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Review

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What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2

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Summary

Key words: atmospheric change, crop yield, elevated [CO_2], FACE (free air CO_2 enrichment), leaf area, photosynthesis, Rubisco.

Free-air CO_2 enrichment (FACE) experiments allow study of the effects of elevated [CO_2] on plants and ecosystems grown under natural conditions without enclosure. Data from 120 primary, peer-reviewed articles describing physiology and production in the 12 large-scale FACE experiments (475–600 ppm) were collected and summarized using meta-analytic techniques. The results confirm some results from previous chamber experiments: light-saturated carbon uptake, diurnal C assimilation, growth and above-ground production increased, while specific leaf area and stomatal conductance decreased in elevated [CO_2]. There were differences in FACE. Trees were more responsive than herbaceous species to elevated [CO_2]. Grain crop yields increased far less than anticipated from prior enclosure studies. The broad direction of change in photosynthesis and production in elevated [CO_2] may be similar in FACE and enclosure studies, but there are major quantitative differences: trees were more responsive than other functional types; C_4 species showed little response; and the reduction in plant nitrogen was small and largely accounted for by decreased Rubisco. The results from this review may provide the most plausible estimates of how plants in their native environments and field-grown crops will respond to rising atmospheric [CO_2]; but even with FACE there are limitations, which are also discussed.

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I. What is FACE?

The rise in atmospheric carbon dioxide concentration [CO_2], is one of the best documented global atmospheric changes of the past half century (Prentice, 2001). Enormous research efforts have been undertaken to understand how plants and ecosystems, both natural and managed, will respond to rising [CO_2]. The primary effects on plants of rising [CO_2] have been well documented and include reduction in stomatal conductance and transpiration, improved water-use efficiency, higher rates of photosynthesis, and increased light-use efficiency (Drake *et al.*, 1997). The majority of these conclusions have come from studies of individual species grown in controlled environments or enclosures (for reviews see Kimball, 1983; Ceulemans & Mousseau, 1994; Gunderson & Wullschleger, 1994; Amthor, 1995; Curtis, 1996; Drake *et al.*, 1997; Curtis & Wang, 1998; Saxe *et al.*, 1998; Norby *et al.*, 1999; Wand *et al.*, 1999). While the conclusions from these experiments form the basis for our knowledge of plant physiological responses to elevated [CO_2], there are serious potential limitations to using enclosure systems when studying the effects of elevated [CO_2] on plants. Enclosures may amplify downregulation of photosynthesis and production (Morgan *et al.*, 2001), and may through environmental modification produce a 'chamber effect' that exceeds the effect of elevating [CO_2]. Chambers also are limited in size and may have limited capacity to allow investigators to follow trees and crops to maturity within a valid experimental design (McLeod & Long, 1999). Further, growing plants in pots restricts the rooting volume and suppresses plant responses to elevated [CO_2] (Arp, 1991).

Large-scale free-air CO_2 enrichment (FACE) experiments allow the exposure of plants to elevated [CO_2] under natural and fully open-air conditions. FACE technology uses no confinement structures, rather an array of vertical or horizontal vent pipes to release jets of CO_2-enriched air or pure CO_2 gas at the periphery of vegetation plots. FACE relies on natural wind and diffusion to disperse the CO_2 across the experimental area. The first FACE systems utilized blowers or fans to inject CO_2-enriched air into the treatment area (Hendrey *et al.*, 1993; Lewin *et al.*, 1994). More recent field studies have employed a FACE technique in which pure CO_2 gas is released as high-velocity jets from emission tubes (through numerous small perforations) positioned horizontally at the periphery of a FACE octagon (Miglietta *et al.*, 2001; Okada *et al.*, 2001). FACE design allows good temporal and spatial control of CO_2 concentrations throughout crop canopies and also relatively young homogeneous forest plantations (Hendrey *et al.*, 1999).

This review focuses on the large-scale FACE facilities (8–30 m diameter) that have been established on forest, grassland, desert and agriculture lands (Table 1). These FACE experiments expose vegetation to elevated [CO_2] of 475–600 ppm, encompass a large number of species and functional groups as well as soil fertilization and stress treatments, and have reduced edge effects compared with small-scale (1–2 m diameter) FACE rings. The results of two multisite, mini-FACE experiments, Bog Ecosystem Research Initiative (BERI) and Managing European Grasslands as a Sustainable Resource in a Changing climate (MEGARICH), were recently reviewed along with some of the large-scale FACE studies (Nowak *et al.*, 2004). In this review the results of large-scale FACE experiments were assessed quantitatively using meta-analytic statistical methods. The second purpose of this review was to compare and contrast the results of chamber-based studies with those of FACE experiments. Only side-by-side tests of open-top chambers and FACE technology, on the same soil with the same level of CO_2 fumigation, will allow a direct comparison of [CO_2] responses in FACE and in open-top chambers. In the absence of such experiments, some guide to differences may be made by quantitatively summarizing results obtained from the two techniques using a meta-analytic approach. This has been done here. It is also evident from Table 1 that FACE experiments have focused on temperate ecosystems, while tropical, boreal and arctic systems have been largely ignored. Any serious commitment to discovering the response of the terrestrial biosphere to atmospheric change will critically require inclusion of these key biomes.

II. Materials and methods

Literature searches of primary FACE research in published peer-reviewed journals were conducted with the *Current Contents* citation index and the *ISI Web of Science* citation database. Data from 124 manuscripts that analyzed more than 40 species from 12 FACE sites were extracted for the analysis of gas exchange, leaf chemistry, leaf area and yield variables (Appendix 1). Response means of variables, standard deviations, and sample sizes from elevated and ambient [CO_2] treatments were either taken from tables, digitized from figures using digitizing software (Morgan *et al.*, 2003), or obtained directly from the authors of the primary studies.

Meta-analytic techniques have been developed for quantitative integration of research results from independent experiments (Hedges & Olkin, 1985), and have been widely adapted to summarize the effects of elevated [CO_2] on vegetation (Curtis,

Table 1 Large-scale free-air CO_2 enrichment (FACE) facilities used in this review

Site	Location	Elevated [CO_2]	Site description reference	Ecosystem	First year of exposure (ppm)
Aspen FACE FACTS 2	Rhinelander, WI, USA 45°36′-N, 89°42′-W	Ambient + 200	Dickson *et al*. (2000)	Aspen forest	1998
BioCON Cedar Creek	Cedar Creek, MN, USA 45°24′-N, 93°12′-W	550	Reich *et al*. (2001)	Natural prairie grassland	1998
ETH-Z FACE Swiss FACE	Eschikon, Switzerland 47°27′-N, 8°41′-E	600	Zanetti *et al*. (1996)	Managed grassland	1993
FACTS 1 Duke Forest	Orange County, NC, USA 35°58′-N, 70°5′-W	Ambient + 200	Hendrey *et al*. (1999)	Loblolly pine forest	1996
Maricopa FACE	Maricopa, AZ, USA 33°4′-N, 111°59′-W	550* Ambient + 200†	Lewin *et al*. (1994)	Agronomic C_3 and C_4 crops	1989
Nevada Desert	Mojave Desert, NV, USA 36°49′-N, 115°55′-W	550	Jordan *et al*. (1999)	Desert ecosystem	1997
Oak Ridge	Roane County, TN, USA 35°54′-N, 84°20′-W	Ambient + 200	Norby *et al*. (2001)	Sweetgum plantation	1998
Pasture FACE	Bulls, New Zealand 40°14′-S, 175°16′-E	475	Edwards *et al*. (2001)	Managed pasture	1997
POPFACE	Viterbo, Italy 42°37′-N, 11°80′-E	Ambient + 200	Miglietta *et al*. (2001)	Poplar plantation	1999
Rapolano Mid FACE	Chianti Region, Italy 43°25′-N, 11°35′-E	560–600	Miglietta *et al*. (1997)	*Vitis vinifera* *Solanum tuberosum*	1995
Rice FACE	Shizukuishi town, Japan 39°38′-N, 140°57′-E	Ambient + 200	Okada *et al*. (2001)	*Oryza sativa*	1998
SoyFACE	Champaign, IL, USA 40°02′-N, 88°14′-W	550		*Glycine max* *Zea mays*	2000

The Brookhaven National Laboratory (BNL) injection method is described in detail by Hendrey *et al*. (1993) and Lewin *et al*. (1994). Pure CO_2 injection methods are described by Miglietta *et al*. (2001) and Okada *et al*. (2001). A detailed map of all FACE experiments, and links to individual websites, are given at the Carbon Dioxide Information Analysis Center website: http://cdiac.esd.ornl.gov/programs/FACE/whereisface.html.
*1989–94; †1996–2000.

1996; Curtis & Wang, 1998; Medlyn *et al.*, 1999, 2001; Kerstiens, 2001; Ainsworth *et al.*, 2002, 2003). For this review, responses of different species, cultivars and stress treatments, and from different years of the FACE experiments, were considered to be independent and suited to meta-analytic analysis. Thus one FACE experiment examining a number of species in a multifactorial design could contribute multiple observations to a given response variable (e.g. Curtis & Wang, 1998; Ainsworth *et al.*, 2003).

The natural log of the response ratio (r = response in elevated [CO_2]/response in ambient [CO_2]) was used as the metric for analyses (Hedges *et al.*, 1999; Rosenberg *et al.*, 2000), and is reported as the mean percentage change [$(r - 1) \times 100$] at elevated [CO_2]. The meta-analysis procedure followed the techniques described by Curtis & Wang (1998), using the statistical software METAWIN (Rosenberg *et al.*, 2000). A mixed-model analysis was used, based on the assumption of random variation in effect sizes between FACE studies. A weighted parametric analysis was used, and each individual observation of response was weighted by the reciprocal of the mixed-model variance, which is the sum of the natural log of the response ratio and the pooled within-class variance (Hedges *et al.*, 1999). If a 95% confidence interval did not overlap with zero, then a significant response to elevated [CO_2] was considered.

Differences in the effect size of different categorical groups were tested according to the method of Curtis & Wang (1998). The approach taken was to partition total heterogeneity within and between levels of each categorical variable. For example, the photosynthetic type was either C_3 or C_4, and by dividing all species into those groups we could test whether there was significant between-group heterogeneity with respect to photosynthetic type. Partitioning of variance proceeded in two steps (Curtis & Wang, 1998). Between-group heterogeneity (Q_B) for each category was examined, then the data were subdivided according to levels of those categorical variables revealing significant between group heterogeneity. The between-group heterogeneity for CO_2 effect size for each variable (A_{sat}, crop yield, etc.) is shown in Table 2.

III. Photosynthetic carbon uptake

Elevated [CO_2] increases photosynthesis by increasing the carboxylation rate of Rubisco and competitively inhibiting

Table 2 Between-group heterogeneity for CO_2 effect size across categorical variables

Variable	k	Photosynthesis type (C_3 vs C_4)	Functional group	Site	Stress
A_{sat}	327	22.90***	127.94***	150.41**	19.19**
A'	146	4.77*	24.09**	58.36***	1.56
AQY	21			24.06*	13.05
g_s	235	1.01	24.09**	41.51***	25.77**
$c_i : c_a$	48		28.27**	24.79***	8.26*
ITE	35	18.87***	26.50***	23.07**	19.51**
$V_{c,max}$	228		15.28*	18.76*	23.99***
J_{max}	168		36.49***	57.03***	12.66*
$V_{c,max}/J_{max}$	97		13.79*	21.03	0.28
Rubisco	24		0.34	2.28	2.59
N_{area}	124		24.21***	25.17**	14.68**
N_{mass}	100		27.95***	28.52***	10.86*
N (%)	33			11.94*	21.19**
Chl_{area}	40		0.085	0.11	0.345
Chl_{mass}	32			2.93	
Chl $a : b$	20		1.76	1.89	0.66
Sugar	31		5.00	4.82	7.52
Starch	31		15.36**	15.72*	13.25**
Plant height	59		15.24**	18.64*	0.42
Stem diameter	54		1.87	10.97*	5.54*
Leaf number	45		8.71	32.45*	2.63
LAI	54		5.32	5.24	1.67
SLA	114	10.26**	15.55*	18.10*	7.25
DMP	175	16.34**	65.26***	12.71	4.13
Crop yield	28	9.65**		3.61	17.21**

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Light-saturated CO_2 uptake (A_{sat}), diurnal carbon assimilation (A'), apparent maximum quantum yield of CO_2 uptake (AQY), stomatal conductance (g_s), ratio of intercellular (c_i) to atmospheric CO_2 concentration (c_a), instantaneous transpiration efficiency (ITE), maximum carboxylation rate ($V_{c,max}$), maximum rate of electron transport (J_{max}), ratio of $V_{c,max} : J_{max}$, Rubisco content in mass/unit area (Rubisco), N content on an area, mass and percentage basis, N_{area}, N_{mass}, N(%), respectively, chlorophyll content on both an area and mass basis (Chl_{area}, Chl_{mass}), chlorophyll a : chlorophyll b (chl a : b), sugar content in mass/unit area (sugar), starch content in mass/unit area (starch), leaf-area index (LAI), specific leaf area (SLA), above-ground dry matter production (DMP). Blank spaces indicate that categorical analysis was not possible because only one category was represented. Blanks occur in the photosynthesis type column when only information for C_3 species was available. Blanks in the functional group column occur when information for only one functional group was available, and in the stress column when no stress treatments were imposed. Each response was represented by k studies.

the oxygenation of Ribulose-1,5-bisphosphate (RubP) (Drake *et al.*, 1997). Exposure to elevated [CO_2] resulted in a 31% increase in the light-saturated leaf photosynthetic rate (A_{sat}) and a 28% increase in the diurnal photosynthetic carbon assimilation (A') when averaged across all FACE experiments and species (Fig. 1; Appendix 2). Apparent maximum quantum yield increased by 12%. Stomatal conductance (g_s) was reduced by 20% with growth at elevated [CO_2] when averaged for 40 species grown at all 12 FACE experiments (Fig. 1). Growth under stressful conditions (low N and drought) exacerbated the decrease in g_s. There was no apparent change in the ratio of intercellular [CO_2] : atmospheric [CO_2] ($c_i : c_a$), and the instantaneous transpiration efficiency of plants grown under elevated [CO_2] was stimulated by ≈ 50% (Fig. 1). A number of experimental variables significantly altered the response of photosynthetic carbon uptake to elevated [CO_2], and are discussed further.

1. C_3 vs C_4 species

The number of C_3 species investigated in large-scale FACE experiments is eight times greater than the number of C_4 species. This is due in part to the assumption, based on photosynthetic theory, that C_4 species would not benefit from increases in atmospheric [CO_2] (Bowes, 1993). However, in a meta-analytic review of wild C_3 and C_4 grass (Poaceae) species, Wand *et al.* (1999) found similar increases in the assimilation response of C_3 and C_4 species (33 and 25% increases, respectively). Our analysis of C_4 species was limited to only five species, but the results contrast very sharply with the analysis of Wand *et al.* (1999). Here, A_{sat} was stimulated by elevated [CO_2] in both C_3 and C_4 species, but the magnitude of the response was three times greater in C_3 than C_4 species (Fig. 2). A_{sat} of three 'wild' C_4 grasses grown at the BioCON experiment was not stimulated with growth at elevated [CO_2], and

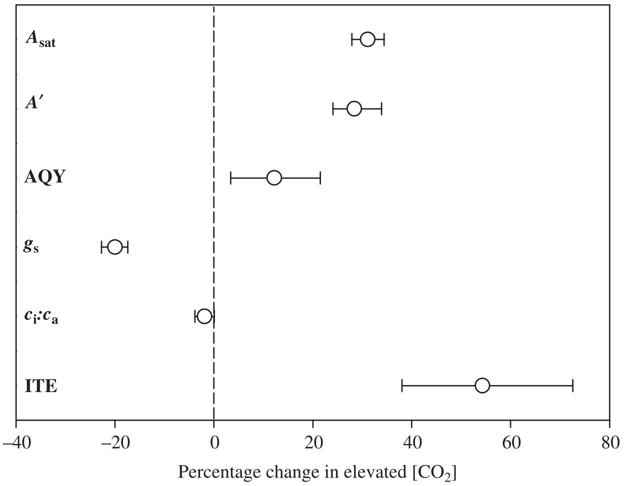

Fig. 1 Mean response to elevated [CO$_2$] (±95% CI) of light-saturated CO$_2$ uptake (A_{sat}), diurnal carbon assimilation (A'), apparent quantum yield of CO$_2$ uptake (AQY), stomatal conductance (g_s), ratio of intercellular (c_i) to atmospheric CO$_2$ concentration (c_a), and instantaneous transpiration efficiency (ITE). Number of species, FACE experiments and individual observations for each response are given in Appendix 2.

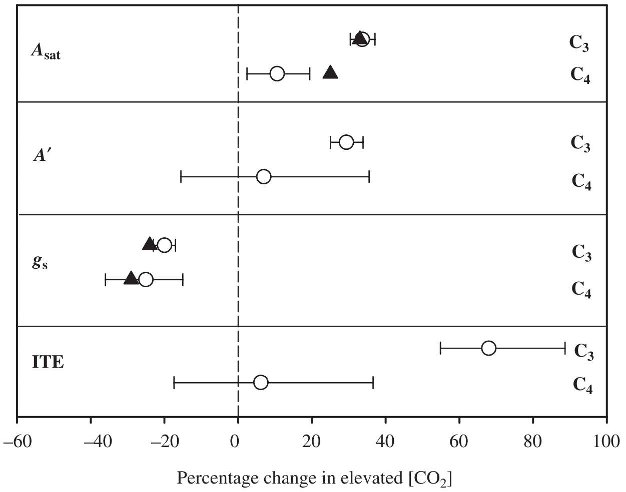

Fig. 2 Comparative photosynthetic responses of C$_3$ and C$_4$ species to elevated [CO$_2$] enrichment. ○, Results from this meta-analysis; ▲, comparative results from a prior meta-analysis of C$_3$ and C$_4$ wild grass (Poaceae) species (Wand *et al*., 1999). Number of species, FACE experiments and individual observations for each response in our meta-analysis are given in Appendix 2.

A_{sat} of C$_4$ crops grown at the Maricopa and SoyFACE sites was increased by 20 and 15%, respectively. Photosynthetic stimulation is not necessarily expected in C$_4$ species because of the CO$_2$-concentrating mechanism in C$_4$ leaves (Bowes, 1993; Ghannoum *et al.*, 2000). There is variation in the CO$_2$ saturation level of C$_4$ leaves. While some species appear to be CO$_2$ saturated at ambient [CO$_2$], other C$_4$ grasses are not necessarily saturated at that level (reviewed by Wand *et al.*, 1999). Wand *et al.* (1999) suggest that this simple explanation may account for the variation in stimulation of photosynthesis in C$_4$ species grown at elevated [CO$_2$].

Stomatal conductance (g_s) decreased on average by 20% in elevated [CO$_2$] and there was no difference between C$_3$ and C$_4$ species (Fig. 2). Wand *et al.* (1999) reported a similar magnitude of decrease in g_s for both C$_3$ and C$_4$ grasses. The instantaneous transpiration efficiency (ITE, A/g_s), a leaf-level measure of water-use efficiency, was significantly different between C$_3$ and C$_4$ species (Fig. 2; Appendix 2). C$_3$ species grown under FACE had a 68% increase in ITE, while ITE was not increased in C$_4$ species, based on six independent measurements of sorghum. However, individual studies reported that elevated [CO$_2$] improved the water status and increased the water-use efficiency in sorghum in the Maricopa FACE experiment (Conley *et al.*, 2001; Wall *et al.*, 2001). The discrepancy between the Wand *et al.* (1999) report and this review illustrates one of the shortcomings of FACE to date. Only five C$_4$ species have been investigated in large-scale FACE experiments, while Wand *et al.* (1999) reviewed 20 wild C$_4$ species from 48 enclosure studies. Further FACE experiments on more C$_4$ species are needed to resolve the discrepancy or confirm the differences between C$_4$ responses to elevated [CO$_2$] in chamber studies and FACE experiments.

2. C$_3$ functional groups and FACE sites

There was a significant difference in the response of A_{sat} to elevated [CO$_2$] in different C$_3$ functional groups (Q_B = 83.928, $P <$ 0.001). Trees showed the greatest response to elevated [CO$_2$], followed by fertilized C$_3$ crops and C$_3$ grasses (Fig. 3). Shrubs and legumes both showed a 21% increase in A_{sat} with growth at elevated [CO$_2$], and forbs showed approximately 15% increase in A_{sat} (Fig. 3). The 47% increase in A_{sat} for trees is significantly higher than the previously reported 31% increase for FACE-grown trees (Curtis & Wang, 1998), but is consistent with the 51% increase in A_{sat} reported for European tree species grown under elevated [CO$_2$] in field chambers (Medlyn *et al.*, 1999; Fig. 3). Nowak *et al.* (2004) also reported that woody species showed a stronger enhancement in A_{sat} relative to herbaceous species. This review includes values for trees grown under both elevated [CO$_2$] and elevated [O$_3$] at the Rhinelander FACE experiment. Ozone considerably increased the percentage response of A_{sat} to elevated [CO$_2$] (59% stimulation with growth under high [O$_3$] and [CO$_2$], relative to plants grown only in elevated [O$_3$]; Appendix 2).

The same trends in functional groups were not observed when photosynthesis was measured and integrated over the diurnal period, although this is based on a much smaller number of studies. A' was stimulated most in shrubs and grasses (Fig. 3). A' was 29% higher in trees and ≈ 20% higher in legumes grown under elevated [CO$_2$].

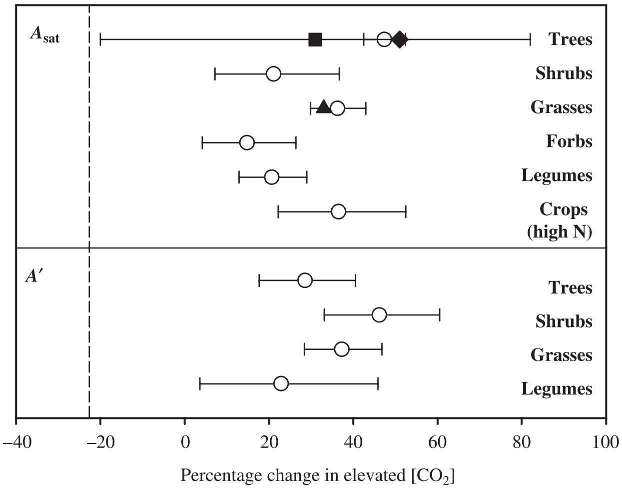

Fig. 3 Comparative photosynthetic responses of different C_3 functional groups to elevated [CO_2]. Results from: ○, this meta-analysis; ■, a meta-analysis of tree species (Curtis & Wang, 1998); ◆, a meta-analysis of European tree species (Medlyn *et al*., 2001); ▲, a meta-analysis of C_3 grasses (Wand *et al*., 1999). Number of species, FACE experiments and individual observations for each response in our meta-analysis are given in Appendix 2.

The experimental site also affected how a functional group responded to elevated [CO_2] (Appendix 2). Photosynthetic stimulation of plants grown at the BioCON experiment was less than that of plants grown at the Swiss FACE and SoyFACE experiments. C_3 grasses grown at the BioCON experiment showed a 16% increase in A_{sat}, while *Lolium perenne* at the Swiss FACE experiment had a 41% increase in A_{sat} (Appendix 2). The difference in response in the two systems was probably caused by nutrient status and reductions in leaf N content in species grown at the BioCON experiment (Nowak *et al.*, 2004). The Swiss FACE experiment was a managed agricultural pasture (with 10–14 or 42–56 g N m^{-2} yr^{-1}; Zanetti *et al.*, 1996), and the BioCON experiment was a natural prairie grassland experiment with no nutrient input on some plots and 4 g N m^{-2} yr^{-1} on other plots (Reich *et al.*, 2001). Even under low N-fertilization input typical of low-intensity grassland management, *L. perenne* showed an approximately 40% increase in A_{sat} on average over the 10 yr experiment (Ainsworth *et al.*, 2003). Legumes grown at the BioCON experiment did not show any stimulation in A_{sat} with growth at elevated [CO_2]. A_{sat} of legumes grown at the Swiss FACE experiment and the SoyFACE experiment was stimulated by 37 and 22%, respectively.

The decrease in g_s with elevated [CO_2] was consistent with previously reported decreases in g_s for European tree species (Medlyn *et al.*, 2001). However, the decrease in g_s varied with site (Table 2). Plants under FACE at the Eschikon experiment, which had the highest elevated [CO_2] (600 ppm; Table 1), showed the greatest decrease in g_s (≈ 33%; Appendix 2). Poplar species in the PopFACE experiment did not show any change in g_s with growth at elevated [CO_2] (Table 2; Appendix 2).

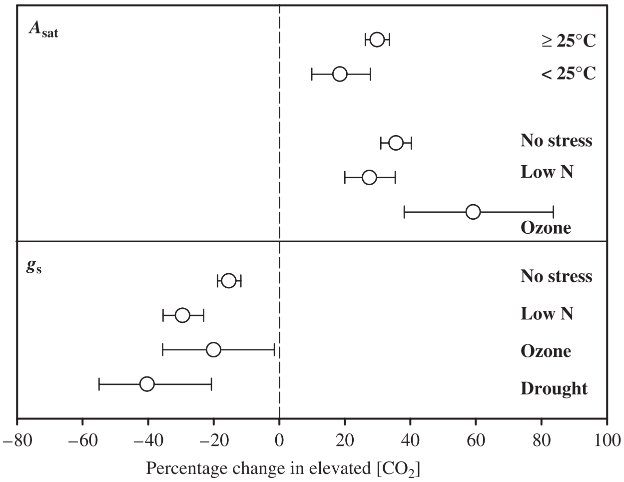

Fig. 4 Comparative responses of light-saturated CO_2 uptake (A_{sat}) and stomatal conductance (g_s) in different growth temperatures and stress treatments. Number of species, FACE experiments and individual observations for each response are given in Appendix 2.

3. Temperature and stress

Stimulation of photosynthesis at elevated [CO_2] is theoretically predicted to be greater at higher temperatures (Drake *et al.*, 1997). When the FACE data were divided between experiments conducted below 25°C and those conducted above 25°C, this prediction was supported. At lower temperatures (< 25°C) A_{sat} was increased by 19%, and at temperatures above 25°C A_{sat} was increased by 30% when plants were grown under elevated [CO_2] ($Q_B = 5.37$, $P < 0.05$; Fig. 4).

Ozone tended to enhance the response of A_{sat} to elevated [CO_2], and low N tended to reduce the response (Fig. 4). On average, plants grown without stress showed a 36% stimulation in A_{sat}, trees in Rhinelander grown under high ozone showed a 59% stimulation, and plants grown under low-N treatment showed a 27.5% stimulation. Stress also significantly affected g_s (Table 2). In general, decreases in g_s with elevated [CO_2] were exacerbated by low N and drought stress (Fig. 4).

IV. Acclimation of photosynthesis

To maintain a balance in N and other resources allocated to the reactions that control photosynthesis, species acclimate to growth in elevated [CO_2] (Sage, 1990; Gunderson & Wullschleger, 1994; Drake *et al.*, 1997). A reduced or acclimated stimulation of *A* has been mechanistically and quantitatively attributed to decreased maximum apparent carboxylation velocity ($V_{c,max}$) and investment in Rubisco (Rogers & Humphries, 2000). Photosynthetic acclimation is frequently reported along with an accumulation of leaf nonstructural carbohydrates and a decrease in N concentration in the leaf and plant (Stitt & Krapp, 1999; Nowak *et al.*, 2004). Plant growth in elevated [CO_2] in FACE experiments resulted in significant acclimation of C_3 photosynthesis (Fig. 5). $V_{c,max}$

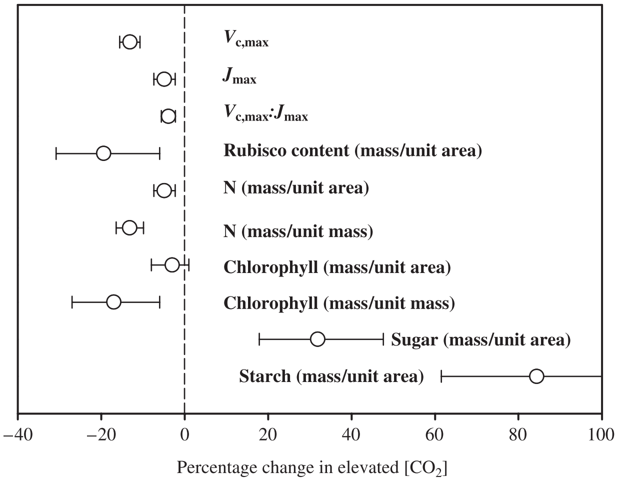

Fig. 5 Mean response of maximum carboxylation rate ($V_{c,max}$), maximum rate of electron transport (J_{max}), ratio of $V_{c,max} : J_{max}$, Rubisco content (mass/unit area), nitrogen content reported on both area and mass basis, chlorophyll content reported on both area and mass basis, sugar and starch content reported on area basis, ±95% CI. Number of species, FACE experiments and individual observations for each response are given in Appendix 2.

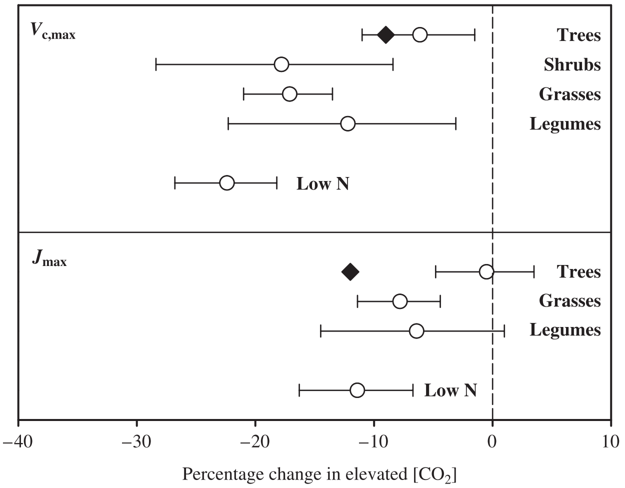

Fig. 6 Comparative acclimation responses of different C_3 functional groups to elevated [CO_2]. Results from: ○, this meta-analysis; ◆, a prior meta-analysis of European tree species (Medlyn *et al*., 2001). Number of species, FACE experiments and individual observations for each response are given in Appendix 2.

was reduced on average by 13%, and the maximum rate of electron transport (J_{max}) was reduced by 5%. There was also a significant 5% shift (reduction) in the ratio of $V_{c,max} : J_{max}$. It has long been recognized that as CO_2 rises, metabolic control of light-saturated photosynthesis by Rubisco ($V_{c,max}$) is decreased, and control by the rate of regeneration of RubP is increased (J_{max}) (Long & Drake, 1992). Along with acclimation of photosynthetic capacity, there were significant reductions in Rubisco content and N content, measured on an area basis. Simultaneously, sugar and starch were increased substantially with growth under elevated [CO_2] (Fig. 5). Variation in acclimation was apparent; functional groups showed different responses and the environmental conditions also altered acclimation.

1. Functional groups and FACE sites

The magnitude of photosynthetic acclimation differed between C_3 functional groups. $V_{c,max}$ tended to be reduced to a greater extent in grasses and shrubs than in trees and legumes (Fig. 6). At the FACTS 1, PopFACE, SoyFACE and New Zealand sites, $V_{c,max}$ was not significantly changed under elevated [CO_2] (Appendix 2). J_{max} was significantly reduced in C_3 grasses, and there was no significant downregulation of J_{max} or N (measured on an area basis) in trees and legumes (Fig. 6). Why would trees and legumes have different responses from other functional groups? The N-fixing ability of legumes generally enhances their response to elevated [CO_2] (Hebeisen *et al*., 1997; Lüscher *et al*., 1998, 2000). In the SoyFACE experiment, non-nodulating soybeans showed downregulation of $V_{c,max}$ in elevated [CO_2], while nodulating varieties maintained the same photosynthetic capacity under ambient and elevated [CO_2] (Ainsworth *et al*., 2004). Lüscher *et al*. (2000) demonstrated the importance of N_2-fixing capacity in the Swiss FACE experiment with effectively and ineffectively nodulating *Medicago sativa*. Under elevated [CO_2], effectively nodulating *M. sativa* strongly increased harvestable biomass and N yield, while ineffectively nodulating plants were negatively affected by FACE. However, at the New Zealand FACE experiment photosynthetic acclimation was stronger in the two N-fixing species than in the grass species (von Caemmerer *et al*., 2001).

Downregulation of photosynthetic capacity in trees in response to FACE is highly variable. Medlyn *et al*. (1999) reported a similar decrease in $V_{c,max}$ for European forest species; however, they also reported a significant 12% decrease in J_{max} for field-grown tree species under elevated [CO_2] (Fig. 6). Much of the data for trees included in this meta-analysis came from the Duke FACE experiment, where both loblolly pine and understorey hardwood species were examined (Ellsworth *et al*., 1995; DeLucia & Thomas, 2000; Naumburg & Ellsworth, 2000; Singsaas *et al*., 2000; Herrick & Thomas, 2001; Rogers & Ellsworth, 2002). DeLucia & Thomas (2000) reported that for four understorey hardwood tree species acclimation of photosynthesis did not involve any decrease in $V_{c,max}$ or Rubisco, but leaves had increased capacity for RubP regeneration, which increased their ability to utilize sunflecks. These results were reflected in this meta-analysis, where J_{max} was significantly increased and $V_{c,max} : J_{max}$ was significantly decreased at the FACTS 1 site (Appendix 2). In the POPFACE experiment, downregulation of $V_{c,max}$ was reported only in the slowest growing of the three poplar clones, *Populus alba*, which probably had the smallest sink capacity (Hovenden, 2003). Sink capacity may also explain variable downregulation of $V_{c,max}$ in *Populus tremuloides* in the Rhinelander FACE experiment. Only mid- and lower-canopy leaves showed significant downregulation of photosynthetic capacity, while upper-canopy leaves with close proximity to rapidly growing sinks did not show any change in photosynthetic capacity (Takeuchi *et al.*, 2001).

2. Nitrogen

Acclimation of photosynthesis to elevated [CO_2] has been reported to be more pronounced when plants are N-limited, and to be absent when N supply is adequate (Stitt & Krapp, 1999; Isopp *et al.*, 2000). Inadequate N supply could restrict the development of new sinks and therefore exacerbate the source–sink imbalance in plants grown under elevated [CO_2] (Stitt & Krapp, 1999; Hymus *et al.*, 2001). The results from the FACE experiments support this hypothesis. Under low N conditions there was a 22% decrease in $V_{c,max}$, and under high N conditions there was only a 12% decrease in $V_{c,max}$ (Fig. 6). Nitrogen reported on an area basis was reduced 12% in plants grown under low-N conditions and elevated [CO_2], but was not changed under unstressed conditions (Appendix 2).

Another explanation for accentuated acclimation under low-N conditions is that the decrease in Rubisco may reflect a general decrease in leaf protein caused by reallocation of N to younger leaves or earlier leaf senescence in N-limited plants (Stitt & Krapp, 1999). However, the results from the FACE experiments suggest that the decrease in Rubisco is specific, and not part of a general decrease in leaf protein. There was no change in chlorophyll content when measured on an area basis (Fig. 5). Assuming Rubisco to account for 25% of leaf N (Spreitzer & Salvucci, 2002), the 20% decrease in Rubisco could account for all of the 5% decrease in leaf N.

V. Growth, above-ground production and yield

Growth and above-ground biomass production generally increased with exposure to elevated [CO_2]; however, the magnitude of the response varied between species, growing seasons and experimental conditions. Elevated [CO_2] resulted in taller plants with larger stem diameter, increased branching and leaf number (Fig. 7). Surprisingly, stimulation of plant height with elevated [CO_2] was greater in the third growing season than in the first and second (Appendix 2). Leaf-area index (LAI) was not significantly affected by growth at elevated [CO_2], although this varied with functional group. Specific leaf area decreased 6% in plants exposed to elevated [CO_2], although this trend also varied with plant functional group and species. One largely unanswered question in forest ecosystems is whether biomass production will be increased along with the increase in photosynthesis (Karnosky, 2003). Our results showed greater allocation to wood and structure in woody plants and a 28% increase in above-ground dry matter production for trees grown under elevated [CO_2] (Fig. 8). Crop yield increased on average by only 17% (Fig. 7), considerably lower than previous estimates of crop yield increase in chambers (Kimball, 1983; Cure & Acock, 1986; Amthor, 2001; Jablonski *et al.*, 2002).

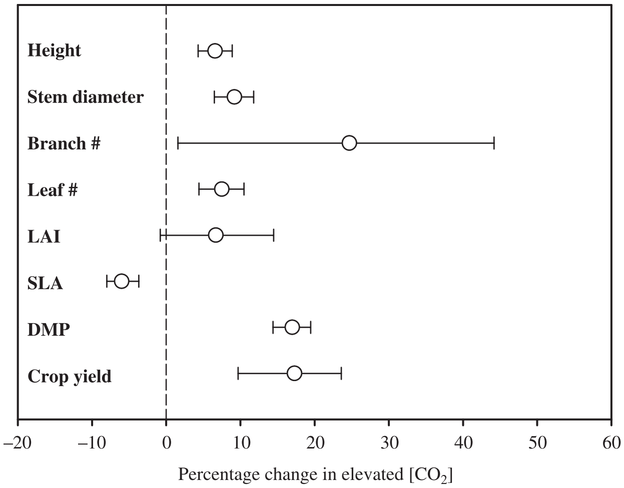

Fig. 7 Mean response to elevated [CO_2] of plant height, stem diameter, leaf number, leaf-area index (LAI), specific leaf area (SLA), above-ground dry matter production (DMP), and crop yield. Number of species, FACE experiments and individual observations for each response are given in Appendix 2.

1. Growth and leaf area

Plant height increased 14% in the third year of exposure to elevated [CO_2], but was not affected in the first 2 yr of exposure ($Q_B = 19.954$, $P < 0.001$; Appendix 2). This result contrasts with the expectation that initial stimulation of growth in response to elevated [CO_2] will diminish over time, possibly because of modifications in biomass allocation and phenology (Ward & Strain, 1999). Plant height increased more in shrubs and trees than C_3 crops (Fig. 8). Thus those FACE experiments with trees and shrubs (FACTS 1, Rhinelander, PopFACE and NV Desert FACE) showed significant increases in plant height, while Maricopa and Rapolano showed no change in plant height (Appendix 2). Stem diameter increased 9% on average, and was unaffected by length of exposure to elevated [CO_2]. Increased stem diameter was significantly affected by stress. *Populus tremuloides* grown under elevated [CO_2] and increased [O_3] showed a marginal 5% increase in stem diameter. Branch number was not highly reported in the FACE literature, but the limited results from six species at three FACE sites suggested an increase of 25% (Fig. 7). These results are consistent with those from a recent review of tree responses to elevated [CO_2], where a persistent growth response and increased branching were reported (Saxe *et al.*, 1998).

Overall, for 12 species in seven FACE experiments, leaf number was increased by 8% with growth at elevated [CO_2]

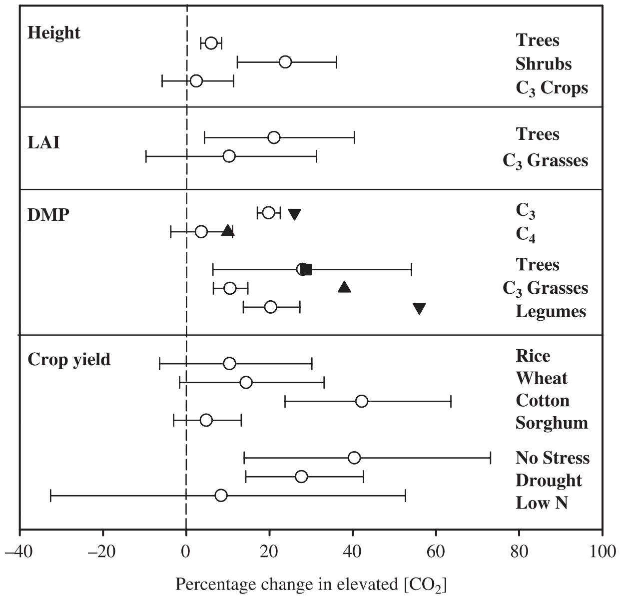

Fig. 8 Comparative responses to elevated [CO_2] of different functional groups and experimental conditions on growth and yield variables. Results from: ○, this meta-analysis; ■, a meta-analysis of tree species (Curtis & Wang, 1998); ▲, a meta-analysis of C_4 grasses (Wand *et al*., 1999). ▼, comparative results from a meta-analysis of 79 crop and wild species (Jablonski *et al*., 2002). Number of species, FACE experiments and individual observations for each response are given in Appendix 2.

(Fig. 7). On average, LAI did not change with growth in elevated [CO_2], but again this response varied with functional type. Trees had a 21% increase in LAI, but herbaceous C_3 grasses did not show a significant change in LAI (Fig. 8). Trees have increased stem diameter and plant height, which allows for more leaves, either by more stems or greater hydraulic conductance per stem. The increase in LAI in trees could result in more rapid canopy closure, which would affect light interception (Ward & Strain, 1999) and potentially increase tree density in mixed grass/tree systems such as savanna and woodland ecosystems (as modeled by Bond *et al*., 2003). The OzFACE experiment in tropical savanna in Yabula, Australia should help answer questions about mixed grassland/woodland dynamics. Results from the Rhinelander experiment (reviewed by Karnosky *et al*., 2003) suggest that while elevated [CO_2] increases LAI in *P. tremuloides*, ozone stress reduces LAI. Therefore when both CO_2 and O_3 are elevated there is no change in LAI (Karnosky *et al*., 2003).

2. Above-ground dry matter production

Above-ground dry matter production increased 20% on average for 29 C_3 species grown in six different FACE experiments (Fig. 8). The increase in C_3 biomass with elevated [CO_2] is consistent with the increase in C_3 plant mass reported by Jablonski *et al.* (2002) (Fig. 8). There was no change in dry matter production for the five C_4 species measured at the Maricopa FACE experiment and the BioCON FACE experiment, and neither C_4 crops nor C_4 wild grasses showed any dry matter production stimulation with growth at elevated [CO_2] (Fig. 8).

Stimulation of dry matter production differed between functional groups (Table 2; Fig. 8). Trees showed the largest response in dry matter production (28%), followed by legumes (24%; Fig. 8). C_3 grasses only showed a 10% increase in above-ground production (Fig. 8). Curtis & Wang (1998) reported a 28.8% increase in total biomass for primarily young or juvenile trees grown under elevated [CO_2] (≈ 700 ppm) in mostly chamber or glasshouse conditions. This suggests that either forests saturate their response at approximate 550 ppm, or the response of trees in FACE experiments differs from the that in growth chamber and glasshouse experiments. Trees grown under nutrient limitation had a nonsignificant 14% stimulation in above-ground biomass, although this is based on only four studies. The increase in legume production is less than that reported in two earlier meta-analyses for soybean biomass (Ainsworth *et al.*, 2002) and legume biomass (Jablonski *et al.*, 2002); however the CO_2 concentration in FACE experiments is lower than the average CO_2 concentration of most growth chamber and glasshouse experiments. The response of C_3 grasses is substantially lower than the 38% increase in above-ground biomass of C_3 Poaceae species reported by Wand *et al.* (1999). However, many of the data for our study come from the BioCON experiment and the low-N treatment at the Eschikon FACE experiment. The response of above-ground biomass to elevated [CO_2] is limited under low-nutrient conditions in wild C_4 grasses (Wand *et al.*, 1999).

3. Crop yield

The average crop yield stimulation of 17% is lower than previous estimates of CO_2 effects on crop yield, which ranged from 28 to 35% (Kimball, 1983; Cure & Acock, 1986; Amthor, 2001; Jablonski, 2002; Kimball *et al.*, 2002). One explanation of the difference is that FACE experiments have not elevated [CO_2] above 600 ppm. However, as a curvilinear increase with increase in [CO_2] is projected, this value is less than expected from chamber studies. Of the four crops analyzed in this meta-analysis, only cotton, a woody crop, showed a significant yield enhancement with growth at elevated [CO_2]. The stimulation in cotton yield with growth at elevated [CO_2] was 42% on average. Mauney *et al.* (1994) found that the primary effect of FACE on cotton was to sustain the initial rate of boll loading in cotton for a longer period. The increased yield is also attributable to more rapid leaf development before fruiting, greater number of flowers, and sustained fruiting for a longer period (Mauney *et al.*, 1994).

Wheat and rice also showed trends towards increases in yield, but these increases were not statistically significant

(Fig. 8). The trend of ≈ 15% increase in wheat yield is in agreement with the estimates of Amthor (2001) and Jablonski *et al.* (2002). Sorghum yield was not affected by growth at elevated [CO_2]. The sorghum data were taken from the Maricopa experiment where sorghum was grown under both wet and dry conditions (Ottman *et al.*, 2001). Ottman *et al.* (2001) reported that sorghum yield was increased in elevated [CO_2] under dry, but not under wet, conditions. The meta-analysis reflected these interactions between growth environment and elevated [CO_2] (Fig. 8; Table 2). The yield under FACE conditions with no reported stress was 40%; however that result was based on only five observations. Under wet conditions, there was no increase in yield with elevated [CO_2], and under dry conditions there was a 28% increase in yield (Appendix 2). Low N fertilization also eliminated any yield response to elevated [CO_2] (Appendix 2).

VI. So, what have we learned?

To date, only two large-scale replicated FACE facilities have reported elevated [CO_2] effects on yields of C_3 food crops, wheat and rice. Both these grains have shown overall smaller increases than were expected based on earlier enclosure studies. Over 3 yr of growth, rice seed yield was increased by 7–5% in elevated [CO_2] (Kim *et al.*, 2003). Spring wheat yield increased only by 8% in two growing seasons (Kimball *et al.*, 1995). These FACE experiments elevated [CO_2] by ≈ 200 ppm above current ambient, whereas the average increase was 350 ppm in the chamber studies surveyed by Kimball (1983). If a linear response of yield to elevated [CO_2] is assumed, then the expected yield increase that would have been predicted in these FACE studies, based on the earlier enclosure studies, is ≈ 19%. Further, this 19% is probably a minimum, as it is expected that increase in production with increase in [CO_2] will show diminishing returns. For example, in open-top chambers grain yield of wheat (cv. Minaret) increased 27% on elevation of [CO_2] from 359 to 534 ppm, but only a further 3% increase was observed when comparing plants grown at 649 to 534 ppm (Fangmeier *et al.*, 1996). A similarly smaller than predicted response has recently been reported for soybean grown at elevated [CO_2] within the SoyFACE experiment (Morgan, 2004).

This discrepancy has wide importance as the chamber values have formed the basis for projecting global and regional food supply, and the stimulation attributed to elevated [CO_2] has commonly been presumed to offset yield losses that would otherwise result from increased stresses, including higher temperature, elevated ground-level ozone and changes in soil moisture. For example, an integrated assessment of Hadley Center (HadCM2) climate-change impacts on agricultural productivity in the contiguous USA predicted climate change for 2090 would diminish wheat yields in most of the northern US wheat belt in the absence of any direct effect of elevated [CO_2] (Izaurralde *et al.*, 2003). When the direct effects of elevated [CO_2] are added, the combined effect that is simulated is an increase in yields. However, a 33% yield increase caused by increasing [CO_2] by 350 ppm is assumed (Izaurralde *et al.*, 2003). If chamber experiments have overestimated the direct effect of increased [CO_2], this would have a major impact on projections of future crop yields and wider implications for extrapolations from chamber studies to terrestrial ecosystems in general.

Could the lower than expected values in FACE be a flaw of the technology? Because of the difficulty of control in the absence of wind and the cost of CO_2, most of the FACE systems do not elevate CO_2 at night. Elevated [CO_2] has been suggested to inhibit dark respiration; however, re-evaluation of the methods used to measure dark respiration under elevated [CO_2] suggests that this apparent effect was an artifact of earlier measurement systems, and is absent when these artifacts are eliminated (Amthor, 2000; Jahnke, 2001; Davey *et al.*, 2004; Long *et al.*, 2004). Using young tropical trees, Holtum & Winter (2003) recently showed that high-frequency fluctuations in [CO_2] of the type produced by FACE technology may diminish the response of photosynthesis to elevated [CO_2]. However, this seems an unlikely explanation of the lower than expected stimulation in the FACE crop experiments. First, Hendrey *et al.* (1997) found no difference between constant and fluctuating elevated [CO_2] on whole-chain photosynthetic electron transport in wheat, provided that oscillations had a half-cycle of 30 s or less, which would include most of the fluctuations observed in FACE systems. Second, large fluctuations in [CO_2] are also observed in open-top chambers (McLeod & Long, 1999), which account for much of the database on effects of elevated [CO_2] on yield (Ainsworth *et al.*, 2002). Third, trees, in contrast to crops, showed greater increases in production than predicted from chamber studies.

The general conclusions from this meta-analysis and a measure of our certainty around them are summarized in Table 3. Functional groups differed in their response to FACE. Trees were generally more responsive than grass, forbs, legumes and crops, showing an average 47% stimulation in A_{sat}. The degree of photosynthetic acclimation was low, and the increase in leaf carbohydrates was also less than the increase for other functional groups. Trees also showed a significant increase in LAI, while there was no change in LAI in crops and grasses grown under FACE. Trees also showed the largest stimulation in dry matter production. While it may be surprising that trees responded more than herbaceous species, it is important to keep in mind that, for the most part, the trees grown under FACE conditions are young and rapidly growing. Nevertheless, in contrast to chamber studies, trees have been grown to canopy closure and to 6–20 m in height. Only with long-term exposure to FACE will the affect of elevated [CO_2] on mature trees be revealed. At present, the indication is that the response is larger than anticipated from chamber studies. C_4 species have shown a far smaller response

Table 3 Comparison of the general results of plant responses to elevated [CO_2] from this analysis of large-scale FACE experiments (FACE) vs previous quantitative reviews of elevated [CO_2] experiments (prior)

Generality	FACE	Prior	Certainty
Order of C_3 functional group responsiveness	Trees > legumes > C_3 grasses	Legumes[1] > grasses[2] > woody plants[3] No difference in functional groups[4]	Low
C_3 vs C_4 response	$C_3 >> C_4$ $C_3 \approx C_4$[2]	$C_3 > C_4$[5]	Low
Sustained increase in carbon uptake	Yes No[5]	Yes[4,8]	High
Acclimation of photosynthesis	$V_{c,max}/J_{max}$	No change in $V_{c,max}/J_{max}$[4,6]	High
Decrease in leaf N	Specific to and accounted for by Rubisco	Dilution effect[6,8]	Medium
Increase in leaf-area index	Trees only No[8]	Yes[7]	Low
Stimulation in crop yield	Small	Large[9,10]	Medium

[1]Jablonski *et al*. (2002); [2]Wand *et al*. (1999); [3]Curtis & Wang (1998); [4]Nowak *et al*. (2004); [5]Bazzaz (1990); [6]Medlyn *et al*. (1999); [7]Saralabai *et al*. (1997); [8]Drake *et al*. (1997); [9]Kimball (1983); [10]Kimball *et al*., 2002).
General level of certainty of our findings is based on sample sizes and confidence intervals around our meta-analytic results.

in FACE than predicted by chamber studies. Most significant is that the decrease in N, often assumed to lead to an expected diminution of the response of vegetation to elevated [CO_2] in the long term, is only marginal in FACE. Nitrogen per unit leaf area was decreased by only 5% (Fig. 5), and this could possibly be explained by the loss of Rubisco alone. The many large differences between the findings within FACE and prior chamber experiments (Table 3) clearly show the need for a wider use of FACE, and most importantly side-by-side experiments to separate technique from site difference. The greater responses of trees to CO_2 in FACE than in chambers, and the lesser responses of crops in FACE relative to chambers, show two urgent needs. More extensive FACE experimentation with the major crops and within the major growing zones will allow better forecasting of the future food supply, given that predictions currently based on chamber experiments appear very optimistic. Similarly, longer-term FACE experiments with forests where responses may have been underestimated will be critical. FACE experiments with tropical forests, which remain completely unrepresented despite representing 50% of C in terrestrial biomass, are an obvious need. The much smaller reduction in N observed in FACE relative to chamber studies also requires some rethinking of effects of elevated [CO_2] on N limitation and terrestrial biogeochemical models of future N and C cycles. Lack of a response in LAI to elevated [CO_2] in all functional types, except trees, similarly suggests a need for adjusting current models that are being used to project future vegetation. Future FACE experiments should also consider multiple levels of elevated [CO_2], ranging from 50 ppm above current ambient to double current ambient [CO_2]. This would allow more accurate scaling of physiological results and validation of ecosystem models. Finally, while large-scale FACE plots provide the most realistic mimic of a future elevated CO_2 atmosphere, they nevertheless have their limitations. While allowing far larger treatment plots than other technologies, a forest FACE ring still has a diameter close to the maximum height of its trees at maturity. This limits the potential for studying interactions with other environmental changes within the plot. Ever-decreasing prices of control hardware, improved control algorithms, and judicious placement near cheap or free sources of CO_2 should allow the development of much larger release arrays that could elevate CO_2 over much larger areas or provide controlled CO_2 gradients. There is therefore a need to improve the technology as well as to maintain and, in some areas, expand FACE.

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Appendix 2. Results of the meta-analysis of FACE effects

Results of the meta-analysis of FACE effects on light-saturated CO_2 uptake (A_{sat}), diurnal carbon assimilation (A'), apparent maximum quantum yield of CO_2 uptake (AQY), stomatal conductance (g_s), ratio of intercellular (c_i) to atmospheric CO_2 concentration (c_a), instantaneous transpiration efficiency (ITE), maximum carboxylation rate ($V_{c,max}$), maximum rate of electron transport (J_{max}), ratio of $V_{c,max} : J_{max}$, Rubisco content, N content, chlorophyll content, sugar content, starch content, plant height, stem diameter, branch number, leaf number, leaf-area index, specific leaf area, crop yield and above-ground dry matter productio

Variable	Interaction	Category	df	Number of species	Number of FACE sites	Effect size (E)	Lower CI	Upper CI
A_{sat}			**326**	**45**	**11**	**1.311**	**1.279**	**1.344**
	C_3 vs C_4	C_3	297	40	11	1.337	1.304	1.371
		C_4	28	5	3	1.106	1.024	1.194
	FACE site (C_4)	BioCON	11	3		0.982	0.886	1.089
		Maricopa	11	1		1.196	1.089	1.313
		SoyFACE	4	1		1.147	0.932	1.41
	Temperature (C_3)	<25°C	31	4	4	1.185	1.099	1.278
		= 25°C	221	32	11	1.299	1.263	1.336
	Functional group (C_3)	Tree	126	12	5	1.474	1.425	1.524
		Shrub	18	3	1	1.211	1.072	1.367
		Grass	62	5	3	1.363	1.299	1.43
		Forb	16	5	2	1.148	1.042	1.264
		Legume	29	6	3	1.207	1.129	1.29
		Crop (high N)	11	2	2	1.365	1.222	1.525
	Stress (C_3)	None	168	28	11	1.356	1.31	1.403
		Ozone	12	1	1	1.592	1.381	1.836
		Low N	55	15	3	1.275	1.2	1.354
	FACE site (C_3 grasses)	BioCON	12	4		1.155	1.036	1.288
		Eschikon	50	3		1.41	1.355	1.468
	FACE site (Legume)	BioCON	9	3		1.076	0.981	1.179
		Eschikon	7	1		1.367	1.213	1.541
		SoyFACE	11	1		1.223	1.134	1.32
A'			**145**	**16**	**6**	**1.284**	**1.241**	**1.339**
	C_3 vs C_4	C_3	142	15	6	1.294	1.25	1.339
		C_4	5	1	1	1.07	0.845	1.355
	Functional group (C_3)	Tree	19	5	2	1.286	1.177	1.405
		Shrub	29	3	1	1.462	1.331	1.605
		Grass	39	2	2	1.373	1.284	1.468
		Legume	6	1	1	1.229	1.036	1.459
	FACE site	Rhinelander	9	1		1.021	0.9	1.16
		Duke	2	1		1.648	0.476	5.705
		NV Desert	34	5		1.425	1.322	1.537
		PopFACE	9	3		1.555	1.353	1.787
		Maricopa	43	2		1.192	1.131	1.256
		Eschikon	38	1		1.366	1.282	1.454
		SoyFACE	12	2		1.162	1.048	1.287
AQY			**20**	**8**	**3**	**1.122**	**1.034**	**1.215**
	FACE site	Rhinelander	3	1		1.085	0.923	1.275
		Duke	11	4		1.255	1.173	1.344
		PopFACE	6	3		0.98	0.88	1.091
g_s			**234**	**40**	**12**	**0.8**	**0.774**	**0.827**
	Functional group	Tree	78	6	3	0.841	0.795	0.891
		Shrub	41	4	1	0.884	0.809	0.965
		C_3 grass	16	6	3	0.778	0.684	0.884
		C_4 grass	11	3	1	0.751	0.62	0.909
		Forb	16	3	1	0.813	0.717	0.922
		Legume	24	4	3	0.771	0.693	0.858
	Site	Rhinelander	12	1		0.803	0.704	0.916
		Oak Ridge	27	1		0.773	0.697	0.858
		Duke	15	6		0.829	0.702	0.98
		NV Desert	44	6		0.88	0.809	0.959
		PopFACE	21	3		0.995	0.886	1.119
		Rapolano	5	4		0.803	0.704	0.916

Appendix 2. *Continued*

Variable	Interaction	Category	df	Number of species	Number of FACE sites	Effect size (*E*)	Lower CI	Upper CI
		BioCON	46	12		0.759	0.704	0.819
		Maricopa	33	3		0.702	0.535	0.922
		Eschikon	16	6		0.667	0.606	0.734
		SoyFACE	12	2		0.834	0.731	0.952
	Stress	None	145	35	10	0.846	0.811	0.883
		Low N	37	12	3	0.705	0.645	0.769
		Ozone	6	1	1	0.8	0.644	0.995
		Drought	6	1	1	0.597	0.45	0.793
$c_i : c_a$			**47**	**12**	**7**	**0.981**	**0.961**	**1.001**
	Site	OakRidge	2	1		1.019	0.639	1.625
		NV Desert	6	1		1.001	0.945	1.06
		Rapolano	7	4		1.019	0.972	1.067
		Eschikon	14	4		1.018	0.981	1.055
		Maricopa	18	1		0.933	0.907	0.959
ITE			**34**	**7**	**4**	**1.543**	**1.38**	**1.726**
	C_3 vs C_4	C_3	28	6	3	1.68	1.549	1.883
		C_4	5	1	1	1.062	0.826	.366
	Functional group	Tree	26	4	3	1.737	1.599	1.887
		C_3 grass	3	1	1	1.258	0.753	2.103
		C_4 grass	5	1	1	1.069	0.84	1.361
$V_{c,max}$			**227**	**25**	**9**	**0.869**	**0.844**	**0.893**
	Functional group (C_3)	Tree	71	11	4	0.939	0.893	0.988
		Shrub	19	4	1	0.822	0.728	0.928
		Grass	97	3	2	0.829	0.793	0.868
		Legume	17	3	3	0.878	0.787	0.979
	Site	Duke	29	7		0.941	0.878	1.009
		PopFACE	29	3		0.939	0.869	1.017
		NV Desert	8	6		0.89	0.803	0.987
		Eschikon	14	6		0.829	0.797	0.864
		SoyFACE	6	1		0.897	0.736	1.093
		New Zealand	6	3		0.75	0.572	1.069
	Environment	Upper canopy	80	14	7	0.902	0.86	0.946
		Lower canopy	14	3	4	0.878	0.771	0.993
		Understorey	17	6	1	0.999	0.878	1.137
		Old	10	7	3	0.876	0.758	1.013
		Young	11	7	3	0.947	0.815	1.106
	Nitrogen	Low N	63	5	4	0.776	0.734	0.82
		High N	48	4	4	0.879	0.826	0.935
J_{max}			**167**	**19**	**8**	**0.951**	**0.926**	**0.977**
	Functional group (C_3)	Tree	57	9	4	0.995	0.955	1.038
		Grass	72	2	3	0.922	0.888	0.958
		Legume	17	2	2	0.936	0.862	1.017
	Site	Duke	33	5		1.089	1.025	1.159
		NV Desert	7	3		0.805	0.678	0.956
		PopFACE	28	3		0.965	0.912	1.02
		Eschikon	79	5		0.914	0.881	0.949
		SoyFACE	5	1		0.991	0.855	1.147
		New Zealand	5	3		0.779	0.56	1.086
	Stress	None	84	17	7	0.995	0.958	1.033
		Low N	39	4	3	0.886	0.839	0.935
$V_{c,max} : J_{max}$			**96**	**19**	**8**	**0.951**	**0.926**	**0.977**
	Functional group (C_3)	Tree	61	11	4	0.968	0.947	0.99
		Shrub	7	2	1	1.054	0.983	1.131
		Legume	16	3	3	0.945	0.912	0.979
Rubisco content (mass/unit area)			**23**	**6**	**3**	**0.806**	**0.692**	**0.94**
N (mass/unit area)			**123**	**21**	**7**	**0.951**	**0.926**	**0.977**
	Functional	Tree	36	3	3	1.02	0.978	1.065

Appendix 2. *Continued*

Variable	Interaction	Category	df	Number of species	Number of FACE sites	Effect size (*E*)	Lower CI	Upper CI
	group	Forb	12	1	3	0.845	0.781	0.914
		Legume	14	6	2	0.903	0.85	1.046
		C_3 grass	22	4	3	0.94	0.877	1.009
		C_4 grass	13	4	2	0.982	0.877	1.113
	Site	Rhinelander	8	1		0.948	0.857	1.049
		OakRidge	6	1		0.987	0.887	1.098
		Duke	28	2		1.031	0.981	1.083
		BioCON	45	13		0.905	0.863	0.949
		Japan	17	1		0.918	0.859	0.982
		Eschikon	6	1		1.02	0.892	1.167
		New Zealand	7	3		0.836	0.741	0.944
	Stress	None	61	9	5	0.99	0.957	1.024
		Low N	31	16	4	0.879	0.829	0.931
	Environment	Upper canopy (trees)	20	3	3	1.063	1.002	1.127
		Lower canopy	17	3	3	0.961	0.901	1.025
N (mass/mass)			**99**	**5**	**11**	**0.868**	**0.836**	**0.901**
	Functional group	Tree	53	6	3	0.899	0.87	0.93
		Shrub	5	2	1	0.852	0.752	0.966
		C_3 grass	8	1	1	0.882	0.807	0.964
		C_3 crop	30	2	1	0.819	0.785	0.854
N (% dry mass)			**32**	**4**	**3**	**0.871**	**0.838**	**0.906**
	Stress	None	19	4	3	0.923	0.889	0.958
		Ozone	14	2	1	0.809	0.77	0.849
Chlorophyll (mass/unit area)			**39**	**7**	**3**	**0.969**	**0.929**	**1.011**
Chlorophyll (mass/mass)			**31**	**6**	**3**	**0.831**	**0.73**	**0.947**
Chlorophyll *a* : chlorophyll *b*			**19**	**6**	**3**	**1.058**	**1.005**	**1.115**
Sugar (mass/unit area)			**30**	**4**	**4**	**1.319**	**1.179**	**1.476**
	Functional group	Tree	10	2	2	1.114	0.901	1.377
		Legume	7	1	1	1.427	1.081	1.884
	Stress	None	18	3	3	1.225	1.077	1.393
		Dry	5	1	1	1.7	1.299	2.225
		Wet	5	1	1	1.26	0.962	1.65
Starch (mass/unit area)			**30**	**4**	**4**	**1.844**	**1.615**	**2.104**
	Functional group	Tree	10	2	2	1.373	1.1	1.715
		Legume	7	1	1	1.842	1.398	2.426
	Site	OakRidge	6	1		1.312	0.982	1.754
		Duke	3	1		1.539	0.844	2.808
		Maricopa	11	1		2.287	1.901	2.755
		SoyFACE	7	1		1.842	1.367	2.429
	Stress	None	18	3	3	1.554	1.327	1.82
		Dry	5	1	1	2.519	1.86	3.41
Plant height			**58**	**10**	**5**	**1.066**	**1.043**	**1.089**
	Functional group	Tree	44	4	2	1.06	1.035	1.085
		Shrub	8	2	1	1.238	1.123	1.361
	Site	Rhinelander	33	1		1.053	1.023	1.085
		PopFACE	9	3		1.075	1.026	1.127
		Rapolano	4	3		1.013	0.919	1.115
		NV Desert	8	2		1.241	1.128	1.365
		Maricopa	3	2		1.108	0.909	1.35
	Growing season	1	14	10	5	1.035	0.998	1.071
		2	16	6	4	1.034	1	1.068
		3	12	6	3	1.138	1.093	1.185
Stem diameter			**53**	**6**	**3**	**1.092**	**1.066**	**1.119**
	Stress	None	34	6	3	1.115	1.081	1.15
		Ozone	20	1	1	1.049	1.004	1.096

Appendix 2. *Continued*

Variable	Interaction	Category	df	Number of species	Number of FACE sites	Effect size (*E*)	Lower CI	Upper CI
Branch number			**12**	**6**	**3**	**1.247**	**1.052**	**1.478**
Leaf number			**44**	**12**	**7**	**1.075**	**1.045**	**1.106**
	Site	Rhinelander	5	1		1.021	0.933	1.116
		Desert	5	1		1.225	1.029	1.459
		Eschikon	11	4		1.394	1.243	1.563
Leaf-area index			**53**	**11**	**6**	**1.067**	**0.999**	**1.142**
	Functional group	Tree	15	6	3	1.211	1.044	1.404
		C_3 grass	10	1	1	1.103	0.92	1.323
Specific leaf area			**113**	**24**	**6**	**0.941**	**0.92**	**0.963**
	C_3 vs C_4	C_3	102	20	6	0.925	0.908	0.952
		C_4	12	2	4	1.025	0.959	1.096
	Functional group	Tree	56	5	14	0.916	0.886	0.947
		Forb	12	1	3	0.944	0.876	1.017
		Legume	10	1	3	0.991	0.917	1.072
		C_3 grass	24	2	4	0.925	0.884	0.968
		C_4 grass	12	1	3	1.026	0.96	1.095
	Site	Duke	41	6		0.903	0.87	0.936
		PopFACE	7	3		0.966	0.892	1.046
		BioCON	45	13		0.982	0.952	1.012
		Eschikon	11	1		0.896	0.84	0.956
Dry matter production			**174**	**34**	**6**	**1.17**	**1.145**	**1.196**
	C_3 vs C_4	C_3	130	29	6	1.198	1.171	1.226
		C_4	11	5	2	1.036	0.963	1.115
	Functional group	Tree	9	7	2	1.28	1.064	1.541
		C_4 crop	6	1	1	1.067	0.978	1.166
		C_3 grass	41	8	3	1.105	1.065	1.148
		C_4 grass	3	4	1	0.963	0.804	1.154
		Legume	18	6	3	1.203	1.137	1.273
	Site	Rapolano	4	3		1.288	1.107	1.498
		Maricopa	27	3		1.205	1.146	1.268
		Eschikon	55	7		1.156	1.113	1.201
		Japan	17	1		1.216	1.141	1.296
		BioCON	46	16		1.118	1.071	1.166
		New Zealand	14	6		1.286	1.115	1.482
Crop yield			**27**	**6**	**3**	**1.173**	**1.102**	**1.249**
	Species	Sorghum	11		1	1.048	0.97	1.132
		Cotton	6		1	1.422	1.237	1.636
		Wheat	4		1	1.144	0.984	1.331
		Rice	5		1	1.104	0.936	1.302
	Stress	None	4			1.404	1.139	1.731
		Wet conditions	7			1.051	0.955	1.156
		Drought	7			1.277	1.143	1.426
		Low N	3			1.084	0.770	1.527

Main effects of FACE in bold font, along with degrees of freedom for each analysis and number of species and FACE sites that the analysis included.

Different categorical groups or interactions were tested further. The between-group heterogeneity (Q_B) across categorical variables and statistical significance of significant categorical differences are reported (e.g. the first categorical test determined the difference in the response of A_{sat} between C_3 and C_4 species).