Review

Fluctuations of CO_2 in Free-Air CO_2 Enrichment (FACE) depress plant photosynthesis, growth, and yield

L.H. Allen[a],[*], B.A. Kimball[b], J.A. Bunce[c], M. Yoshimoto[d], Y. Harazono[e], J.T. Baker[f], K.J. Boote[g], J.W. White[b]

[a] U.S. Department of Agriculture, Agricultural Research Service, CMAVE, Gainesville, FL, United States
[b] U.S. Department of Agriculture, Agricultural Research Service, U.S. Arid-Land Agricultural Research Center, Maricopa, AZ, United States
[c] U.S. Department of Agriculture, Agricultural Research Service, Beltsville, MD, United States
[d] Institute for Agro-Environmental Sciences, NARO, Tsukuba, Japan
[e] International Arctic Research Center, UAF, Fairbanks, AK, United States
[f] U.S. Department of Agriculture, Agricultural Research Service, Big Spring, TX, United States
[g] Agronomy Department, University of Florida, Gainesville, FL, United States

ABSTRACT

Free-Air CO_2 Enrichment (FACE) was conceived as an experimental method to measure plant responses to elevated CO_2 in natural environments rather than in chambered or controlled environments. However, due to the difficulty of controlling elevated CO_2 concentrations in turbulent air, the range of fluctuations of CO_2 in FACE experiments are more than 10-fold greater than plants experience in natural conditions. One early study reported that photosynthetic increases of leaves in 40- and 80-s periods of oscillating elevated CO_2 were only about 68% of those in leaves exposed to constant elevated CO_2 with the same mean CO_2 concentration. Later whole-plant studies reported smaller increases of responses in 60-s periods of oscillating elevated CO_2 compared to constant elevated CO_2 with the same mean concentration. After eliminating problematic data from studies that predicted plant responses in FACE to be only 45% of responses in open top chambers, we calculated that yields increased 65% as much in fluctuating elevated CO_2 of FACE as in constant elevated CO_2. The smaller plant responses in fluctuating elevated CO_2 can be attributed partially to the non-linear, convex-upward curved response of photosynthesis to CO_2 concentration, but other unknown mechanisms must exist. Future leaf chamber studies and FACE studies should include fundamental photosynthetic physiologists who can focus on uncovering the mechanisms responsible for lower photosynthetic, biomass, and yield response in both regular waveform oscillating and irregular fluctuating elevated CO_2. Because CO_2 fluctuates in FACE and recent experiments indicate reduced photosynthesis and growth under fluctuating CO_2, responses of plants in FACE are likely to underestimate the benefits of rising CO_2. We found that a correction factor of about 1.5 needs to be applied to FACE results. While responses to elevated CO_2 in FACE experiments are smaller than those in chamber experiments, FACE responses are obtained in natural conditions not available in chambers and thus are conservative regarding future projections of agricultural productivity.

1. Introduction

Interest in quantifying the response of plants to rising carbon dioxide concentration ($[CO_2]$) expanded rapidly during the 1980′s (Allen, 1979; Sionit et al., 1982; Kimball, 1983; Jones et al., 1984; Rogers et al., 1984a, 1984b; Dahlman et al., 1985; Strain and Cure, 1985; Allen et al., 1987; Allen, 1990). Most early studies reported plant responses from open top chambers (OTC) or sunlit, controlled-environment chambers (SCEC, such as Soil-Plant-Atmosphere Research or SPAR) facilities. Recognizing that chamber environments differ

substantially from natural environments, researchers developed systems for open-air CO_2 enrichment, culminating in the Free-Air CO_2 Enrichment (FACE) method (Allen, 1992). A prototype FACE technology was developed by Brookhaven National Laboratory, NY (Hendrey, 1993), and early testing was conducted at Yazoo City, MS (Hileman et al., 1992). This system became fully operational at Maricopa, AZ USA (Kimball et al., 1992, 1994) and has since been adapted in various systems worldwide (LeCain et al., 2015) (see also https://facedata.ornl.gov/global_face.html, accessed 29 April 2018). FACE systems were promoted because they provided (a) natural aerial environment (wind, temperature, and humidity) for plants; (b) natural sunlight; (c) natural, non-limiting rooting environment in contrast to plants grown in small containers, which may affect results (Arp, 1991; Thomas and Strain, 1991; Heagle et al., 1999); (d) field-plot size of experimental units with sufficient plant material for multiple studies, all having bordered plants, and potential for scaling up to tall plant studies, including trees; (e) lower cost per unit plot area; and (f) field data from both treatment plots and control plots for validating plant growth models. Other outdoor, sunlit, exposure systems such as OTC, SCEC, SPAR chambers, and Temperature-Gradient Greenhouses/ Tunnels/ Chambers (TGG/TGT/TGC) did not provide all these advantages. Artificially illuminated growth chambers or facilities with plants grown in pots with root restriction were deemed unnatural and would provide less meaningful assessments of plant responses. However, controlled plant-growth systems can accommodate a higher and lower range of environmental variables ([CO_2], temperature, water availability, and nutrients) than open-field plots (Ziska and Bunce, 2007).

In this paper, the term "elevated [CO_2]" will be designated "e[CO_2]." The term "oscillating e[CO_2]" will be applied to orderly e[CO_2] variations with a large fixed oscillation pattern (i.e., fixed frequency and fixed amplitude). "Fluctuating e[CO_2]" will be applied to e[CO_2] variations with a wide range of uncontrolled, effectively random, varying frequencies and amplitudes as produced in FACE enrichment systems. Leaf and plant responses to both oscillating e[CO_2] and fluctuating FACE e[CO_2] will be compared with constant e[CO_2]. By constant e[CO_2], we mean no rapid fluctuations of e[CO_2], with a steady e[CO_2] nearly constant to within a few ppm.

Early measurements indicated that e[CO_2] variability around the [CO_2] setpoint was pronounced in FACE systems (Hileman et al., 1992). However, few efforts were made to quantify this variability or to determine if fluctuating e[CO_2] might influence plant responses. Instead, the focus was on quantifying the percentage of time that [CO_2] was within a given range of setpoint e[CO_2] (Nagy et al., 1994). For example, grab samples at the control point (each value representing a 4-s average of instantaneous concentrations recorded each minute) in 1995 at Duke Forest, NC USA were within ± 20% of setpoint [CO_2] [± 110 ppm of the 550 ppm setpoint) for 62% of the time (Hendrey et al., 1999)]. Consequently, [CO_2] deviations from setpoint were more than ± 110 ppm for 38% of the time for this sampling method. The distribution of [CO_2] in these grab samples exhibited a sharp cut-off slightly below the ambient [CO_2] of 350 ppm but exhibited a long tail that exceeded 800 ppm at the high end of the distribution (Hendrey et al., 1999). Likewise, 1-min averages of [CO_2] were within ± 10% of target (± 55 ppm of the 550 ppm setpoint) for 69% of the time, and within ± 20% of target (± 110 ppm of the 550 ppm setpoint) for 92% of the time (Hendrey et al., 1999). Smoothing observations across 1-min intervals caused an apparent better fit to setpoint of fluctuating FACE e[CO_2], which is misleading because it causes short-term fluctuations to disappear. Similar levels of [CO_2] control were obtained in other FACE systems (Okada et al., 2001; Miglietta et al., 2001). A summary of 11 FACE sites indicated 1-min average [CO_2] to be within ± 10% of setpoint an average of 79% of the time, with a range of 59% to 92% for various sites and systems (Hendrey and Miglietta, 2006). However, these summary data gave no indication of the rapid and wide fluctuations of [CO_2] within FACE systems at very short time steps.

Early leaf chamber studies of wheat indicated the potential for a 20% maximum reduction of plant photosynthetic response under oscillating e[CO_2] compared to constant e[CO_2] at periods of 120 to 240 s with no reduction at periods of 20 s and less (Hendrey et al., 1997). While this study was made on the effect of oscillating e[CO_2] on electron transport of Photosystem II, it should provide information of photosynthetic CO_2 uptake rates in oscillating e[CO_2].

Because plants were exposed to e[CO_2] in natural open-air environments in FACE systems, and because possible artifacts of fluctuating [CO_2] were not obvious or were considered to be minor and unimportant, FACE became the *accepted standard* for studies of CO_2 enrichment effects on plants (Hendrey, 1993; Hendrey et al., 1999; Kimball et al., 2002; Hendrey and Miglietta, 2006; Ainsworth et al., 2003; Long et al., 2004, 2005, 2006; Ainsworth and Long, 2005; Ainsworth et al., 2008a; Leakey et al., 2009). Acceptance of FACE was so strong that no formal experiments were conducted to compare FACE with on-site chamber systems. Prior to studies in Beltsville, MD (Bunce, 2014a, 2016) the only study where FACE and OTC systems were deployed together was in a wheat trial in Maricopa, AZ (Kimball et al., 1997).

Our hypothesis is that plant responses in fluctuating e[CO_2] are depressed (i.e., less) compared to plant responses in constant [CO_2] of the same mean concentration. This hypothesis is based on numerous experimental observations rather than a testable physiological mechanism. Our objectives are to (1) describe the fluctuations in [CO_2] as reported for various FACE systems, then (2) review and critically compare responses of plants grown in both oscillating e[CO_2] systems and fluctuating e[CO_2] of FACE systems with respect to responses of plants grown in constant e[CO_2] of chambered-plant studies, and (3) provide new insights into reports of differing photosynthetic, biomass, and seed yield outcomes of FACE versus non-FACE systems of CO_2 enrichment of plants.

2. Characterizing fluctuating [CO_2] in various conditions

2.1. Magnitude of fluctuations of [CO_2] in FACE systems

For measuring fluctuations of [CO_2] in FACE and control plots, two open-path infrared gas analyzers (model E009A and E009B, Advanet Inc., Okayama, Japan) were positioned 0.4 m above a wheat canopy at Maricopa, AZ USA on 26–27 March 1997. One analyzer was placed in a non-CO_2-enriched control "Blower" plot and one in an enriched FACE plot. The CO_2 analyzers were placed northeast of the center of the plots, downwind of the predominant southwest wind. The field layout of the Maricopa FACE facility was documented in detail (Kimball et al., 1999). The ambient [CO_2] within the control Blower plot was steady (nearly constant) but e[CO_2] within the FACE plot was not well maintained near the + 200 ppm setpoint (Fig. 1). In this example, the lower (bounded) limit to the fluctuations was about 370 ppm (the natural ambient [CO_2]) and the upper (unbounded) limit was > 770 ppm (sometimes much greater than 770 ppm (Fig. 1). Other reports also indicate upper unbounded [CO_2] of greater than 200 ppm above target in FACE systems (Hendrey et al., 1999; Okada et al., 2001; Bunce, 2011). Control to the fixed [CO_2] setpoint was variable in other systems as well (compare Fig. 1 with Supplementary Fig. S2).

The Maricopa FACE system used the first FACE system, the Brookhaven National Laboratory design (Hendrey, 1993) wherein single blowers forced CO_2-enriched air through a circular array of vertical vent pipe injectors that were controlled to emit typically on the upwind side of each FACE plot. Operational details and most of the data from the experiment are published (Kimball et al., 2017). The injected air was prediluted to about 1 to 3% CO_2 (Lipfert et al., 1992; He et al., 1996). The Rice FACE system or "Okada" design (Okada et al., 2001) injected pure CO_2 at high velocity from 0.5 to 0.9 mm diameter holes in horizontal porous polyethylene tubing (supported 50–60 cm above the plant height) with a wall thickness of 0.5 mm. Injection rate was
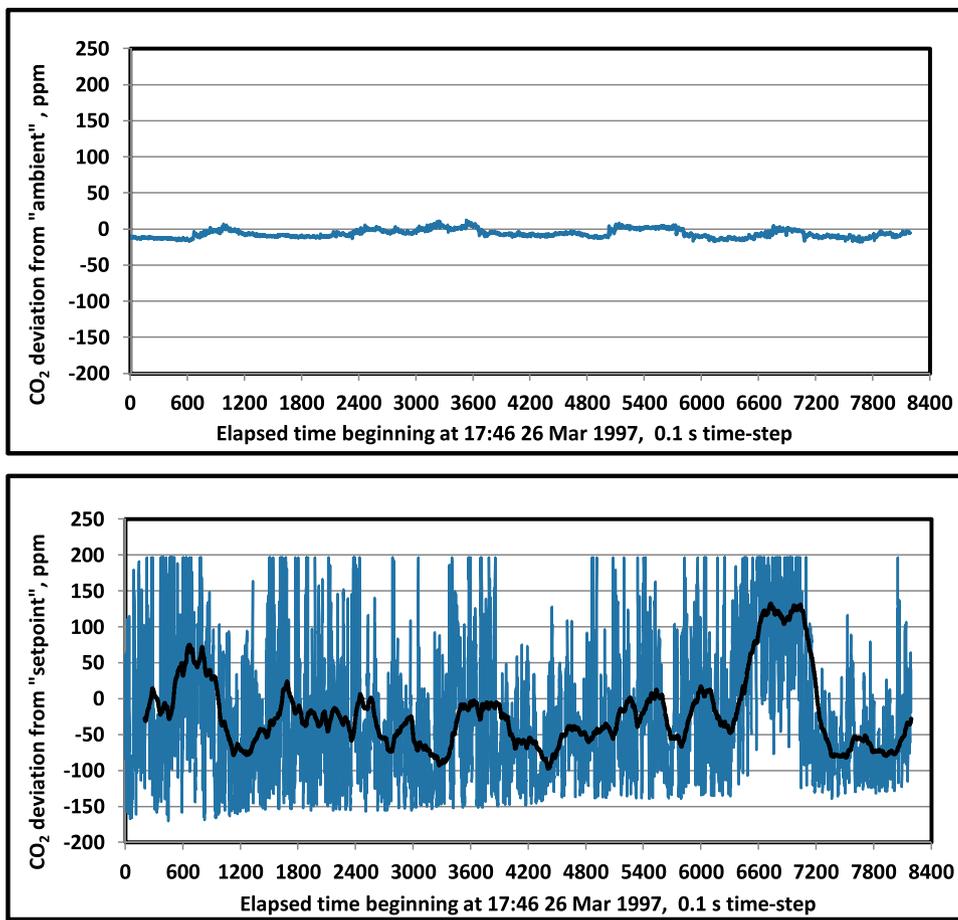
Fig. 1. Variation in $[CO_2]$ in a non-enriched control FACE Blower plot with no CO_2 injection (top panel) and in an enriched FACE plot (bottom panel) at Maricopa, AZ USA. Observations began at 17:46 h, 26 March 1997 with time steps of 0.1 s and a time span of 819.2 s. A 20-s moving average is shown by the black trace (bottom panel) which illustrates irregular oscillation periods of about 1 to 2 min.

controlled by varying pressure (up to 200 kPa) in the tubing. The POPFACE system or "Miglietta" design (Miglietta et al., 2001) also injected pure CO_2 at high pressure and high velocity through 0.3 mm holes in 20-mm diameter horizontal polyethylene pipes suspended at the height of the plant canopy. Jet-flow delivery of CO_2 through holes of each horizontal pipe was controlled by adjusting pressure at 8 steps ranging from 150 to 450 kPa.

Few of the numerous FACE publications provided figures of real-time $e[CO_2]$ fluctuations (Hendrey et al., 1999; Long et al., 2004). None show sampling intervals as short as 0.1 s such as shown in Fig. 1. Other reports showed a 24-h data set of FACE $[CO_2]$ averaged at 5 s (Okada et al., 2001) and one hour of "1-sec" $[CO_2]$ concentrations (Hendrey and Miglietta, 2006). However, these reports observed $[CO_2]$ from systems with inherent lag-time and concentration-smoothing conditions, namely with sample air pumped through lengths of tubing to closed-path analyzers. These systems thus lacked the ability to measure large deviations from the desired setpoint at very short time intervals.

Turbulent transport due to variable wind causes fluctuations of $[CO_2]$ on all scales of frequency and amplitude. However, inherent design and time-lags also contribute, including the various systems that depend on (1) time for CO_2 to get from emitters at the plot border to center-of-plot sampling point which depends on distance and wind speed, (2) flow rate of sampled air to CO_2 analyzer, (3) software control integration for CO_2 injection and measurement, and (4) degree of mixing of injected CO_2 with ambient air. These factors likely contribute to some of the slower but larger fluctuations.

Other types of FACE systems have shown large deviations from setpoint, especially high CO_2 concentration spikes (e.g., Web-FACE (Pepin and Körner, 2002) and area-distributed FACE (Bunce, 2011). An injection system that distributes CO_2 directly within a plant canopy

using dangling injection tubes has been proposed (Fangmeier et al., 2016) but this system would inject pure CO_2 near plants and exacerbate the problems of fluctuating $e[CO_2]$ and bursts of very high $[CO_2]$ as discussed later. Fluctuations in FACE were prevalent in both diluted CO_2 delivery via vertical vent pipes and pure CO_2 delivery via high-pressure systems and were prevalent at all wind speeds (Supplementary Figs. S1 and S2).

2.2. Magnitude of fluctuations of [CO2] in natural atmospheres within and above crops

Much smaller fluctuations of $[CO_2]$ occur in natural atmospheres of vegetation than in FACE systems. Standard deviations of $[CO_2]$ for 10-min periods within a corn crop canopy near midday (21 August 1969) ranged from 2.4 ppm (mean = 309.0 ppm) to 5.3 ppm (mean = 302.4 ppm) (Desjardins et al., 1978). The respective relative standard deviations were 2.4/309.0 = 0.0078 and 5.3/302.4 = 0.018. Turbulent intensities of wind speed (i.e., relative standard deviations of wind speed) ranged from 0.348 to 0.486. In contrast, the near-continuous FACE data set at Maricopa, AZ (Figs. 2–4) with ninety-three, 819.2-s periods, had an average standard deviation of 85 ppm and a relative standard deviation of 85/570 = 0.15. This relative standard deviation of FACE data was about 8 to 19 times as large as the relative standard deviation of $[CO_2]$ in the natural atmosphere. Similarly, in a FACE control plot data set from Maricopa (17:46 h on 26 March 1997), the average $[CO_2]$ was 333.9 ppm, the standard deviation was 5.5 ppm, and the relative standard deviation was 0.0165 ppm/ppm. The relative standard deviation of FACE data was about 9 times as large as the relative standard deviation of [CO2] in the natural Maricopa atmosphere.

The maximum deviation of $[CO_2]$ in the cornfield was about 18 ppm (Desjardins et al., 1978) and the maximum deviation of $[CO_2]$ in the

Frequency of occurance of [CO₂], 26-27 March 1997, Maricopa FACE.
Data fitted for values less than -180 ppm and greater than +180 ppm.
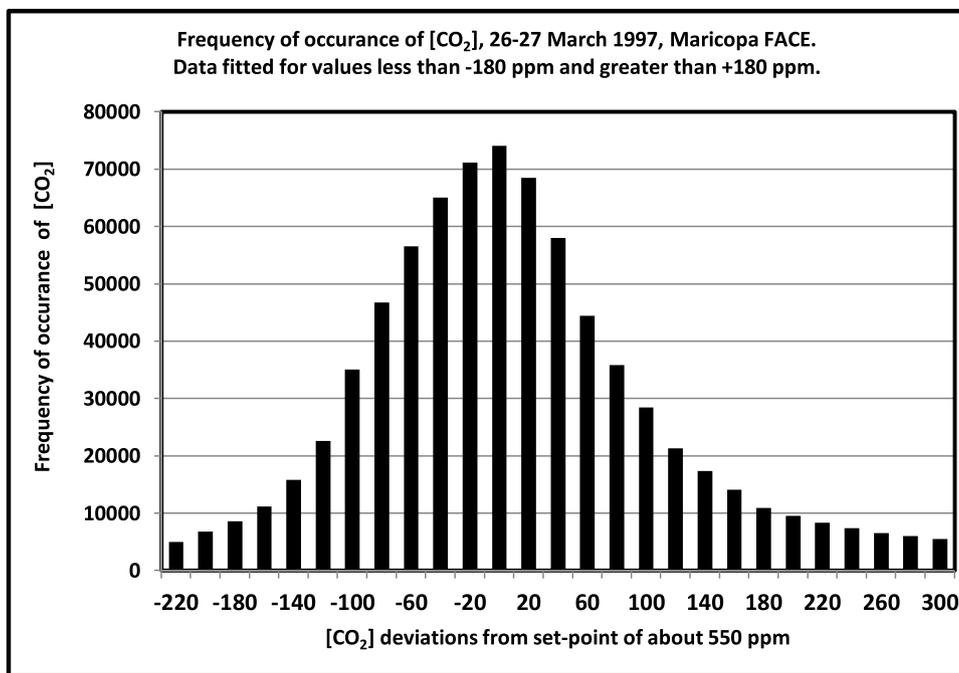

Fig. 2. Histogram of FACE deviations from target CO_2 concentration, Maricopa, AZ wheat FACE measured with a rapid-response (0.1 s sampling time step) CO_2 analyzer. Data were collected for 13.6533 min at 15-min intervals continually from 17:31 h on 26 March through 16:31 h on 27 March 1997.

Maricopa wheat-field example was about 20 ppm. Thus, the ratio of maximum deviation to mean [CO₂] was about 18/306 = 0.059 in the cornfield and about 20/334 = 0.060 at Maricopa. At a target enrichment of +200 ppm CO₂ (e.g., Kimball et al., 1999; Ainsworth et al., 2008a) and an ambient of 400 ppm CO₂ (ambient [CO₂] itself a moving target), the range of deviations could be ± 200 ppm or greater and the ratio of maximum deviations to background e[CO₂] would be 400/600 = 0.667 or greater. The minimum ratio of 0.667/0.060 = 11 represents a more than 10-fold larger range in [CO₂] maximum-to-minimum fluctuations in FACE compared to natural fields. Thus, FACE systems exhibit [CO₂] fluctuations that are *much larger than natural*.

2.3. Magnitude and frequency distributions of fluctuations of [CO₂] in FACE systems

Fig. 1 compares the magnitude of the [CO₂] fluctuations within a FACE plot with that of a non-enriched control plot during a 26–27 March 1997 study at Maricopa, AZ. The small fluctuations of [CO₂] within a control plot (top panel of Fig. 1) are similar to the small fluctuations observed in a corn-field (Desjardins et al., 1978). Fig. 2 illustrates a histogram of [CO₂] distributions from about 220 ppm below target to > 220 ppm above the 570-ppm target [CO₂] for the entire 23.15 h period at Maricopa. Fig. 3 illustrates the percentage of
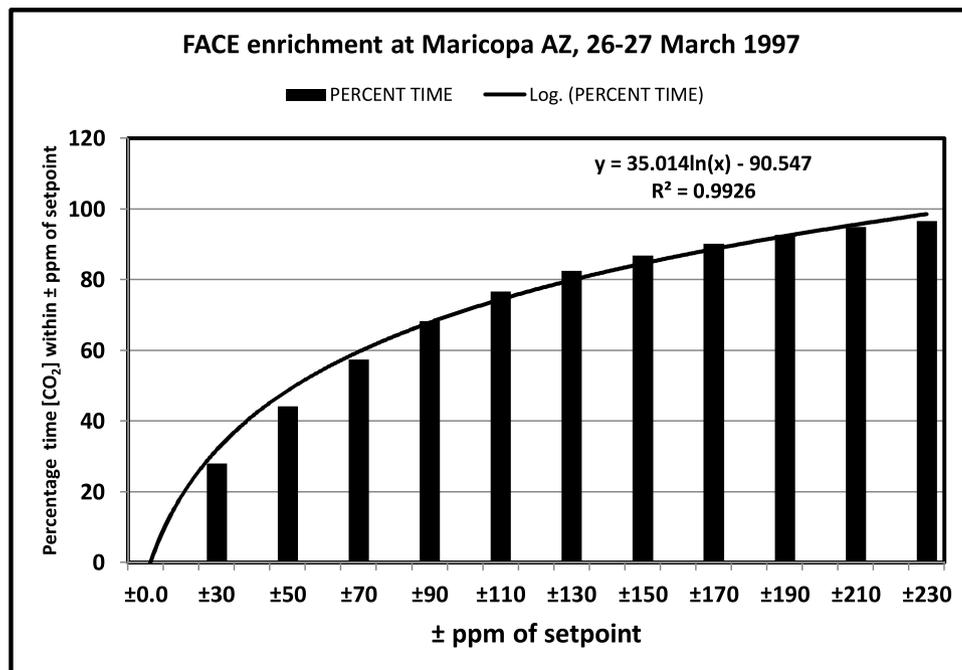

Fig. 3. Histogram of the cumulative percentage of time that 0.1 s observations of [CO₂] were within a given ± ppm of setpoint from ± 30 up to ± 230 ppm. A logarithmic curve trend-line fits well. Across almost 24 h, [CO₂] concentration was within ± 10% of setpoint (± 57 ppm of setpoint) for about 50% of the time, and within ± 20% of setpoint (± 114 ppm of setpoint) for about 77% of the time.
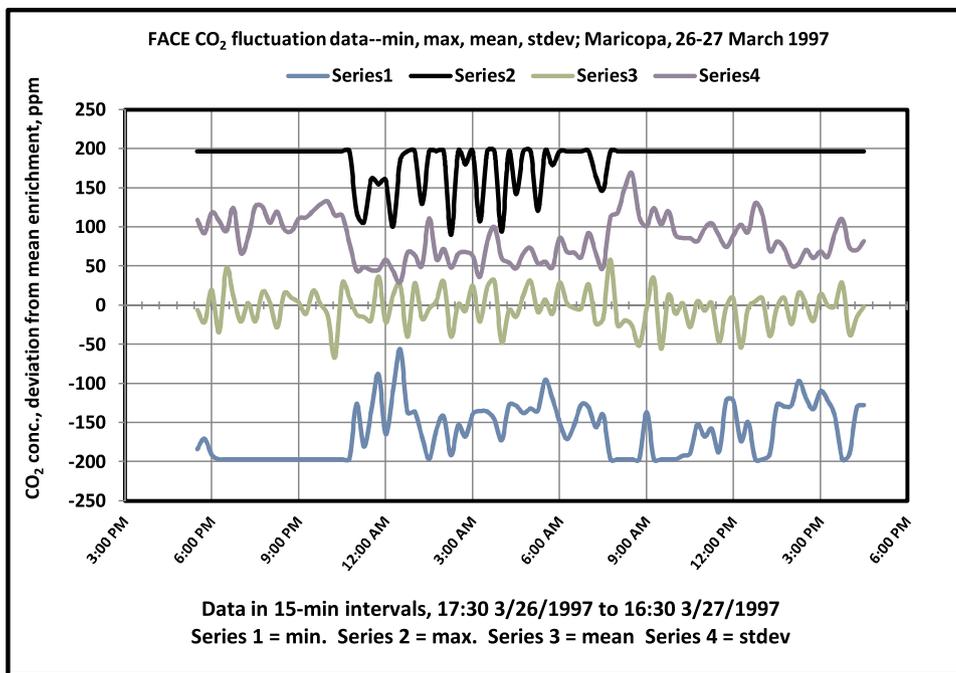
Fig. 4. Minimum (blue), maximum (black), mean (green), and standard deviation (purple, positive direction only shown) about the set-point of 0.1-sec observations of CO_2 concentrations in a FACE sampling, 26–27 March 1997, Maricopa, AZ USA. Means for the 13.6533-min segments each 15 min were close to zero, mostly within 50 ± ppm of setpoint. The range limits of the CO_2 analyzer prevented data collection below - 200 ppm and above + 200 ppm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

time the $[CO_2]$ was within a specified ± range of the target FACE $[CO_2]$. Across 23.15 h, $[CO_2]$ was within ± 55 ppm of setpoint $[CO_2]$ (± 10% of setpoint $[CO_2]$) for about 50% of the time, and within ± 110 ppm of setpoint $[CO_2]$ (± 20% of setpoint $[CO_2]$) for about 77% of the time. Expressed in terms of the actual enrichment of 200 ppm CO_2, level of control is not as impressive. The values were within ± 27.5% of 200 ppm $e[CO_2]$ for about 50% of the time, and within ± 55% of 200 ppm $e[CO_2]$ for about 77% of the time. For 1990 and 1991 studies using the same FACE system (Nagy et al., 1994), 3-s averages of $[CO_2]$ recorded every minute were within ± 55 ppm of setpoint $[CO_2]$ (± 10% of setpoint $[CO_2]$) for about 67% of the time, and within ± 110 ppm of setpoint $[CO_2]$ (± 20% of setpoint $[CO_2]$) for about 91% of the time. Likewise, the values were within ± 27.5% of 200 ppm $e[CO_2]$ for about 67% of the time, and within ± 55% of 200 ppm $e[CO_2]$ for about 91% of the time. (Supplementary material: Expressing FACE observations as ± 10% or ± 20% of setpoint.)

Because averaging smooths out short, rapid extremes of $[CO_2]$, the actual range of values for 0.1-s $[CO_2]$ data _are not nearly as close_ to setpoint $[CO_2]$ as the 3-s averages of $[CO_2]$ or the 1-min integrals of $[CO_2]$ cited earlier (Hendrey et al., 1999; Hendrey and Miglietta, 2006). Minimum, maximum, mean, and standard deviation of $[CO_2]$ from our ninety-three 819.2-s periods at 15-min intervals are plotted in Fig. 4. Averaging data across 1.6 s (Fig. 5) eliminated most extremes of $[CO_2]$, indicating that out-of-range $[CO_2]$ was of short duration. Fig. 5 also shows that running averages calculated across 20 data points (32 s) smoothed $[CO_2]$ peaks and valleys so that variable longer-term periodicities appeared (Supplementary material, Periodicities in Fluctuating FACE $[CO_2]$).

One question for selection of FACE setpoint has been whether to control to a fixed $e[CO_2]$ or to control to a fixed elevation setpoint above ambient $[CO_2]$, with ambient $[CO_2]$ measured near the top of the plant canopy. During the growing season, both the regional air-mass $[CO_2]$ decreases and the average $[CO_2]$ profiles decrease from aloft toward the crop surface (Wright and Lemon, 1966; Lemon et al., 1969; Desjardins et al., 1978). The basis of this question is addressed by Supplementary Fig. 3 embedded in Supplementary material, setpoint control target for $e[CO_2]$).

3. CO_2 uptake, growth, and yield in oscillating or fluctuating $e[CO_2]$

3.1. Terminology of plant responses to systems of CO_2 enrichment

We define Relative Response Ratio as the plant relative response in fluctuating FACE $e[CO_2]$ or oscillating $e[CO_2]$ (OSC $e[CO_2]$) divided by the plant relative response in constant $e[CO_2]$ (CON $e[CO_2]$, shown below:

Relative Response Ratio of FACE $e[CO_2]$
= (Value at FACE $e[CO_2]$ – 1.00)/ (Value at CON $e[CO_2]$ – 1.00)
Relative Response Ratio of OSC $e[CO_2]$
= (Value at OSC $e[CO_2]$ – 1.00)/(Value at CON $e[CO_2]$ – 1.00)
Derivations are provided in Supplementary material: Derivation of Relative Response Ratio of fluctuating FACE $e[CO_2]$/Constant $e[CO_2]$.

3.2. Leaf photosynthetic response to oscillating $e[CO_2]$: electron transport

The effects of oscillating $e[CO_2]$ at various frequencies on _in vivo_ electron transport of Photosystem II via fluorescence measurements of wheat leaves were investigated (Hendrey et al., 1997). Using an asymptotically-saturating generalized steady-state response curve of C_3 leaf CO_2 assimilation rate versus $[CO_2]$, they stated that CO_2 uptake rates by leaves exposed continuously to an $e[CO_2]$ of 650 ppm should be greater than CO_2 uptake rates of leaves exposed alternately to 425 and 875 ppm for equal durations (a _square waveform_ of $e[CO_2]$ exposure), given enough time for leaves to equilibrate (Hendrey et al., 1997).

The half-life of CO_2 in the gas space in the interior of a wheat leaf was calculated to be ~ 0.20 s (Hendrey et al., 1997). An earlier study indicated that most of the CO_2 in the airspace inside an aspen leaf should be used up within 0.05 s (Laisk and Oya, 1975). The small storage capacity for gaseous CO_2 inside leaves indicates that potential effects of $[CO_2]$ oscillations, such as a relatively rapid stomatal closure response to increasing $[CO_2]$ coupled with a relatively slow stomatal
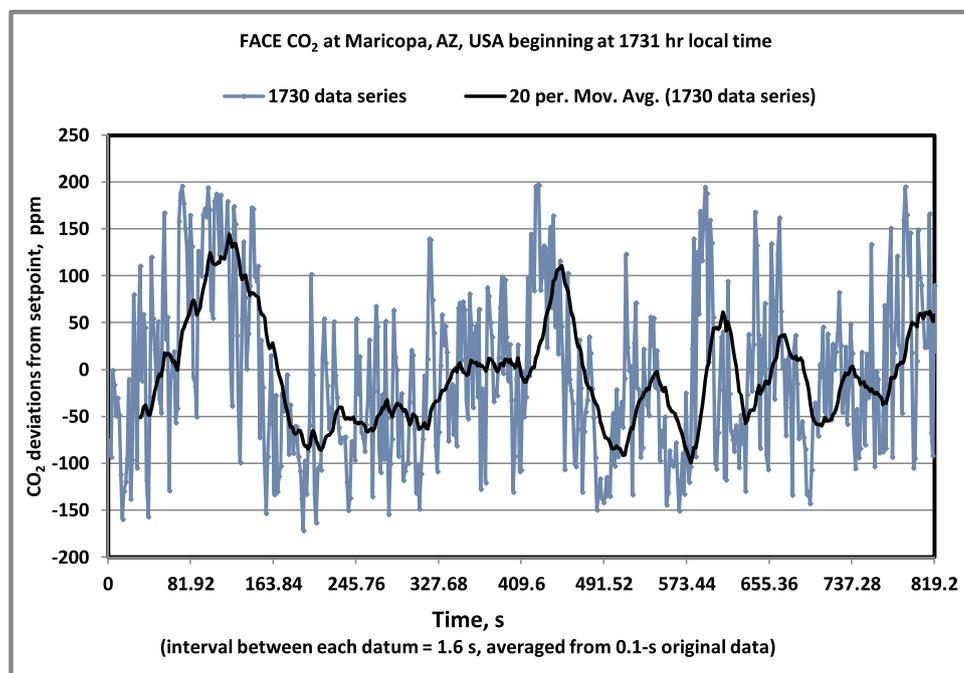
Fig. 5. Carbon dioxide concentration deviation from setpoint in a FACE plot at Maricopa, AZ, USA beginning at 17:31 h 26 March 1997. Original data at 0.1-s intervals were averaged over 16 values (to provide 1.6 s averaged data). Most overshoots and undershoot of data are eliminated in comparison with top panel of Supplementary Fig. 2. The 20 points moving average represents a 32 s moving average ($1.6 \times 20 = 32$). The right half of the figure shows 6 well-defined peaks at a regular interval of about 1 cycle per min.

opening response to decreasing $[CO_2]$ (Vodnik et al., 2013), would be experienced immediately by internal leaf photosynthetic biochemistry. Oscillating $e[CO_2]$ with periods < 20 s had no effect on *in vivo* electron transport through PS II of wheat leaves (Hendrey et al., 1997). Rates of electron transport decreased linearly from a period of $e[CO_2]$ oscillation of 20 s to a period of 120 s, and then remained constant up to a period of 240 s, but were not investigated at longer periods (Hendrey et al., 1997). Electron transport through PS II decreased by 20% in oscillating $e[CO_2]$ with periods of 120 to 240 s (2 to 4 min). This is a noteworthy reduction that compares well to the durations corresponding to the general peaks in periodograms noted earlier. Later, the possibility that a systematic understatement of the effect that fluctuating FACE $e[CO_2]$ might have on carbon gain by vegetation compared to constant $e[CO_2]$ was recognized (Hendrey and Miglietta, 2006). (Supplementary material: Periodicities in Fluctuating FACE $[CO_2]$ and Supplementary material: Leaf response to oscillating $e[CO2]$: Electron transport.)

3.3. Leaf photosynthetic response to oscillating $e[CO_2]$: CO_2 uptake rate

Studies of oscillations of $[CO_2]$ with fixed frequency and fixed large amplitude about the mean CO_2 enrichment level showed decreased photosynthetic responses of leaves of small plants of two tropical tree species, *Tectona grandis* L. f. (Verbenaceae) and *Pseudobombax septenatum* (Jacq.) Dug. (Bombacaceae) compared to leaves maintained at constant $e[CO_2]$ (Holtum and Winter, 2003). The periods of symmetrical *triangular waveform* $e[CO_2]$ oscillations were either 40 s or 80 s. Ambient $[CO_2]$ was 370 ppm, the constant $e[CO_2]$ was 600 ppm, and the $\pm$ 230 ppm oscillating $e[CO_2]$ averaged 600 ppm.

When *T. grandis* was exposed to a constant $e[CO_2]$ of 600 ppm, the rate of net CO_2 uptake was 28% greater than at a constant $amb[CO_2]$ of 370 ppm (Holtum and Winter, 2003). The net CO_2 uptake rate increase was only 19% when the seedling leaves were exposed to oscillations with a period of 40 s and mean $[CO_2]$ of 600 ppm. In a subset of plants exposed to oscillations with a period of 80 s, the CO_2 uptake rate increase was 30% at constant 600 ppm vs. 20% for oscillating 600 ppm. The Relative Response Ratios were $0.19/0.28 = 0.68$ and $0.20/0.30 = 0.67$, respectively.

Similarly, the response of *P. septenatum* to constant $e[CO_2]$ of 600 ppm, compared to constant 370 ppm, resulted in CO_2 uptake rate increase of 52%. In oscillating $e[CO_2]$ with mean of 600 ppm, the

response to enrichment was 36%. Based on the individual data of 6 runs (Holtum and Winter, 2003), the Relative Response Ratio was 0.69. Thus, the Relative Response Ratio in oscillating $e[CO_2]$ compared to constant $e[CO_2]$ was always about 0.68 for the two species and periods (40 and 80 s) of oscillating $e[CO_2]$ (Fig. 6, bar #1).

Leaf responses to oscillating $e[CO_2]$ reached steady state within 10 min (Holtum and Winter, 2003). Since there appeared to be no long-term time lags, models of leaf response to oscillating $e[CO_2]$ could be initiated from an equilibrated state rather than be processed from initial to steady-state conditions. The reduction in photosynthetic responses due to exposure to oscillating $e[CO_2]$ appears similar to photosynthetic induction responses in fluctuating light, but there is no clear connection. The effect could possibly be on stomatal lag responses rather than light-reactions biochemistry (Supplementary material: Does photosynthesis have an induction period (time lag) in fluctuating $[CO_2]$?)

3.4. Plant photosynthetic, biomass, and yield responses to oscillating and constant $e[CO_2]$ in chambers

Carbon dioxide enrichment studies were conducted in OTCs on cotton and wheat exposed to a 60-s period, *triangular-waveform* of oscillating maximum and minimum concentrations and compared to exposure at constant $e[CO_2]$ (Bunce, 2012). The constant $e[CO_2]$ target setpoint was 180 ppm above ambient air, and the oscillating $e[CO_2]$ ranged between 30 and 330 ppm above ambient air. The oscillating $e[CO_2]$-to-constant $e[CO_2]$ ratio of photosynthetic rates was $34.5/41.8 = 0.83$, and the ratio of stomatal conductances (mol m^{-2} s^{-1}) was $0.745/1.180 = 0.63$. Calculated intercellular $[CO_2]$ (i.e., C_i) values were similar, 418 and 413 µmol mol^{-1} in constant $e[CO_2]$ and oscillating $e[CO_2]$, respectively. At 27 days after sowing, cotton shoot biomass was 1.31 g plant^{-1} for constant $e[CO_2]$ and 0.92 g plant^{-1} for oscillating $e[CO_2]$ (Bunce, 2012).

For one cotton experiment that included $amb[CO_2]$ exposures, cotton increased 1.47-fold in biomass for the constant $e[CO_2]$ exposure over $amb[CO_2]$ compared to a 1.25-fold increase for the oscillating $e[CO_2]$ exposure over background $amb[CO_2]$ (Bunce, 2012). This represents a Relative Response Ratio of $0.25/0.47 = 0.53$ for biomass yield (Fig. 6, bar #2 and (Supplementary Table 1). Subsequent summaries of these Bunce (2012) data are also in Supplementary Table 1.

The photosynthesis rate of wheat leaves in oscillating $e[CO_2]$ was
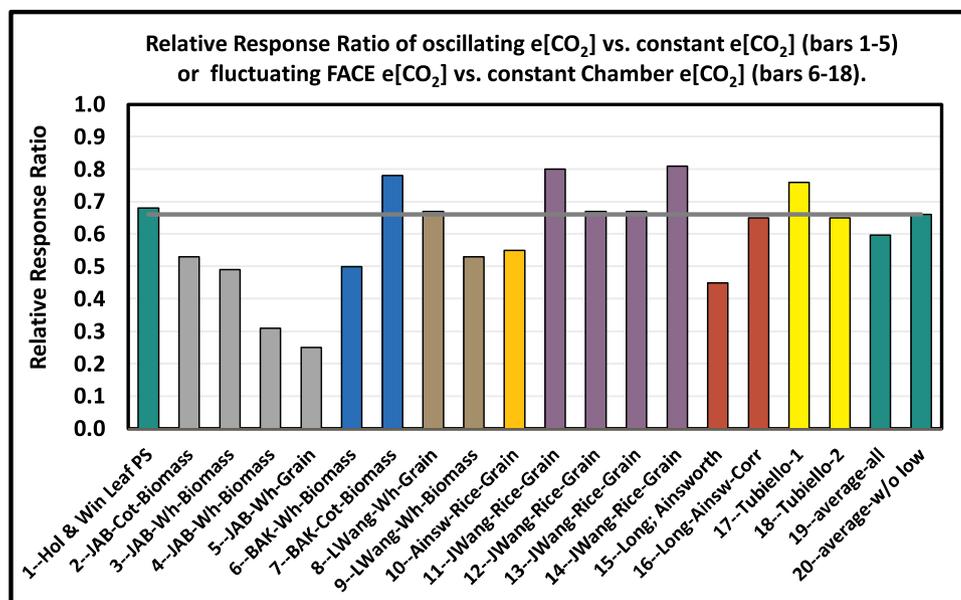
Fig. 6. Relative Response Ratios by number as cited in the manuscript. The grey horizontal line represents our convergent value of 0.66. The left green bar (#1) is from the leaf photosynthetic rate study of Holtum and Winter (2003). The gray bars (bar #2 to bar #5) are from oscillating e[CO_2] studies of Bunce (2012, 2016) and the various colored bars (bar #6 to bar #18) are from fluctuating FACE e[CO_2] reports. The blue bars are from Kimball et al. (1997), the brown bars from L. Wang et al. (2013), the orange bar from Ainsworth (2008), the purple bars from J. Wang et al. (2015), the red bars from Long et al. (2005, 2006) & Ainsworth et al. (2008a), and the yellow bars from Tubiello et al. (2007). Bar #15 is the Relative Response Ratio of 0.45 derived from Long et al. (2005, 2006) and Ainsworth et al., 2008a). Bar #16 (Relative Response Ratio = 0.65) is the change in bar #15 after eliminating problematic data. Bar # 19 and bar #20 are averages, with and without Relative Response Ratios that were smaller than 0.50. The average with the lowest four Relative Response Ratios included is 0.60 (bar # 19) and average with the lowest four Relative Response Rations excluded is 0.66 (bar # 20). Abbreviations in the horizontal axis are: PS is Photosynthesis, Cot is cotton, Wh is wheat, Ainsw is Ainsworth, Corr is Corrected. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.93 of that in constant e[CO_2] (Bunce, 2012) (Supplementary Table 1). At day 44, shoot biomass (g plant^{-1}) was 0.98 for the amb[CO_2] treatment, 1.43 for constant e[CO_2], and 1.20 for oscillating e[CO_2], giving a Relative Response Ratio of 0.49 (Fig. 6, bar #3 and Supplementary Table 1). Wheat shoot biomass at maturity was 373, 445, and 395 g/plant for amb[CO_2], constant e[CO_2], and oscillating e[CO_2], respectively, providing a small Relative Response Ratio of 0.31 (Fig. 6, bar #4 and Supplementary Table 1). Wheat grain yields were 125, 149, and 131 g m^{-2} for amb[CO_2], constant e[CO_2], and oscillating e[CO_2], respectively (Bunce, 2012), providing a small Relative Response Ratio of 0.25 (Fig. 6, bar #5 and Supplementary Table 1). These observations of inhibitory effects of oscillating e[CO_2] could be either larger or smaller in FACE e[CO_2] systems with wide variations of frequencies and amplitudes of fluctuations (Bunce, 2012).

4. Compilations and meta-analyses: FACE vs. chambers

This analysis avoided studies where severe water stress or high temperature stress were evident, because in those situations biomass partitioning into yield may be affected more by these stresses than CO_2 effects on photosynthesis and biomass production.. We also avoided complications of nutrient deficiencies and high vapor pressure deficit effects.

4.1. Wheat and cotton

Wheat and cotton data from FACE were compared with OTC experiments in similar conditions (Kimball et al., 1997). Although the responses of wheat to e[CO_2] were relatively small in both FACE and OTC, the Relative Response Ratio was (0.06/0.12) = 0.50 (Fig. 6, bar #6). Regression equations (Kimball et al., 1997) quantified the relative responses of cotton experiments that spanned 1983–1987 for OTC studies and 1989–1991 for FACE studies. The Relative Response Ratio for increase of cotton biomass in FACE/OTC studies of enrichment from 350 to 550 ppm CO_2 was (0.31/0.40) = 0.78 (Fig. 6, bar #7).

Grain yield increases of wheat in response to e[CO_2] from studies conducted using laboratory chambers, glasshouses, SCECs, OTCs, and FACE systems have been summarized (Amthor, 2001). Expressed in terms of a 200 ppm [CO_2] enrichment, increases were 24%, 28%, 16%, 14.8%, and 13.6% for the respective enrichment systems

(Supplementary Table 2).

We extracted wheat data from a meta-analysis (Wang et al., 2013) that indicated a 14% increase in grain yield for FACE studies and a 21% increase in grain yield for OTC studies (wheat section of Supplementary Table 2). Thus, the FACE/OTC Relative Response Ratio was 0.14/0.21 = 0.67 (Fig. 6, bar #8) which is in general agreement with responses found in other meta-analyses. Extractions from Fig. 3 of that meta-analysis indicated that wheat photosynthesis was increased by 24% in FACE and by 42% in OTC studies (Wang et al., 2013) for a Relative Response Ratio of 0.57. Above ground biomass at maturity showed a Relative Response Ratio of 0.53 (Fig. 6, bar #9).

4.2. Rice

The earliest meta-analysis reviewed rice responses to both [CO_2] and ozone concentration (Ainsworth, 2008). Averaged over all studies in all systems of enrichment, increasing [CO_2] from an average of 365 to 627 ppm resulted in a light-saturated leaf photoassimilation rate (A_{sat}) increase of 38%, a stomatal conductance decrease of 25%, and both rice seed yield and biomass increases of 23%. Also analyses at three enrichment levels of 500–599 ppm, 600–699 ppm, and >700 ppm were compared (Ainsworth, 2008). As expected, A_{sat} values and seed yields increased with increasing [CO_2] enrichment. At the enrichment level 500–599 ppm, A_{sat} rates increased slightly more than 50% above controls in OTC, sunlit chambers, and greenhouse enrichment studies, but increased an average of only 18% in FACE studies. From this meta-analysis, we estimated an overall 22% increase in rice yields for OTC and SCEC chambers (Ainsworth, 2008). Overall yield increase for rice FACE was 12%. Rice had a FACE/chamber yield Relative Response Ratio of about 0.55 (Fig. 6, bar #10) based on combined OTC and SCEC studies (Supplementary Table 2).

A later meta-analysis of 125 studies of rice reported lower responses to e[CO_2] in FACE systems than in other exposure systems(Wang et al., 2015). Seed yield increases in FACE, OTC, and growth chamber studies were 16%, 20%, and 24%, respectively, providing a Relative Response Ratio for FACE/OTC studies of 0.80 (Fig. 6, bar #11 and Supplementary Table 2) and 0.67 (Fig. 6, bar #12) for FACE/chamber studies. We calculated that the above-ground biomass increases in FACE, OTC, and growth chamber studies were 17.6%, 26.4%, and 21.7%, respectively, indicating a Relative Response Ratio of 0.176/0.264 = 0.67 for FACE/

OTC studies (Fig. 6, bar #13 and Supplementary Table 2) and 0.176/0.217 = 0.81 for FACE/chamber studies (Fig. 6, bar #14).

4.3. Converging to a general FACE/chamber relative response ratio

Several studies indicate that above ground biomass and seed yield of crops grown in FACE systems were less than those of crops grown in field-based chamber enrichment studies (Long et al., 2005, 2006; Morgan et al., 2005; Hendrey and Miglietta, 2006; Ainsworth, 2008; Ainsworth et al., 2008a, 2008b; Leakey et al., 2009). Rice, wheat, and soybean FACE studies had a mean yield response ratio of 1.14 for average amb$[CO_2]$ of 367 ppm and average e$[CO_2]$ of 583 ppm (difference = 216 ppm), whereas wheat and soybean enclosure studies had a mean grain yield response ratio of 1.31 for average ambient and average e$[CO_2]$ of 373 and 565 ppm, respectively (Long et al., 2006; Ainsworth et al., 2008a; Long and Ort, 2010). This reported response results in a Relative Response Ratio of FACE/chamber experiments of 0.14/0.31 = 0.45 (Fig. 6, bar #15).

Examination of data in Supplementary Tables 1 and 2 of reference (Ainsworth et al., 2008a) revealed that seven responses to e$[CO_2]$ compared to ambient CO_2 in OTC studies should likely be excluded because of confounding ancillary SO_2 or O_3 treatments. (Supplementary material online at: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-8137.2008.02500.x, or https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-8137.2008.02500.x, last accessed 8 August 2018.) In addition, two of the Arizona FACE Wheat experiments (1993 and 1994) had blowers in the FACE plots but not in the ambient Control plots. Because intake air was higher in the nocturnal inversion, the blower air warmed the FACE plots at night, thereby shortening the growth period and decreasing grain yields. This problem has been termed the "blower effect" and has been rectified by setting up blowers in the Control plots (Pinter et al., 2000; Kimball, 2013). (Supplementary material: The Blower effect.)

We recalculated the response in e$[CO_2]$with respect to amb$[CO_2]$ of the OTC data without the confounding ancillary SO_2 and O_3 treatments and obtained a Response Ratio of 1.23 rather than 1.31. Furthermore, the FACE stimulation data included some responses involving low nitrogen (not likely in modern agriculture). Eliminating these data resulted in an average FACE Response Ratio of 1.15. Thus, the likely Relative Response Ratio would be 0.15/0.23 = 0.65 (Fig. 6, bar # 16). Further elimination of the 1993 and 1994 Maricopa wheat data because of "blower effect" imbalance between control and FACE plots led to no detectable change in Relative Response Ratio (0.15/0.23 = 0.65) (Fig. 6, bar #16). Mean values of an aggregated wheat dataset (Amthor, 2001) indicated a Relative Response Ratio of 0.124/0.164 = 0.76 (Fig. 6, bar #17) in a FACE/OTC comparison and 0.124/0.190 = 0.65 (Fig. 6, bar # 18) in a FACE/non-FACE comparison (Tubiello et al., 2007). These values are consistent with the short-term Relative Response Ratio of photosynthetic rates of tropical tree seedlings of 0.68 (Holtum and Winter, 2003). The adjusted outcomes of the yield meta-analysis (Ainsworth et al., 2008a) provided an overall Relative Response Ratios of ∼ 0.65 which is a representative value (Fig. 6, bar #16). Finally, the overall average of Relative Response Ratios for bars #1 to #18 was 0.60 (Fig. 6, bar #19) and the average Relative Response Ratio for all bars excluding those with values less than 0.50 was 0.66 (Fig. 6, bar #20).

4.4. Differences in cultivar responses?

Following the "Food for Thought" paper (Long et al., 2006) that indicated a Relative Response Ratio of 0.45 (Fig. 6, bar #15) in FACE relative to chamber studies, comparisons that considered a wider population of chamber studies demonstrated additional variation not considered in that assessment, with statistical overlap among methodologies (Tubiello et al., 2006; Ziska and Bunce, 2007; Kimball, 2011). The greater overlap may indicate differences in cultivar responses to

elevated CO_2. For example, other FACE studies with hybrid rice (Liu et al., 2008; Yang et al., 2009; Lai et al., 2014) and with a range of rice varieties (Hasegawa et al., 2013; Zhu et al., 2015) reported larger responses to e$[CO_2]$ for Indica types and Indica hybrids than earlier FACE studies with Japonica cultivars. In a hot, dry environment, various wheat cultivars have also shown a wide range of yield increases to 550 ppm CO_2 enrichment ranging from 55% down to −10%, with an average of 30% (Seneweera et al., 2010). In a combination of two wheat cultivars, three years, two planting dates, two water regimes, and two locations (in a hot, dry environment), the range of yield increases to 550 ppm CO_2 enrichment ranged from 79% to −17%, with an average of 31% (Fitzgerald et al., 2016). Moreover, earlier studies (not in FACE systems) also showed a wide range of rice cultivars responses to CO_2 enrichment (Ziska and Teramura, 1992; Ziska et al., 1996; Baker, 2004). These recent and past wide-ranging responses indicate that use of FACE for identifying plant genetic materials adapted to maximal responses in e$[CO_2]$ would be a viable pursuit (Ainsworth et al., 2008b). Finally, the magnitude of any difference between FACE and chamber studies seems likely to be smaller than stated earlier (Long et al., 2006).

4.5. Rapid responses of leaves to $[CO_2]$ oscillations or pulses

Leaf-scale experiments with oscillatory e$[CO_2]$ show decreased CO_2 uptake rates that apparently occur within about 10 min (Holtum and Winter, 2003). Furthermore, pulsed e$[CO_2]$ experiments show decreased CO_2 uptake rates immediately that persist for at least 20 min and recover slowly thereafter (Bunce, 2013). These studies indicate that diminished response to oscillating or pulsed e$[CO_2]$ occurs rapidly and persists.

4.6. Lack of night-time CO_2 enrichment and potential ozone effects

Few FACE experiments provided e$[CO_2]$ both day and night, largely because of costs of CO_2. Thus, it is possible that, besides fluctuating e$[CO_2]$, a lack of CO_2 enrichment during night-time altered plant responses relative to 24-h FACE (Ferris and Taylor, 1994; Griffin et al., 1999; Heagle et al., 1999; Bunce, 2005, 2014a, 2014b). For example, four grassland herbs were exposed continuously with either 350 or 590 ppm CO_2 for a 16-h light period followed by an 8-h dark period (Ferris and Taylor, 1994). Dark period leaf extensions were 2.3- to 3.6-fold greater when exposed to 8-h dark period $[CO_2]$ of 590 ppm compared to 8-h dark period $[CO_2]$ of 350 ppm (Ferris and Taylor, 1994). Nighttime CO_2 enrichment might result in more rapid leaf expansion and thereby increase the capture of sunlight for photosynthesis by plants the following day.

Two cultivars of common bean (*Phaseolus vulgaris* L.) showed an average seed yield increase of 25% for 24-h e$[CO_2]$ exposure compared to daytime-only e$[CO_2]$ exposure in OTCs (Bunce, 2014b). Continuous, 24-h e$[CO_2]$ increased the area of leaflets by about 40% which likely led to higher yields via increased light capture and greater photosynthesis. Possibly some of the effect of diminished response to e$[CO_2]$ in FACE could be ascribed to the prevalence of daytime-only FACE enrichment rather than fluctuating e$[CO_2]$.

Ground-level tropospheric ozone causes reductions in plant performance in the field (Pang et al., 2009; Betzelberger et al., 2012). Possibly exclusion of ground-level ozone from a closed system such as SPAR chambers could cause a greater plant response to e$[CO_2]$ in SPAR chambers compared to FACE. However, the possibility of diminished plant responses due to reduced ozone exposure in an OTCs is not likely because (in the absence of charcoal air filters) most ground-level ozone passes into the OTC through the blower housing. Fluctuating e$[CO_2]$ in FACE remains implicated for the response differences between OTCs and FACE.

Other factors might contribute to an apparent Relative Response Ratio value less than 1.0 in FACE exposure systems. In the Maricopa

research, the daytime elevation of $[CO_2]$ in the FACE plots averaged 185 ppm above the blower control plots rather than the target setpoint of 200 ppm (Kimball et al., 1999). This would lead to a value of photosynthetic response of about 0.925 of that expected from an actual enrichment of 200 ppm. Furthermore, the average contamination of the blower control plots with CO_2 from the FACE plots was 15 ppm above the upwind ambient $[CO_2]$ (Kimball et al., 1999). However, contamination of blower control plots does not impact the response to elevated CO_2 much since growth and yield responses to elevated $[CO_2]$ are relative to the blower control plot CO_2 concentration This factor of 0.925 does not approach the convergent value of 0.66 for the Relative Response Ratio, but it might contribute to the apparent less than expected photosynthetic responses in FACE systems. For SPAR chambers, this type of problem should be much less.

4.7. Future directions

The scientific question remains: What causes plants to demonstrate smaller photosynthetic, growth, and yield responses in fluctuating $e[CO_2]$ environments than in constant $e[CO_2]$ environments? The answer certainly resides in the leaf (Supplementary material: Factors that might influence plant response to fluctuating CO_2). More leaf scale studies of the effects of oscillating or fluctuating $[CO_2]$ on plant photosynthesis are needed to explain the controlling processes at biochemical, mesophyll conductance, and stomatal conductance levels. In addition, for large-plot FACE systems, novel FACE plus OTC chamber experiments should be initiated. Plant responses with OTCs located within FACE plots (having inputs of fluctuating $e[CO_2]$ FACE air directly into the OTCs, preferably into the top) could be compared directly with constant $e[CO_2]$ treatments outside FACE plots. (Supplementary material: A potential field method for determining effects of FACE $[CO_2]$ fluctuations.) Such experiments should be done in combination with experiments that identify crops that perform better in FACE environments (Ainsworth et al., 2008b). At least part of the technology of the Canopy EvapoTranspiration and Assimilation (CETA) chamber could be adapted as well as OTCs for evaluating plant responses to real FACE fluctuations (Baker et al., 2009, 2014).

For some plants, the closing response of stomata to increasing $e[CO_2]$ is more rapid than the opening response of stomata to decreasing levels of $[CO_2]$ (Supplementary Fig. 8a). Thus, response in oscillating or fluctuating $[CO_2]$ is likely to be a reduction in average stomatal conductance and photosynthetic rate compared to steady enrichment (Hladnik et al., 2009; Vodnik et al., 2013). However, modeling these stomatal effects led to minor effects on photosynthetic Relative Response Ratio and might indicate that reductions in leaf performance in fluctuating $e[CO_2]$ may be metabolically more complex than effects on stomatal conductance alone.

Leaf models that describe photosynthetic responses could be employed to predict stomatal behavior and leaf CO_2 photoassimilation rates in oscillating $e[CO_2]$ conditions. Predictions using either a (1) derivation of the Farquhar-von Caemmerer-Berry (FvCB) leaf photosynthesis model (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982; Boote and Pickering, 1984; Pickering et al., 1995) or a (2) stomatal closing and opening model (in response to increasing and decreasing oscillations of $[CO_2]$) were employed (Supplementary material: Modeling leaf photosynthesis in oscillating or fluctuating $[CO_2]$).

The FvCB leaf photosynthesis model was used to compute the Relative Response Ratio under several conditions. This process is discussed in detail in Supplementary material: Modeling leaf photosynthesis in oscillating or fluctuating $[CO_2]$: Modeling I. In Example 1 of this Supplementary material, the square waveform $[CO_2]$ oscillation (with $[CO_2]$ held for equal lengths of time at a maximum value and a minimum value) indicated that the shape of the photosynthetic rate versus $[CO_2]$ curve could cause a Relative Response Ratio of 0.83, which accounts for only a (1.00–0.83) X 100 = 17% reduction in photosynthesis, whereas the nominal Relative Response Ratio is 0.66

indicates a 34% reduction in photosynthesis. Likewise, in Example 3, the triangular waveform $[CO_2]$ oscillation caused a Relative Response Ratio of 0.94, which accounts for only (1.00–0.94) X 100 = 6% reduction in photosynthesis.

The most important calculations were obtained from actual fluctuating $e[CO_2]$ of a FACE experiment using Maricopa AZ data from 10:01:00 h through 11:29:39 h, 27 March 1997 (Supplementary Table 3 and Supplementary Fig. 4). The calculated Relative Response Ratio was 0.96, which indicates that, despite excursions of high $[CO_2]$, FACE systems operate close to the midpoint $[CO_2]$. Only about 11%, that is (1.00–0.96)/ (1.00–0.66) X 100 of the nominal 0.66 Relative Response Ratio can be attributed to the shape of the photosynthesis rate vs $[CO_2]$ response curve. Because the Relative Response Ratio was much higher than 0.66, clearly some unknown factor diminishes leaf photosynthesis rates under fluctuation $e[CO_2]$ of FACE systems. *Clearly, processes other than responses to a non-linear leaf photosynthesis versus $[CO_2]$ are leading to depressed photosynthetic rates, biomass, and seed yield) in fluctuating FACE exposures.*

5. Summary and conclusion

1 Magnitudes of $[CO_2]$ fluctuations in FACE systems are more than 10-fold greater than in nature. Thus, exposures to $e[CO_2]$ in FACE are not representative of exposure to atmospheric $e[CO_2]$ (with natural fluctuations) projected to occur in the future.

2 Oscillations and fluctuations of $e[CO_2]$ decrease observed leaf photosynthetic rates compared to steady levels of $e[CO_2]$. It is unclear which frequencies and amplitudes are involved, but fluctuating periods around one min are implicated.

3 Leaf photosynthetic rates, crop biomass accumulation, and crop yield responses in fluctuating FACE environments, compared to other sunlit systems (OTC, SPAR, or TGG), had a Relative Response Ratio of about 0.66 (Fig. 6). Therefore FACE data may not be the only basis for predicting plant responses to rising atmospheric CO_2.

4 One study of leaf photosynthetic responses to oscillating $e[CO_2]$ compared to constant $e[CO_2]$ of the same enrichment provided a Relative Response Ratio of 0.67, near the convergent value of 0.66 for FACE $e[CO_2]$/constant $e[CO_2]$. However, several field experiments (e.g., Bunce, 2012, 2016;) provided Relative Response Ratios lower than 0.50, for which we have no explanation.

5 Despite limitations, FACE systems may be well suited for evaluating various crop germplasm responses and ecosystem processes to future $[CO_2]$. Further, control plots of FACE can provide data for validating growth models under field conditions.

6 New investigations are needed to evaluate leaf-level physiological mechanisms of responses to fluctuating $e[CO_2]$ with a focus on a relatively rapid closing response of stomata to increasing $[CO_2]$ and the possible effects of a lingering decrease in stomatal and mesophyll conductance, or possibly Rubisco activation, caused by exposures to peaks of $e[CO_2]$.

7 OTCs located within FACE plots (with inputs of fluctuating $e[CO_2]$ air directly into the OTCs) should be compared with OTC constant $e[CO_2]$ treatments outside FACE plots. Direct use of fluctuating $e[CO_2]$ air could confirm reduction of plant responses that appear to occur in FACE.

8 Accurate modeling of plant growth and yield responses to $e[CO_2]$ utilizing FACE data for verification will be less certain until the plant responses to fluctuating $e[CO_2]$ versus constant $e[CO_2]$ are understood.

9 Although responses to elevated CO_2 in FACE experiments have been smaller than those in chamber experiments, FACE responses have been obtained in otherwise natural conditions not available with chambers, and they should be conservative regarding future projections of agricultural productivity.

10 Prior conclusions of the response of plants to $e[CO_2]$ under FACE conditions may need to be reassessed by applying an adjustment factor (about 1.5) for photosynthesis, biomass, and yield to

conclusions reached in experimental and modeling studies. Future work should include independent studies focused on photosynthetic physiology in both fluctuating and oscillating e[CO_2] as suggested in item 6 above and the incorporation of other studies within FACE studies as suggested in item 7 above.

Author contributions

L.H.A. drafted the original manuscript. All authors contributed to revising and editing the manuscript. M.Y. and Y.H. provided the CO_2 concentration data from open-path, rapid response analyzers related to FACE systems in Arizona and Japan. K.J.B. provided the "Farquhar-type" leaf photosynthesis model and conducted simulations. B.A.K initiated a model and conducted simulations that predicted leaf stomatal conductance and photosynthetic rate for symmetrical oscillating elevated CO_2 based on "faster" closing of stomata in the higher CO_2 part of the oscillation and "slower" opening of stomata in the lower CO_2 part of the oscillation. L.H.A. conducted some of the simulations with both the K.J.B. model and the B.A.K. model. B.A.K., J.W.W., and L.H.A. conducted spectral analysis (Fast Fourier Transforms) on segments of the Arizona CO_2 data set. J.T.B. developed a Canopy EvapoTranspiration and Assimilation chamber which might be useful for incorporating into future FACE studies.

EEO/Non-discrimination statement

"The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720–2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, D.C. 20,250–9410, or call (800) 795–3272 (voice) or (202) 720–6382 (TDD). USDA is an equal opportunity provider and employer."

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.107899.

References

Ainsworth, E.A., Davey, P.A., Hymus, G.J., Osbourne, C.P., Rogers, A., Nösberger, A., Long, S.P., 2003. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO_2 Enrichment (FACE). Plant Cell Environ. 26, 705–714.

Ainsworth, E.A., Leakey, A.D.B., Ort, D.R., Long, S.P., 2008Aa. FACE-ing the facts: inconsistencies and interdependence among field, chamber and modeling studies of elevated [CO_2] impacts on crop yield and food supply. New Phytol. 179, 5–9.

Ainsworth, E.A., Long, S.P., 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analysis of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol. 165, 351–372.

Ainsworth, E.A., 2008. Rice production in a changing climate: a meta-analysis of responses to elevated carbon dioxide and elevated ozone concentration. Global Change Biol. 14, 1642–1650. https://doi.org/10.1111/j.1365-2486.2008.01594.x.

Ainsworth, E.A., Beier, C., Calfapietra, C., Ceulemans, R., Durand-Tardif, M., Farquhar, G.D., Godbold, D.L., Hendrey, G.R., Hickler, T., Kaduk, J., Karnosky, D.F., Kimball, B.A., Körner, C., Koornneef, M., Lafarge, T., Leakey, A.D.B., Lewin, K.F., Long, S.P., Manderscheid, R., McNeil, D.L., Mies, T.A., Miglietta, F., Morgan, J.A., Nagy, J.,

Norby, R.J., Norton, R.M., Percy, K.E., Rogers, A., Soussana, J.-F., Stitt, M., Weigel, H.-J., White, J.W., 2008Ab. Next generation of elevated [CO_2] experiments with crops: a critical investment for feeding the future world. Plant Cell Environ. 31, 1317–1324.

Allen, L.H., 1979. Potentials for carbon dioxide enrichment. In: Barfield, B.J., Gerber, J.F. (Eds.), Modification of the Aerial Environment of Crops. Am. Soc. Agric. Eng., St. Joseph, Michigan, pp. 500–519.

Allen, L.H., Boote, K.J., Jones, J.W., Jones, P.H., Valle, R.R., Acock, B., Rogers, H.H., Dahlman, R.C., 1987. Response of vegetation to rising carbon dioxide: photosynthesis, biomass, and yield of soybean. Global Biogeochem. Cycles 1, 1–14.

Allen, L.H., 1990. Plant responses to rising carbon dioxide and potential interactions with air pollutants. J. Environ. Qual. 19, 15–34.

Allen, L.H., 1992. Free-air CO_2 enrichment field experiments: an historical overview. Crit. Rev. Plant Sci. 11, 121–134 Also, co-published as Allen, L.H., 1993. Free-air CO2 enrichment field experiments: An historical overview, in: Hendrey, G.R. (Ed.), Free-Air CO2 Enrichment for Plant Research in the Field. C.K. Smoley (CRC Press), Boca Raton, FL, pp. 121-134.

Amthor, J.S., 2001. Effects of atmospheric CO_2 concentration on wheat yield: review of results from experiments using various approaches to control CO_2 concentration. Field Crops Res. 73, 1–34.

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

Baker, J.T., 2004. Yield responses of southern US rice cultivars to CO_2 and temperature. Agric. For. Meteorol. 122, 129–137.

Baker, J.T., Van Pelt, R.S., Gitz, D.C., Payton, P., Lascano, R., McMichael, B., 2009. Canopy gas exchange measurements of cotton in an open system. Agron. J. 101, 52–59. https://doi.org/10.2134/agronj2008.0007x.

Baker, J.T., Gitz, D.C., Payton, P., Broughton, K.J., Bange, M.P., Lascano, R.J., 2014. Carbon dioxide control in an open system that measures canopy gas exchanges. Agron. J. 106, 789–792.

Betzelberger, A.M., Yendrek, C.R., Sun, J., Leisner, C.P., Nelson, R.L., Ort, D.R., Ainsworth, E.A., 2012. Ozone exposure response for U.S. soybean cultivars: linear reductions in photosynthetic potential, biomass, and yield. Plant Physiol. 160, 1827–1839.

Boote, K.J., Pickering, N.B., 1994. Modeling photosynthesis of row crop canopies. Hort. Sci. 29, 1423–1434.

Bunce, J.A., 2005. Seed yields of soybeans with daytime or continuous elevation of carbon dioxide under field conditions. Photosynthetica 43, 435–438.

Bunce, J.A., 2011. Performance characteristics of an area distributed free air carbon dioxide enrichment (FACE) system. Agric. For. Meteorol. 151, 1147–1152. https://doi.org/10.1016/j.agrformet.2011.04.004. dx.doi.org/.

Bunce, J.A., 2012. Responses of cotton and wheat photosynthesis and growth to cyclic variation in carbon dioxide concentration. Photosynthetica 50, 395–400.

Bunce, J.A., 2013. Effects of pulses of elevated carbon dioxide concentration on stomatal conductance and photosynthesis in wheat and rice. Physiol. Plant. 149, 214–221.

Bunce, J.A., 2014a. Limitations to soybean photosynthesis at elevated carbon dioxide in free-air enrichment and open top chamber systems. Plant Sci. 226, 131–135. https://doi.org/10.1016/j.plantsci.2014.01.002. doi.org/.

Bunce, J.A., 2014b. CO_2 enrichment at night affects the growth and yield of common beans. Crop Sci. 54, 1744–1747. https://doi.org/10.3145/cropsci2013.12.0803.

Bunce, J.A., 2016. Crop responses of soybeans and wheat to elevated CO_2 in free-air and open top chamber systems. Field Crops Res. 186, 78–85.

Dahlman, R.C., Strain, B.R., Rogers, H.H., 1985. Research on the response of vegetation to elevated atmospheric carbon dioxide. J. Environ. Qual. 14, 1–8.

Desjardins, R.L., Allen, L.H., Lemon, E.R., 1978. Variations of carbon dioxide, air temperature, and horizontal wind within and above a maize crop. Boundary-Layer Meteorol. 14, 369–380.

Fangmeier, A., Torres-Toledo, V., Franzaring, J., Damsohn, W., 2016. Design and performance of a new FACE (free air carbon dioxide enrichment) system for crop and short vegetation exposure. Environ. Exp. Bot. 130, 151–161.

Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 78–90.

Farquhar, G.D., von Caemmerer, S., et al., 1982. Modeling of photosynthetic response to environment. In: Lange, O.L. (Ed.), Encyclopedia of Plant Physiology, New Series, Vol. 12B, Physiological Plant Ecology II. Springer-Verlag, Berlin, pp. 549–587.

Ferris, R., Taylor, G., 1994. Elevated CO_2, water relations and biophysics of leaf expansion in four chalk grassland herbs. New Phytol. 127, 297–307.

Fitzgerald, G.J., Tausz, M., O'Leary, G., Mollah, M.R., Tausz-Posch, S., Seneweera, S., Mock, I., Löw, M., Partington, D.L., McNeil, D., Norton, R.M., 2016. Elevated atmospheric [CO_2] can dramatically increase wheat yields in semi-arid environments and buffer against heat waves. Global Change Biol. 22, 2269–2284. https://doi.org/10.1111/gcb.13263.

Griffin, K.L., Sims, D.A., Seemann, J.R., 1999. Altered night-time CO_2 concentration affects the growth, physiology and biochemistry of soybean. Plant Cell Environ. 22, 91–99.

Hasegawa, T., Sakai, H., Tokida, T., Nakamura, H., Zhu, C.U., Y., Y., M., F., M., W., H., K., N., M., T., K., Y., S., T., T., F., S., R., O., M., M., T., M.A., 2013. Rice cultivar responses to elevated CO_2 at two free-air CO_2 enrichment (FACE) sites in Japan. Funct. Plant Biol. 40, 148–159.

He, Y., Yang, X., Miller, D.R., Hendrey, G.R., Lewin, K.F., Nagy, J., 1996. Effects of FACE systems operation on the micrometeorology of a loblolly pine stand. Trans. ASAE 39, 1551–1556.

Heagle, A.S., Booker, F.L., Miller, J.E., Pursley, W.A., Stefanski, L.A., 1999. Influence of daily carbon dioxide exposure duration and root environment on soybean response to elevated carbon dioxide. J. Environ. Qual. 28, 666–675.

Hendrey, G.R., 1993. Free-air Carbon Dioxide Enrichment for Plant Research in the Field.

C. K. Smoley, Boca Raton, FL.

Hendrey, G.R., Ellsworth, D.S., Lewin, K.F., Nagy, J.A., 1999. Free-air enrichment systems for exposing tall forest vegetation to elevated atmospheric CO_2. Global Change Biol. 5, 293–309.

Hendrey, G.R., Miglietta, F., 2006. FACE technology: past, present, and future. In: Nösberger, J., Long, S.P., Norby, R.J., Stitt, M., Hendrey, G.R., Blum, H. (Eds.), Managed Ecosystems and CO_2: Case Studies, Processes, and Perspectives, Ecological Studies, Vol. 187. Springer-Verlag, Berlin Heidelberg, pp. 15–43.

Hendrey, G.R., Long, S.P., McKee, I.F., Baker, N.R., 1997. Can photosynthesis respond to short-term fluctuations in atmospheric carbon dioxide? Photosynthesis Res. 51, 179–184.

Hileman, D.R., Bhattacharya, N.C., Ghosh, P.P., Biswas, P.K., Allen, L.H., Lewin, K.F., Hendrey, G.R., 1992. Distribution of carbon dioxide within and above a cotton canopy growing in the FACE system. Crit. Rev. Plant Sci. 11, 187–194. https://doi.org/10.1080/07352689209382338. URL. http://dx.doi.org/10.1080/07352689209382338.

Hladnik, J., Eler, K., Kržan, K., Pintar, M., Vodnik, D., 2009. Short-term dynamics of stomatal response to sudden increase in CO_2 concentration in maize supplied with different amounts of water. Photosynthetica 47, 422–428.

Holtum, J.A.M., Winter, K., 2003. Photosynthetic CO_2 uptake in seedlings of two tropical tree species exposed to oscillating elevated concentrations of CO_2. Planta 218, 152–158. https://doi.org/10.1007/s00425-003-1089-1.

Jones, P., Allen, L.H., Jones, J.W., Boote, K.J., Campbell, W.J., 1984. Soybean canopy growth, photosynthesis, and transpiration responses to whole-season carbon dioxide enrichment. Agron. J. 75, 633–637.

Kimball, B.A., 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. Agron. J. 75, 770–786.

Kimball, B.A., Pinter, P.J., Mauney, J.R., 1992. Cotton leaf and boll temperatures in the 1989 FACE experiment. Crit. Rev. Plant Sci. 11, 233–240.

Kimball, B.A., LaMorte, R.L., Seay, R., Pinter, P.J., Rokey, R.R., Hunsaker, D.J., Dugas, W.A., Heuer, M.L., Mauney, J.R., Hendrey, G.R., Lewin, K.F., Nagy, J., 1994. Effects of free-air CO_2 enrichment on energy balance and evapotranspiration of cotton. Agric. For. Meteorol. 70, 259–278.

Kimball, B.A., Kobayashi, K., Bindi, M., 2002. Responses of agricultural crops to Free-Air CO_2 Enrichment. Advances in Agronomy 77 Elsevier Science, USA.

Kimball, B.A., Pinter, P.J., Wall, G.W., Garcia, R.L., LaMorte, R.L., Jak, P.M.C., Frumau, K.F.A., Vugts, H.F., 1997. Comparisons of responses of vegetation to elevated carbon dioxide in free-air and open-top chamber facilities. In: Allen, L.H., Kirkham, M.B., Olszyk, D.M., Whitman, C.E. (Eds.), Advances in Carbon Dioxide Research. American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, Madison, WI, pp. 113–130.

Kimball, B.A., LaMorte, R.L., Pinter, P.J., Wall, G.W., Hunsaker, D.J., Adamsen, F.J., Leavitt, S.W., Thompson, T.L., Matthias, A.D., Brook, T.J., 1999. Free-air CO_2 enrichment and soil nitrogen effects on energy balance and evapotranspiration of wheat. Water Res. Res. 35, 1179–1190.

Kimball, B.A., Pinter, P.J., LaMorte, R.L., Leavitt, S.J., Hunsaker, D.J., Wall, G.W., Wechsung, F., Wechsung, G., Bloom, A.J., White, J.W., 2017. Data from the Arizona FACE (Free-Air CO_2 Enrichment) experiments on wheat at ample and limiting levels of water and nitrogen. Open Data J. Agric. Res. 3, 29–38.

Kimball, B.A., 2013. Comment on "Improving ecophysiological simulation models to predict the impact of elevated CO_2 concentration on crop productivity" by X. Yin. Ann. Bot. 112, 477–478.

Kimball, B.A., 2011. Lessons from FACE: CO_2 effects and interactions with water, nitrogen, and temperature. In: Hillel, D., Rosenzweig, C. (Eds.), Handbook of Climate Change and Agroecosystems: Impacts, Adaptation, and Mitigation. Imperial College Press, London, pp. 87–107.

Lai, S., Zhou, S., Gu, W., Zhuang, S., Zhou, J., Zhu, J., Yang, L., Wang, Y., 2014. Effects of CO_2 concentration, nitrogen supply and transplanting density on yield formation of hybrid rice Shanyou 63: a FACE study. J. Agro-Environ. Sci. 33, 836–843.

Laisk, A.K., Oya, V.M., 1975. Photosynthesis of leaves subjected to brief impulses of CO_2: the carboxylation reaction *in vivo*. Soviet Plant Physiol. 21, 928–935 Institute of Astrophysics and Atmospheric Physics, Academy of Sciences of the Estonian SSR, Tartu. Translated from Fiziolologiya Rastenii. 21(6), 1123-1131, November-December, 1974. ©1975 Plenum Publishing Corporation, 227 West 17th Street, New York, N. Y. 10011.

Leakey, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., Ort, D.R., 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. J. Exp. Bot. 60, 2859–2876. https://doi.org/10.1093/jxb/erp096.

LeCain, D., Smith, D., Morgan, J., Kimball, B.A., Pendall, E., Miglietta, F., 2015. Microclimatic performance of a Free-Air warming and CO_2 enrichment experiment in windy Wyoming, USA. PLoS ONE 10 (2), e0116834. https://doi.org/10.1371/journal.pone.0116834.

Lemon, E.R., Wright, J.L., Drake, G.M., 1969. Photosynthesis under field conditions. XB. Origins of short-time CO_2 fluctuations in a cornfield. Agron. J. 61, 411–413.

Lipfert, F.W., Alexander, Y., Hendrey, G.R., Lewin, K.F., Nagy, J., 1992. Performance analysis of the BNL FACE gas injection system. Crit. Rev. Plant Sci. 11, 143–163.

Liu, H., Yang, L., Wang, Y., Huang, J., Zhu, J., Yunxia, W., Dong, G., Liu, G., 2008. Yield formation of CO_2-enriched hybrid cultivar Shanyou 63 under fully open-air field conditions. Field Crops Res. 108, 93–100.

Long, S.P., Ort, D.R., 2010. More than taking the heat: crops and global change. Curr. Opin. Plant Biol. 13, 241–248.

Long, S.P., Ainsworth, E.A., Rogers, A., Ort, D.R., 2004. Rising atmospheric carbon dioxide: plants FACE the future. Annu. Rev. Plant Biol. 55, 591–628. https://doi.org/10.1146/annurev.arplant.55.031903.141610.

Long, S.P., Ainsworth, E.A., Leakey, A.D.B., Morgan, P.B., 2005. Global food insecurity.

Treatment of major food crops with elevated carbon dioxide or ozone under large-scale fully open-air conditions suggests recent models may have overestimated future yields. Phil. Trans. R. Soc. B 360, 2011–2020.

Long, S.P., Ainsworth, E.A., Leakey, A.D.B., Nösberger, J., Ort, D.R., 2006. Food for thought: lower-than-expected crop yield stimulation with rising CO_2 concentrations. Science 312, 1918–1921. https://doi.org/10.1126/science.1114722.

Miglietta, F., Peressotti, A., Vaccari, F.P., Zaldei, A., deAngelis, P., Scarascia-Mugnozza, G., 2001. Free-air CO_2 enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. New Phytol. 150, 465–476.

Morgan, P.B., Bollero, G.A., Nelson, R.L., Dohleman, F.G., Long, S.P., 2005. Smaller than predicted increase in aboveground net primary production and yield of field-grown soybean under fully open-air [CO_2] elevation. Global Change Biol. 11, 1856–1865.

Nagy, J., Lewin, K.F., Hendrey, G.R., Hassinger, E., LaMorte, R., 1994. FACE facility CO_2 concentration control and CO_2 use in 1990 and 1991. Agric. For. Meteorol. 70, 31–48.

Okada, M., Lieffering, H., Nakamura, H., Yoshimoto, M., Kim, H.Y., Kobayashi, K., 2001. Free-air CO_2 enrichment (FACE) using pure CO_2 injection: system description. New Phytol. 150, 251–260.

Pang, J., Kobayashi, K., Zhu, J., 2009. Yield and photosynthetic characteristics of flag leaves in Chinese rice (*Oryza sativa* L.) varieties subjected to free-air release of ozone. Agric. Ecosyst. Environ. 132, 203–211.

Pepin, S., Körner, C., 2002. Web-FACE: a new canopy free-air CO_2 enrichment system for tall trees in mature forests. Oecologia 133, 1–9. https://doi.org/10.1007/s00442-002-1008-3.

Pickering, N.B., Jones, J.W., Boote, K.J., 1995. Adapting SOYGRO V5.42 for prediction under climate change conditions. In: Rosenzweig, C., Jones, J.W., Allen, L.H. (Eds.), Climate Change and Agriculture: Analysis of Potential International Impacts. ASA-CSSA-SSSA, Madison, WI, pp. 77–98 ASA Spec. Pub. No. 59.

Pinter, P.J., Kimball, B.A., LaMorte, R.L., Wall, G.W., Hunsaker, D.J., Adamsen, F.J., Frumau, K.F.A., Vugts, H.F., Hendrey, G.R., Lewin, K.F., Nagy, J., Johnson, H.B., Thompson, T.L., Matthias, A.D., Brooks, T.J., 2000. Free-air CO_2 enrichment (FACE): blower effects on wheat canopy microclimate and plant development. Agric. For. Meteorol. 103, 319–332.

Rogers, H.H., Cure, J.D., Thomas, J.F., Smith, J.M., 1984Aa. Influence of elevated CO_2 on growth of soybean plants. Crop Sci. 24, 361–366.

Rogers, H.H., Sionit, N., Cure, J.D., Smith, J.M., Bingham, G.E., 1984Ab. Influence of elevated carbon dioxide on water relations of soybeans. Plant Physiol. 74, 233–238.

Seneweera, S., Posch, S., Norton, R., Tausz, M., Fitzgerald, G., Korte, C., Rebetzke, G., Mollah, M., Barlow, S., 2010. Intraspecific variation of growth and yield response of wheat to elevated CO_2 in Australian Grains Free Air Carbon Dioxide Enrichment (AGFACE). In: Dove, H., Culvenor, R.H. (Eds.), Food Security from Sustainable Agriculture. Proceedings of the 15th Australian Agronomy Conference. Australian Society of Agronomy, Lincoln, New Zealand 15-18 November 2010. http://www.agronomyaustraliaproceedings.org/index.php/2-uncategorised/558-2010-index (accessed 28 January 2019).

Sionit, N., Helmers, H., Strain, B.R., 1982. Interaction of atmospheric CO_2 enrichment and irradiance on plant growth. Agron. J. 74, 721–725.

Strain, B.R., Cure, J.D. (Eds.), 1985. Direct effects of increasing carbon dioxide on vegetation. United States Department of Energy, Office of Energy Research, Office of Basic Energy Sciences, Carbon Dioxide Research Division, Washington, D.C. 20545. DOE/ER-0238, December 1985. https://www.osti.gov/servlets/purl/6134866#page=198(accessed 13 August 2018).

Thomas, R.B., Strain, B.R., 1991. Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. Plant Physiol. 96, 627–634.

Tubiello, F.N., Amthor, J.S., Boote, K.J., Donatelli, M., Easterling, W., Fischer, G., Gifford, R.M., Howden, M., Reilly, J., Rosenzweig, C., 2007. Crop response to elevated CO_2 and world food supply. A comment on "Food for Thought." by Long et al. Science 312, 1918–1921 2006. Eur. J. Agron. 26, 215-223.

Vodnik, D., Hladnik, J., Vrešak, M., Eler, K., 2013. Interspecific variability of plant stomatal response to step changes of [CO_2]. Env. Exp. Bot. 88, 107–112.

Wang, J., Wang, C., Chen, N., Xiong, Z., Wolf, D., Zou, J., 2015. Response of rice production to elevated [CO_2] and its interaction with rising temperature or nitrogen supply: a meta-analysis. Climate Change 130, 529–543. https://doi.org/10.1007/s10584-015-1374-6.

Wang, L., Feng, Z., Schjoerring, J.K., 2013. Effects of elevated atmospheric CO_2 on physiology and yield of wheat (*Triticum aestivum* L.): a meta-analytic test of current hypotheses. Agric. Ecosys. Envir 178, 57–63.

Wright, J.L., Lemon, E.R., 1966. Photosynthesis under field conditions. IX. Vertical distribution of photosynthesis within a corn crop. Agron. J. 58, 265–268.

Yang, L., Liu, H., Wang, Y., Zhu, J., Huang, J., Liu, G., Dong, G., Wang, Y., 2009. Yield formation of CO_2-enriched inter-subspecific hybrid rice cultivar Liangyoupeijiu under fully open-air field condition in a warm sub-tropical climate. Agric. Ecosys. Environ. 129, 193–200.

Zhu, C., Xu, X., Wang, D., Zhu, J., Liu, G., 2015. An indica rice genotype showed a similar yield enhancement to that of hybrid rice under free air carbon dioxide enrichment. Sci. Rep. 5, 12719. https://doi.org/10.1038/srep12719.

Ziska, L.H., Bunce, J.A., 2007. Predicting the impact of changing CO_2 on crop yields: some thoughts on food. New Phytol. 175, 607–618.

Ziska, L.H., Teramura, A.H., 1992. Intraspecific variation in response of rice (*Oryza sativa*) to increased CO_2-photosynthetic, biomass and reproductive characteristics. Physiol. Plant 84, 269–276.

Ziska, L.H., Manalo, P.A., Ordonez, R.A., 1996. Intraspecific variation in the response of rice (*Oryza sativa*. L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. J. Exp. Bot. 47, 1353–1359.