P < 0.001$) and Yaqui 54 ($y = -8.4 + 0.081x$, $r^2 = 0.85$, $P < 0.001$) on CO_2. Dotted lines depict 95% confidence intervals for regression lines.

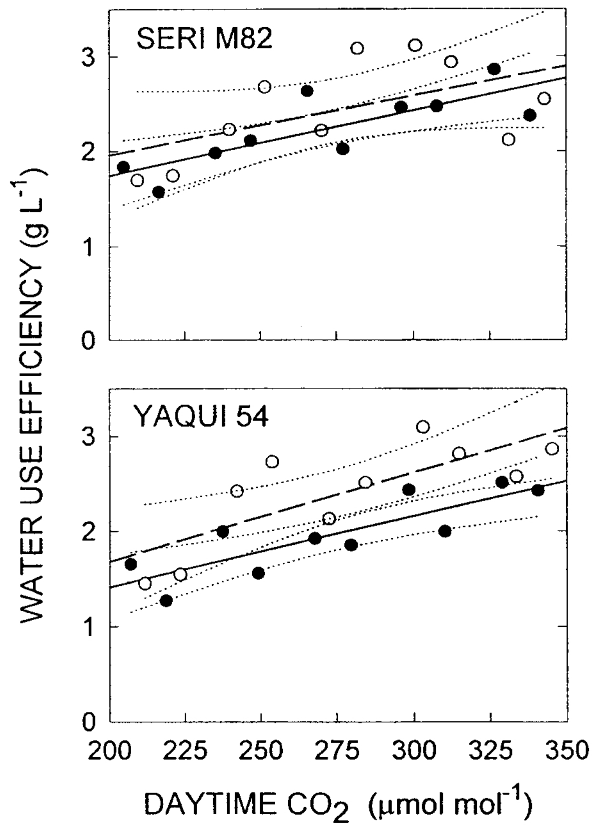

Fig. 8 Water use efficiency of above-ground biomass production (WUE) of well-watered (filled symbols) and droughted (open symbols) plants of two cultivars of spring wheat grown across a subambient CO_2 gradient. Solid lines are linear regressions of WUE of well-watered Seri M82 ($y = 0.37 + 0.007x$, $r^2 = 0.64$, $P = 0.006$) and Yaqui 54 ($y = -0.08 + 0.007x$, $r^2 = 0.71$, $P = 0.002$) on CO_2. Dashed lines are linear regressions of WUE of droughted Seri M82 ($y = 0.70 + 0.006x$, $r^2 = 0.31$, $P = 0.10$) and Yaqui 54 ($y = -0.19 + 0.009x$, $r^2 = 0.61$, $P = 0.008$) on CO_2. Dotted lines depict 95% confidence intervals for regression lines.

per spike in both well-watered and droughted plants (Fig. 7). Mass per grain, tillering, and numbers of fertile spikes per plant were not consistently affected by CO_2. In previous experiments with wheat, number of grains per spike increased with (Krenzer & Moss 1975; Gifford 1977, 1979; Chaudhuri *et al.* 1990) or was not affected by CO_2 (Sionit *et al.* 1980), but number of grains per plant or per unit area invariably increased. Irrespective of water or other stresses, tillering and the number of spikes per plant or per unit area are yield components that often respond positively to elevated CO_2 (Gifford 1979; Sionit *et al.* 1980; Sionit *et al.* 1981 a, b; Chaudhuri *et al.* 1990). No significant increase in tillering occurred in this experiment, perhaps because of the high plant density (355 plants m^{-2}) relative to other reports, although density in our experiment was equivalent to that recommended for the field in our geographical area. The progressive thinning of plants during this experiment may also have lessened CO_2 effects on tillering. Wheat was at or beyond the boot stage and, thus, the period when tillering would be responsive to CO_2 when plants were thinned to final density. In a previous experiment conducted in the same chamber, above-ground biomass of oats (*Avena sativa* L.) increased nearly 300% from about 150–330 µmol mol^{-1} CO_2 when grown at a density of 15 plants m^{-2} (Polley *et al.* 1992). The increase in oat biomass reflected a 65% increase in tillers per plant and 76% increase in biomass per tiller.

Mass per grain of wheat increased in some (Krenzer & Moss 1975; Sionit *et al.* 1980; Sionit *et al.* 1981b; Chaudhuri *et al.* 1990), but not all (Combe 1981; Gifford 1979) studies at the current and elevated CO_2 levels. Atmospheric CO_2 had little or no effect on the mass of individual grains in well-watered plants in this study

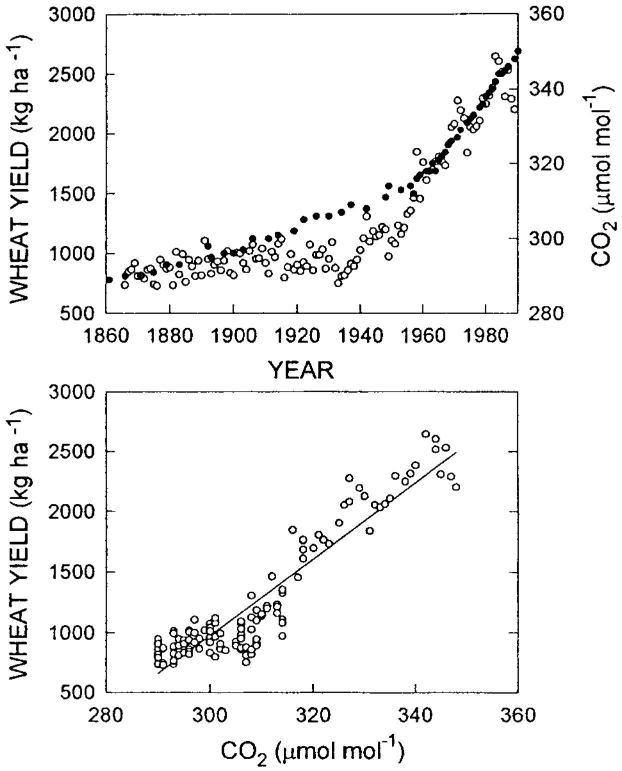

Fig. 9 Average United States wheat yields from 1866 to 1989 (open symbols) and atmospheric CO_2 concentration (filled symbols) over the same time period (upper), and the linear regression of national annual average wheat yields against CO_2 concentration (lower; $y = 31.6x - 8501$, $r^2 = 0.87$, $P = 0.0001$). Yields include all types of wheat and were compiled from the United States Department of Agriculture's *Agricultural Statistics* (1936 through 1990). Atmospheric CO_2 data are from Friedli *et al.* (1986).

(Fig. 6). Withholding water during grain-filling, eliminated any positive effect of CO_2 on mass per grain inYaqui 54 and caused grain mass to decrease as CO_2 rose in the later-maturing Seri M82. This decrease in mass per grain in Seri M82 resulted in lower grain yield (Fig. 3) and harvest index (Fig. 4) under drought, particularly at CO_2 concentrations approaching the current level.

The drought treatment had a more detrimental effect on yield of Seri M82 than Yaqui 54 and at the current than lower CO_2 concentrations. These trends partly reflected the timing of water deprivation and differences in cumulative water supplied. Because water was withheld from the early boot stage to maturity, the severity of stress increased progressively after the midpoint of the growing season. Stress developed too late to significantly influence tillering and spike density. Water deficits developed after floral initiation and spikelet number was established, so the number of grains per spike was not greatly affected by drought. Drought did influence mass per grain, however, especially in the later-maturing cultivar Seri M82.

Differences in cumulative irrigation also contributed to the greater sensivity of yield to drought treatments at the current than lower CO_2 concentrations, especially in Seri M82. About 25 L less water was added to droughted than well-watered compartments with Yaqui 54 over the experiment, regardless of CO_2 treatment. By contrast, the difference in water added to well-watered compared to droughted compartments with Seri M82 increased from about 13–36 L as CO_2 rose.

Factors contributing to yield responses to CO_2

The highly positive responses of above-ground biomass and grain yield to CO_2 in wheat resulted from a variety of physiological changes (Polley *et al.* 1993). Daytime net assimilation of Seri M82 and Yaqui 54 canopies more than doubled as CO_2 rose, while the ratio of night-time respiration to daytime net assimilation declined linearly with CO_2 concentration (Polley *et al.* 1993). Consequently, daily (24-h) net CO_2 accumulation per unit soil surface area increased dramatically from low to high CO_2 concentration, from about 180 to 450 µmol CO_2 m^{-2} d^{-1} during March and from 120 to 500 µmol m^{-2} d^{-1} during the first 2 weeks of April. The light compensation point of wheat canopies (the daily total of PPFD required for positive carbon assimilation) declined as CO_2 rose, suggesting that light use efficiency, like WUE (Fig. 8), increased with CO_2 concentration. The large increases in above-ground biomass and grain yield thus reflected positive contributions of carbon assimilation and retention that were proportionally greater than the increase in CO_2 concentration over a broad subambient range.

Historical wheat yields and CO_2

Annual world wheat production during recent decades rose 86% but the total area sown to wheat increased only 25.4%, suggesting that yields increased 'due to improved varieties and cultural practices' (Arnon 1972). Atmospheric CO_2 concentration also rose rapidly during recent decades. Growth and yield of wheat are highly sensitive to subambient CO_2 concentrations, implying that rising atmospheric CO_2 has been partly responsible for the upward trend in yield of this crop (Gifford 1979).

Goudriaan & Unsworth (1990) found a near-perfect relationship between world average cereal grain yield per unit area and CO_2 measurements at Mauna Loa, Hawaii from 1959 to 1986. They reasoned that rising CO_2 contributed about 1/14, or 7%, of the yield increase because the relative increase in grain yield has been seven times the relative increase in CO_2 concentration and the biotic growth (or yield enhancement) factor observed in experiments (ratio of proportional yield increase to proportional CO_2 increase) rarely exceeds 0.5. Yield enhancement factors calculated for grain from our experiment range from 1.0 to 1.4 for the two cultivars when droughted, and are ≈ 1.7 and 1.8 for well-watered Seri M82 and Yaqui 54, respectively. Using these values, corresponding proportions of the increase in world average grain yield attributable to rising CO_2 concentration for the period addressed by Goudriaan & Unsworth (1990) are 14–20% under drought and approach 25% under well-watered conditions.

Average wheat yields in the United States (U.S. Department of Agriculture 1936–90) and atmospheric CO_2 concentration are correlated over the 123-year period for which yield data are available (r^2 = 0.87; Fig. 9), but the correlation is especially strong during the last few decades when the rate of increase in CO_2 concentration was greatest. National average yields increased about 1250 kg ha^{-1} (from 1350 to 2600 kg ha^{-1}) between 1955 and 1990, while atmospheric CO_2 concentration rose 40 μmol mol^{-1} (from 312 to 352 μmol mol^{-1}). Regressions of grain yields on CO_2 concentration for the two spring wheat cultivars in this experiment (Fig. 3) indicate a mean increase of 242 and 602 kg ha^{-1} in grain yield when droughted and well-watered, repectively, with the 40 μmol mol^{-1} increase in CO_2 from 312 to 352 μmol mol^{-1} that occurred between 1955 and 1990. These suggest that rising CO_2 concentration has accounted for 19–48% of the observed increase in average yields of wheat in the U.S. over the last few decades, or fully a third, 33%, if these experimentally determined increases in grain yields of droughted and well-watered wheat are averaged.

The observed response of wheat to CO_2 and, consequently, both of our estimates of the contribution of CO_2 to historical increases in wheat yield should be regarded as near maximal. Plants were grown in fertile soil at relatively high temperatures and in narrow stands. Attenuation of lateral light by neighbouring plants thus was minimal compared to the shading that occurs in field plantings. Under well-watered conditions, plants experienced no water stress, and wheat grown near today's CO_2 level used 22–37% more water over the experiment than plants grown at the lowest concentration. The data do, however, demonstrate the extreme sensitivity of wheat yield to past increases in CO_2 concentration.

Each of the methods used to calculate the contribution of rising CO_2 to the recent increase in wheat yield produced lower-range estimates of about 15–20%. These estimates are two- to three-times those calculated without the benefit of experimental data on the response of wheat yield to subambient CO_2 concentrations (Goudriaan & Unsworth 1990; Amthor 1995).

Much of the recent increase in wheat yield undoubtedly reflects development of varieties better adapted to specific wheat-growing areas and with greater disease-resistance and physiological yield potential (Deckerd *et al.* 1985; Perry & D'Antuono 1989). These examples of progress in breeding, like cultural innovations such as effective pesticides and widespread use of nitrogen fertilizers, however, were introduced or widely employed in some areas, like the U.S., well after wheat yields began to climb rapidly during the 1950s.

Acknowledgements

Anne Gibson, Katherine Jones and Mark Dumesnil assisted in data collection, analysis, and presentation. Milton McDaniel advised us on the selection of cultivars, and Charles Erickson, John Heaton, and Cal Qualset provided seed. Jeffrey Baker, Al Frank, Thomas Gerik, Bruce Kimball, and Jim Kiniry provided helpful comments on the manuscript. Research was supported in part by the U.S. Department of Agriculture, Cooperative State Research Service under agreement no. 91–37100–6633 and National Research Initiative Competitive Grants Program/USDA under agreement no. 94–37100–0692.

References

Allen LH Jr, Bisbal EC, Boote KJ, Jones PH (1991) Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. *Agronomy Journal*, **83**, 875–883.

Amthor JS (1995) Terrestrial higher-plant response to increasing atmospheric [CO_2] in relation to the global carbon cycle. *Global Change Biology*, **1**, 243–274.

Arnon I (1972) *Crop Production in Dry Regions, Vol. II: Systematic Treatment of the Principal Crops*. Barnes & Noble, New York.

Baker JT, Allen LH Jr, Boote KJ (1990) Growth and yield response of rice to carbon dioxide concentration. *Journal of Agricultural Science*, **11**, 313–320.

Bacastow RB, Keeling CD, Whorf TP (1985) Seasonal amplitude increase in atmospheric CO_2 concentration at Mauna Loa, Hawaii, 1959–1982. *Journal of Geophysical Research*, **90**, 10529–10540.

Chaudhuri UN, Kirkham MB, Kanemasu ET (1990) Carbon dioxide and water level effects on yield and water use of winter wheat. *Agronomy Journal*, **82**, 637–641.

Combe L (1981) Effect of carbon dioxide and culture under artificial climate on the growth and yield of a winter wheat. *Agronomie*, **1**, 177–186.

Cure JD, Acock B (1986) Crop responses to carbon dioxide doubling: A literature survey. *Agriculture and Forest Meteorology*, **38**, 127–145.

Deckerd EL, Busch RH, Kofoid KD (1985) Physiological aspects of spring wheat improvement. In: *Exploitation of Physiological and Genetic Variability to Enhance Crop Productivity* (eds Harper JE, Schrader LE, Howell RW), pp. 46–54. American Society of Plant Physiologists, Rockville, MD.

Delmas RJ, Ascencio J-M, Legrand M (1980) Polar ice evidence that atmospheric CO_2 20 000 year BP was 50% of present. *Nature*, **284**, 155–157.

Dippery JK, Tissue DT, Thomas RB, Strain BR (1995) Effects of low and elevated CO_2 on C_3 and C_4 annuals I. Growth and biomass allocation. *Oecologia*, **101**, 13–20.

Ehleringer JR, Sage RF, Flanagan LB, Pearcy RW (1991) Climate change and the evolution of C_4 photosynthesis. *Trends in Ecology and Evolution*, **6**, 95–99.

Friedli H, Lotscher H, Oeschger H, Siegenthaler U, Stauffer B (1986) Ice core record of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries. *Nature*, **324**, 237–238.

Gifford RM (1977) Growth pattern, carbon dioxide exchange and dry matter distribution in wheat growing under differing photosynthetic environments. *Australian Journal of Plant Physiology*, **4**, 99–110.

Gifford RM (1979) Growth and yield of CO_2-enriched wheat under water-limited conditions. *Australian Journal of Plant Physiology*, **6**, 367–378.

Goudriaan J, de Ruiter HE (1983) Plant growth in response to CO_2 enrichment, at two levels of nitrogen and phosphorous supply. 1. Dry matter, leaf area and development. *Netherland Journal of Agricultural Science*, **31**, 157–169.

Goudriaan J, Unsworth MH (1990) Implications of increasing carbon dioxide and climate change for agricultural productivity and water resources. In: *Impact of Carbon Dioxide, Trace Gases, and Climate Change on Global Agriculture* (eds Kimball BA, Rosenberg NR, Allen Jr LH), pp. 111–130. Special Publication Number 53. American Society of Agronomy, Madison.

Huckabee JW Jr, Thompson DR, Wyrick JC, Paulat EG (1977) *Soil Survey Bell County Texas*. USDA Soil Conservation Service, Washington, D.C., 165 pp.

Johnson HB, Polley HW, Mayeux HS (1993) Increasing CO_2 and plant–plant interactions: effects on natural vegetation. *Vegetatio*, **104/105**, 157–170.

Keeling CD, Whorf TP (1994) Atmospheric CO_2 records from sites in the SIO air sampling network. In: *Trends '93: A Compendium of Data on Global Change* (eds Boden TA, Kaiser DP, Sepanski RJ, Stoss FW), pp. 16–26. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN.

Kimball BA (1983) Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal*, **75**, 779–788.

Kimball BA, Pinter PJ Jr, Garcia RL *et al.* (1995) Productivity and water use of wheat under free-air CO_2 enrichment. *Global Change Biology*, **1**, 429–442.

Krenzer EG Jr, Moss DN (1975) Carbon dioxide enrichment effects upon yield and yield components in wheat. *Crop Science*, **15**, 71–74.

Lawlor DW, Mitchell RAC (1991) The effects of increasing CO_2 on crop photosynthesis and productivity: a review of field studies. *Plant, Cell, and Environment*, **14**, 807–818.

Loomis RS (1983) Productivity of agricultural systems. In: *Physiological Plant Ecology IV* (eds Lange OL, Nobel PS, Osmond CB, Ziegler H), pp. 151–172. Springer-Verlag, Berlin.

Mayeux HS, Johnson HB, Polley HW, Dumesnil MJ, Spanel GA (1993) A controlled environment chamber for growing plants across a subambient CO_2 gradient. *Functional Ecology*, **7**, 125–133.

Neftel A, Oeschger H, Staffelbach T, Stauffer B (1988) CO_2 record in the Byrd ice core 50 000 year BP. *Nature*, **331**, 609–611.

Perry MW, D'Antuono MF (1989) Yield improvement and associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982 *Australian Journal of Agricultural Research*, **40**, 457–472

Polley HW, Johnson HB, Mayeux HS (1992) Growth and gas exchange of oats (*Avena sativa*) and wild mustard (*Brassica kaber*) at subambient CO_2 concentrations. *International Journal of Plant Sciences*, **153**, 453–461.

Polley HW, Johnson HB, Mayeux HS, Malone SR (1993) Physiology and growth of wheat across a subambient carbon dioxide gradient. *Annals of Botany*, **71**, 347–356.

Sage RF (1995) Was low atmospheric CO_2 during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biology*, **1**, 93–106.

Sionit N, Hellmers H, Strain BR (1980) Growth and yield of wheat under CO_2 enrichment and water stress. *Crop Science*, **20**, 687–690.

Sionit N, Mortensen DA, Strain BR, Hellmers H (1981a) Growth response of wheat to CO_2 enrichment and different levels of mineral nutrition. *Agronomy Journal*, **73**, 1023–1027.

Sionit N, Strain BR, Hellmers H (1981b) Effects of different concentrations of atmospheric CO_2 on growth and yield components of wheat. *Journal of Agricultural Science*, **79**, 335–339.

Strain BR (1992) Atmospheric carbon dioxide: a plant fertilizer? *New Biologist*, **4**, 87–89.

Trabalka JR, Edmonds JA, Reilly JM, Gardner RH, Voorhees LD (1985) Human alterations of the global carbon cycle and the projected future. In: *Atmospheric Carbon Dioxide and the Global Carbon Cycle* (ed. Trabalka JR), pp. 247–287. U.S. Department of Energy, Washington, D.C.

United States Department of Agriculture (1936–1990) *Agricultural Statistics*, 1936, 1952, 1966, 1975 and 1990. U. S. Government Printing Office, Washington, D.C.

Weisberg S (1980) *Applied Linear Regression*. John Wiley & Sons, New York, 283 pp.