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TECHNICAL REPORT

Facility for studying the effects of elevated carbon dioxide concentration and increased temperature on crops

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ABSTRACT

The requirements for the experimental study of the effects of global climate change conditions on plants are outlined. A semi-controlled plant growth facility is described which allows the study of elevated CO_2 and temperature, and their interaction on the growth of plants under radiation and temperature conditions similar to the field. During an experiment on winter wheat (cv. Mercia), which ran from December 1990 through to August 1991, the facility maintained mean daytime CO_2 concentrations of 363 and 692 cm^3 m^{-3} for targets of 350 and 700 cm^3 m^{-3} respectively. Temperatures were set to follow outside ambient or outside ambient +4 °C, and hourly means were within 0·5 °C of the target for 92% of the time for target temperatures greater than 6 °C. Total photosynthetically active radiation incident on the crop (solar radiation supplemented by artifical light with natural photoperiod) was 2% greater than the total measured outside over the same period.

Key-words: CO_2 enrichment; $CO_2 \times$ temperature; environmental control; climate change.

INTRODUCTION

The potential effects of global climate change on local, national and world food supplies may be very severe. Therefore, it is important to assess the effects of environmental conditions associated with global climate change, i.e. increased CO_2 concentration and temperature, on the productivity of agricultural crops. The information derived from assessment of crop responses under experimental conditions may be included in crop simulation models, and thus, used to estimate the consequences of changes in particular environmental factors, different combinations of factors and interactions with other conditions (e.g. soil nutrition) on the productivity of plants.

The effects of the rapidly increasing CO_2 concentration, currently increasing at 1·5 cm^3 m^{-3} $annum^{-1}$, have been examined for some of the most important food crops (e.g. soy bean and spring wheat), but fewer studies have been made of the response of crops with a very long growing season, such as winter wheat (Kimball 1983; Cure & Acock 1986; Lawlor & Mitchell 1991). The majority of the studies on crop plants have been conducted in controlled environments, usually at reduced radiation and at warmer temperatures relative to field conditions (Lawlor & Mitchell 1991). It has been suggested that a decrease in photosynthetic capacity in response to CO_2 enrichment is more likely to be observed in controlled environments than in the field (Arp 1991; E. Delgado, personal communcation). In any case, the response of plants to elevated CO_2 is very dependent upon other environmental factors, particularly water supply, temperature and nutrition (Lawlor & Mitchell 1991). This is illustrated by the variability of crop responses to a doubling of CO_2 concentration (Cure & Acock 1986); for example, increases in wheat yield ranging from 0 to 37% have been reported even under optimal water and nutrient conditions (Fischer & Aguilar 1976; Krenzer & Moss 1975).

Temperature has profound effects on crop production, affecting the rate of organ development, respiration and senescence and altering the source-sink relations of plants (Farrar & Williams 1991). Photorespiration increases in importance with temperature so that a positive interaction between the effects of increased temperature and CO_2 concentration on photosynthesis is expected in C_3 plants (Long 1991). Studies by Idso, Kimball & Mauney (1987) indicate that such an interaction may occur on the productivity of several species, but similar studies have not been made in wheat. Increases in temperature of up to 4 °C towards the end of the next century have been predicted by global circulation models to accompany increases of CO_2 from the current 350 to as high as 700 cm^3 m^{-3}. These conditions represent extremes but provide a base line for testing the response of plants from which responses to less extreme conditions can be judged.

The complexity of the interactions between CO_2 and temperature and other environmental variables means that quantification of plant responses to novel climates requires simulation models of the processes. However,

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since these models of necessity contain approximations and empirical relationships, it is necessary to establish other conditions as close as possible to those currently experienced, and expected in the future, in the field (e.g. natural day length and radiation). However, this is difficult to do in the field; increasing CO_2 around crops by free air CO_2 enrichment (FACE) (Hendrey *et al.* 1988) is technically demanding and extremely expensive in equipment and use of CO_2. Also, temperature cannot be modified, so that CO_2 × temperature interactions are impossible to study except by exploiting (uncontrolled) temperature variability between years. The advantage of FACE experiments is in the large areas of crop exposed to elevated CO_2. Open-top fumigation chambers are a practical solution to the problem of exposing crops to altered atmospheres (Drake *et al.* 1989). However, they do modify the environment substantially, increasing temperatures, decreasing radiation and rainfall (Ashenden, Baxter & Rafarel 1992). The relative merits of alternative methods of studying the effects of elevated CO_2 on crops have been compared in detail elsewhere (Lawlor & Mitchell 1991).

Here we describe a facility comprised of compartments within a glass house, which allows comparison of the effects of elevated CO_2 and increased temperature and their interaction, otherwise not possible in field studies. The performance of the system in achieving target environments throughout the growing season of winter wheat is reported.

MATERIALS AND METHODS

Controlled environment facility

Four chambers of approximately 2 × 3 m in area and 2 m high, were constructed of 6-mm double-skinned polycarbonate sheet within a glasshouse (Fig. 1). The chambers were surrounded externally with reflective aluminium foil to improve light distribution within the chamber. Natural radiation was decreased by approximately 30% by the glasshouse structures, chamber roof *et cetera*. To maintain the total photosynthetically active radition (PAR) incident on the crop over the day close to the natural radiation, supplementary lighting of ca. 200 μmol quanta m^{-2} s^{-1} at floor height is provided by six 400-W SON-T lamps mounted above the chamber roof. The lamps are programmed to switch on at day break and off at sunset via a glasshouse control system (Envirocon 3, Rothamsted Experimental Station, Harpenden, UK). Temperature control of the main glasshouse is provided by the Envirocon manipulating the air vents and heating. Cooling for the chambers is provided by a central refrigeration plant (Airwell 'Split System' GC6 CMS4, L'Air Conditionné Entreprises SA, Montigny-le-Brettoneux, France) with compressor and heat exchange outside the glass house and individual floor mounted heat exchange units in each chamber. These have integral fans (airflow ca. 560 m^3 h^{-1}), cooling coils (3·2–4·3 kW) and heaters (2 kW), to increase the background heating when required. Ambient air is blown by a fan into the compartment through a filter to remove insects. Temperature of the chamber air entering the air handler (taken as that of the whole compartment) is sensed with platinum resistance thermometers. Ambient air temperature is similarly measured outside in a Stevenson screen 10 m away from the glass house. Temperature profiles within the chambers are determined by an array of type T thermocouples. Humidity is determined at regular intervals using a portable humidity meter (model SL126, Eurisem Technics, Earl Shilton, UK). Total radiation incident in each room is measured by 0·9-m-long tube solarimeters (model TSL, Delta T Devices, Cambridge, UK) which are adjustable in height and are moved so that they are positioned just above the crop. Ambient radiation is measured by a Kipp solarimeter at a meteorological site 500 m away from the experimental facility.

The CO_2 content of the air within a chamber is measured by an individual infra-red gas analyser (IGD RMS 862; FKI Krypton, Yeovil, UK) for each chamber. The analyser samples air from several points within the chamber with a response time of c. 45 s. Pure CO_2 is supplied to the chamber from a bank of four, 12 kg cylinders via a pressure regulator and a solenoid valve controlled by the software of a computer system. The CO_2 is injected into the air handler inlet to ensure rapid and uniform dispersal of the gas within the compartment.

Data logging and control of conditions

Temperature sensor readings for control of the chamber temperature are interfaced via a data logger/controller (CIL MFI System 1010, incorporating CIL 200 and CIL 100 programmable controls units; CIL, Lancing, UK) interfaced with a computer (PC standard), which provides user access to the CIL MFI system. The infra-red gas analyser output signal is compared to the set point for CO_2 concentration required for the chamber which is input to the CIL MFI System via the PC. When the infra-red gas analyser's reading falls below the set point (with a dead band of 20 cm^3 m^{-3}), the solenoid is activated via the CIL MFI System and CO_2 flows into the chamber until the concentration rises beyond the set point and the solenoid closes. Software developed at Rothamsted Experimental Station (HIGHCOAM, G. Harrison and R. Lefevre) provides for data logging and storage on hard and floppy disk, and for user input of set points for CO_2 and temperature, and real-time display of data. The temperature sensor measurements are compared with the set point, which is the ambient temperature plus a user-defined offset, and the heating and cooling functions are activated as required to maintain the target temperature. Additional logging of thermocouple and light sensor data is performed by Campbell CR10 loggers (Campbell Scientific, Loughbo-

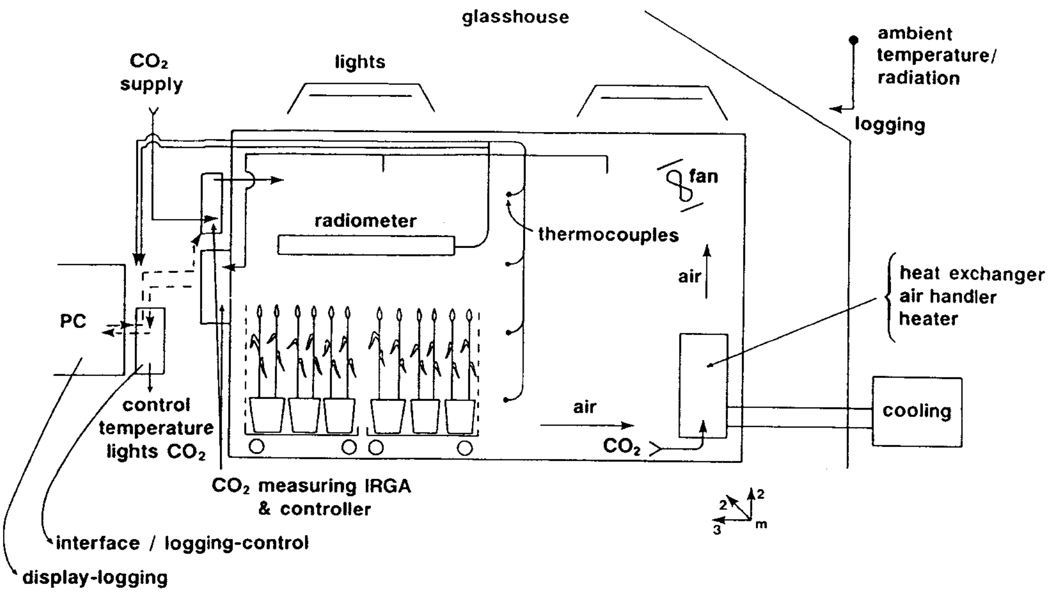


Figure 1. Diagram of the controlled CO_2 and temperature chambers used to study the response of winter wheat to climate change conditions. Details of the equipment are given in the text.

rough, UK) the data being down-loaded regularly to the PC.

Four chambers of the design described were used in the studies, so that replication of the four treatment conditions was not possible. To minimize bias due to differences in the light or temperature conditions, due to small differences in sensor calibration between chamchambers or to the position of the chambers, the plants were moved between chambers weekly, so that each crop experienced each chamber in succession; the CO_2 and temperature set points were re-set to maintain the treatment conditions. Plants were also moved around within each chamber systematically so that each pot was at the edge of the crop for the same length of time to minimize positional effects.

Plant growth

Plants of winter wheat (*Triticum aestivum* L. cv. Mercia) were grown in 5 dm^3, 17 cm diameter plastic pots containing sintered arcillite rooting medium (Terra-green, Silvaperl Products Ltd, Harrogate, UK). Pots were arranged in trays (3×3 array) mounted on 10 cm tall wheeled trolleys to allow movement of plants within and between rooms.

RESULTS

The target levels for the experiment, which ran from 5 December 1990 to 2 August 1991, were temperatures following outside air ambient (called ambient) or ambient plus 4°C and CO_2 concentrations of 350 and 700 $cm^3\ m^{-3}$. Temperatures attained by each treatment during the experiment are shown in Fig. 2, together with the ambient temperature. The target temperatures were easily achieved, except when the ambient went below 6°C during the very coldest winter period, when the refrigeration unit was unable to operate without danger of icing and damage. During this period, the temperature in the rooms was kept at 6°C, and some growth of the plants proceeded, thus accelerating growth compared to that of field grown plants. Above the minimum temperature, all treatments were within 0·5°C of the temperature target for 92% of the time. Independent thermocouples attached to the plant stems at the base of the canopy showed that coupling between

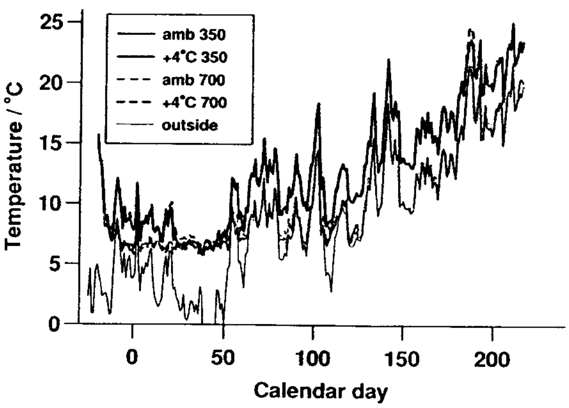


Figure 2. Mean daily temperatures attained in the controlled CO_2 and temperature chambers compared with the outside (ambient) temperature. The chambers were set to track ambient or 4°C above ambient for temperatures greater than 6°C; temperatures below this were not attainable because of possible damage to equipment.

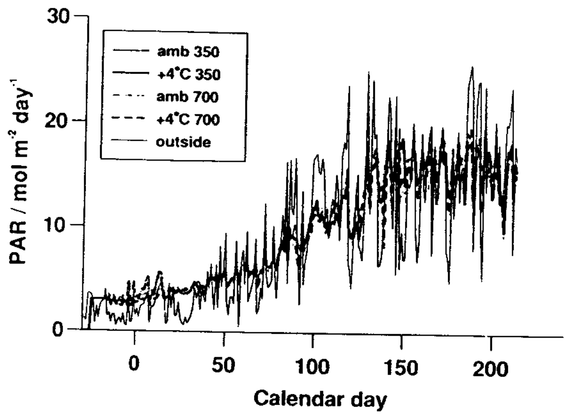


Figure 3. The daily total PAR incident on plants in the CO_2 and temperature facility and the daily measured PAR outside the glasshouse. Note the different CO_2 and temperature treatments experienced the same PAR and that during periods in winter the radiation exceeded the natural radiation. In summer, radiation in the chambers incident upon the plants exceeded the natural radiation when sunlight was dim, but did not reach the maxima obtained in very bright periods. The total radiation experienced by plants within the chamber was very similar to the total radiation in the open air (see text).

the mean hourly stem and air temperature was within 1 °C for 68% of the time and within 2°C for 90% of the time. Overall, stem temperature was 0·2 °C warmer than air temperature. Maximum hourly mean temperatures reached were 28 and 32°C for the ambient and ambient +4°C treatment, respectively. The mean seasonal temperatures were 1·5 °C (almost entirely due to the 6 °C lower limit of the system) and 4·1 °C above ambient for the ambient and ambient +4°C treatments, respectively.

Daily total photosynthetically active radiation incident on the plants was comparable to the ambient incident PAR solar radiation (Fig. 3). The supplementary lighting increased the radiation to the crop so that it exceeded the ambient during the very dim winter days. In bright days in summer, the peak radiation inside the chambers was less than the ambient, but on dull days, the chambers experienced greater radiation than ambient. Consequently, the average total PAR radiation experienced by the crops over the growing season in the compartments (5364 mol quanta m^{-2}) was very similar to that measured outside (5253 mol quanta m^{-2}) and the totals received by the four treatments were all

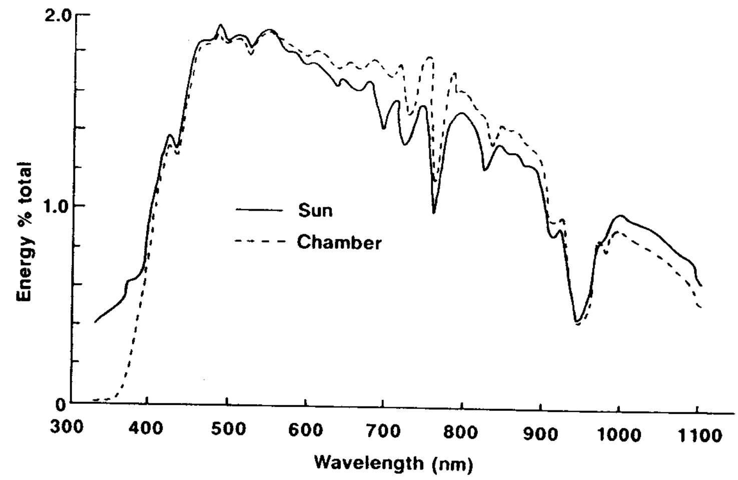
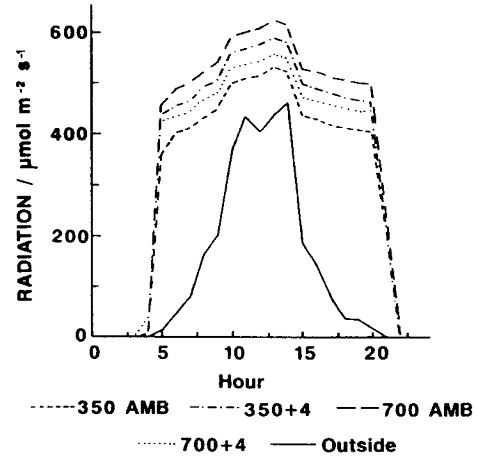


Figure 4. Spectral distribution of radiation experienced by crops grown in the CO_2 and temperature facility from combined solar radiation and artifical light (SON-T lamps) compared to solar radiation. Measurements were made with a LI-COR 1800 spectral meter with a wave-band of half power and above of 4 nm.

Table 1. CO_2 concentrations achieved during the winter wheat experiment. Mean hourly concentrations of CO_2 (cm^3 m^{-3}) are shown ± SD

	Target	350	700	*n*
January–March	Night	377 ± 35	656 ± 115	1709
	Day	353 ± 41	690 ± 37	1085
April–May	Night	380 ± 40	702 ± 28	972
	Day	367 ± 35	692 ± 39	2058
Overall	Night	380 ± 41	673 ± 92	2682
	Day	363 ± 39	692 ± 39	3143

(a) 25 June (cloudy)



(b) 5 July (sunny)

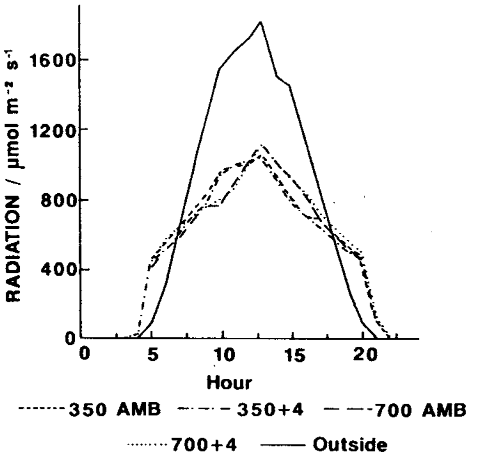


Figure 5. Examples of the diurnal distribution of day-length in the CO_2 and temperature chambers compared with radiation outside. Contribution of solar radiation and artifical lamps (SON-T lamps) depends on the absolute level of solar radiation: (a) a day with little solar radiation; (b) a very sunny day.

within 2% of each other. The spectral quality of the radiation was similar to sunlight over the range 400–700nm (PAR) with a relative reduction at the shorter wavelengths and increase at the longer (Fig. 4). The compartment walls and green house removed radiation below 370nm and enhanced the wavelengths above 700nm.

The pattern of diurnal radiation was 'squarer' than in ambient conditions, with greater intensities early and late in the day, but less at high solar elevations (Fig. 5). This was largely due to the contribution of the supplementary lighting.

The CO_2 content of the air in the chambers over the growing season is shown in Fig. 6. The main problem in maintaining the chamber CO_2 targets was local ambient concentrations exceeding $350cm^3\ m^{-3}$, especially at night (Table 1) with occasional very marked peaks particularly during the winter months. Concentrations were within $50cm^3\ m^{-3}$ of the target in $350cm^3\ m^{-3}$ and within $20cm^3\ m^{-3}$ in the $700cm^3\ m^{-3}$ treatment for 90% of the time. As Fig. 6 shows, there were very few occasions when the CO_2 concentration dropped (or increased) substantially below the $700cm^3\ m^{-3}$ set point. The distribution of CO_2 in the rooms was very uniform (data not shown).

DISCUSSION

The system described and characterized here fulfils a number of criteria for the effective study of the effects and interaction of increased CO_2 and temperature on crops, with application of well-controlled, clearly defined treatments under radiation and temperature very similar to the field. However, several problems are also apparent in the approach—the control of saturation vapour deficit is one; dehumidification followed by re-humidifying the air is expensive for the relatively low-cost system described here. However, the humidities measured in the facility were consistently above the range in which water stress effects occur (data not shown). Another problem is the spectral difference with decrease of short wavelengths (including UV-B) (Fig. 4) which could alter plant responses to the other variables. Effects owing to the small soil volume used are also possible, since although the regular provision of ample nutrients and water means that interaction with water or nutrient deficiency was not a problem, restricted root volume may lead to the production of ABA which may affect organ growth, stomatal activity and hence total production (Davies & Zhang 1991). However, the very large dry matter production observed in the experiment on winter wheat (Mitchell *et al.* 1993)

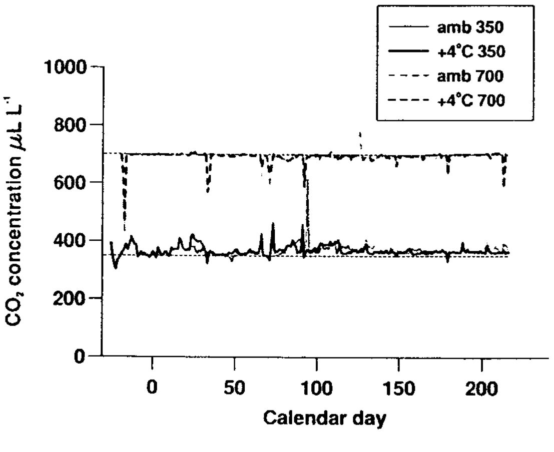


Figure 6. Daily mean carbon dioxide (CO_2) concentrations of the air in the controlled CO_2 and temperature chambers during the course of an experiment examining the effects of atmospheric conditions on winter wheat over approximately 250d. The set points for the system were 700 and $350cm^3\ m^{-3}$ each at two temperatures, ambient and ambient + 4°C.

does not suggest that a major limitation to growth occurred. The control over root medium conditions and the timing and rates of application of nutrients have distinct advantages for experimentation, compared to the field. Also, dates of sowing can be controlled more easily. By monitoring the consumption of CO_2 in the chambers, the facility also affords the possibility of measuring total crop CO_2 exchange with the atmosphere.

In conclusion, the facility described here is a low-cost means of applying increases in CO_2 concentration and temperature over ambient conditions, in a light environment comparable to UK field conditions.

REFERENCES

Arp W.J. (1991) Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. *Plant, Cell and Environment* **14**, 869–875.

Ashenden T.W., Baxter R. & Rafarel C.R. (1992) An inexpensive system for exposing plants in the field to elevated concentrations of CO_2. *Plant, Cell and Environment* **15**, 365–372.

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

Davies W.J. & Zhang J. (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology* **42**, 55–76.

Drake B.G., Leadley P.W., Arp W.J., Nassiry D. & Curtis P.S. (1989) An open-top chamber for field studies of elevated atmospheric CO_2 concentrations on salt marsh vegetation. *Functional Ecology* **3**, 363–371.

Farrar J.F. & Williams M.L. (1991) The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment* **14**, 819–830.

Fischer R.A. & Aguilar I.M. (1976) Yield potential in a dwarf spring wheat and the effect of carbon dioxide fertilization. *Agronomy Journal* **68**, 749–752.

Hendrey G.R. Lipfert F.W., Kimball B.A., Hileman D.R. & Bhattacharya N.C. (1988) *Free air carbon dioxide enrichment (FACE) facility development. II. Field tests at Yazoo city, MS, 1987.* Report 046, US Dept of Energy, Carbon Dixoide Research Division, Office of Energy Research, Washington, DC.

Idso S.B., Kimball B.A. & Mauney J.R. (1987) Atmospheric carbon dioxide enrichment effects on cotton midday foliage temperature: implications for plant water use and crop yield. *Agronomy Journal* **79**, 667–672.

Kimball B.A. (1983) Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**, 779–782.

Krenzer E.G. & Moss D.N. (1975) Carbon dioxide enrichment effects upon yield and yield components in wheat. *Crop Science* **15**, 71–74.

Lawlor D.W. & Mitchell R.A.C. (1991) The effects on increasing CO_2 on crop photosynthesis and productivity: a review of field studies. *Plant, Cell and Environment* **14**, 807–818.

Long S.P. (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**, 729–739.

Mitchell R.A.C., Mitchell V.J., Driscoll S.P., Franklin J. & Lawlor D.W. (1993) Effects of increased CO_2 concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant, Cell and Environment* **16**, 521–529.

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