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Review

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Functional responses of plants to elevated atmospheric CO_2 – do photosynthetic and productivity data from FACE experiments support early predictions?

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Contents

Key words: net assimilation, photosynthetic downregulation, primary production, bog, forest, grassland, desert, plant functional type.

Summary

Results from 16 free-air CO_2 enrichment (FACE) sites representing four different global vegetation types indicate that only some early predictions of the effects of increasing CO_2 concentration (elevated $[CO_2]$) on plant and ecosystem processes are well supported. Predictions for leaf CO_2 assimilation (A_{net}) generally fit our understanding of limitations to photosynthesis, and the FACE experiments indicate concurrent enhancement of photosynthesis and of partial downregulation. In addition, most herbaceous species had reduced leaf nitrogen (N)-content under elevated $[CO_2]$ and thus only a modest enhancement of A_{net}, whereas most woody species had little change in leaf N with elevated $[CO_2]$ but a larger enhancement of A_{net}. Early predictions for primary production are more mixed. Predictions that enhancement of productivity would be greater in drier ecosystems or in drier years has only limited support. Furthermore, differences in productivity enhancements among six plant functional types were not significant. By contrast, increases in productivity enhancements with increased N availability are well supported by the FACE results. Thus, neither a resource-based conceptual model nor a plant functional type conceptual model is exclusively supported by FACE results, but rather both species identity and resource

availability are important factors influencing the response of ecosystems to elevated $[CO_2]$.

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I. Introduction

The increase in atmospheric CO_2 concentration ($[CO_2]$) during the last 250 yr is unequivocal, and atmospheric $[CO_2]$ will continue to increase at least for the next several decades. The direct measurements of atmospheric $[CO_2]$ at Mauna Loa, Hawaii by Keeling and colleagues clearly show a 55 μmol mol^{-1} increase since 1959 (Keeling & Whorf, 2002). Longer-term data indicate an atmospheric $[CO_2]$ near 280 μmol mol^{-1} before 1750 (Houghton *et al.*, 2001). Thus, the atmospheric $[CO_2]$ of 370 μmol mol^{-1} in 2001 represents a 32% increase in the last 250 yr, with more than half of that increase occurring in the last 42 yr. Although predictions of future atmospheric $[CO_2]$ require a number of assumptions about economic growth, technological advances, and carbon sequestration by biological and geological processes, estimates of atmospheric $[CO_2]$ in the year 2100 range between 540 μmol mol^{-1} and 970 μmol mol^{-1} (Houghton *et al.*, 2001). Note that for convenience and familiarity, we use concentration units (i.e. μmol mol^{-1}) rather than partial pressures (i.e. Pa) to express the content of CO_2 in air, recognizing that changes in elevation among sites, and hence differences in total atmospheric pressure, require appropriate adjustments to the concentration units for physiological processes such as photosynthesis.

Elevated atmospheric $[CO_2]$ has interested biological scientists, especially ecologists and plant physiologists, because of the potential biological impacts from CO_2-induced global warming and from direct effects of elevated $[CO_2]$ on vegetation that are independent of global warming. This latter interest is the focus of this review, and readers interested in the effects of global warming on biological systems are referred to Watson *et al.* (1998) and Melillo *et al.* (2001). The current review augments previous reviews (Ceulemans & Mousseau, 1994; Medlyn *et al.*, 2001) and special issues of *New Phytologist* (Volume 147, Issue 1, 2000; Volume 150, Issue 2, 2001) on the effects of elevated $[CO_2]$ on specific plants or ecosystems. Our review differs from these earlier papers in that it focuses on whole-ecosystem free-air CO_2 enrichment (FACE) experiments, which currently represent the best technology to manipulate $[CO_2]$ for ecosystems under natural conditions, and explicitly contrasts the results from these FACE experiments in the context of early predictions made *c.* 20 yr ago on how elevated $[CO_2]$ may affect different plants and ecosystems.

II. Early assessments of $[CO_2]$ responses in natural ecosystems

Although elevated $[CO_2]$ has long been known to stimulate plant growth, particularly within the field of horticulture, the realization that increasing $[CO_2]$ would have potentially important effects on crops, forests, and natural ecosystems did not generate interest until the later part of the twentieth century. An early set of reviews on the subject (Kramer, 1981; Kimball, 1983; Pearcy & Björkman, 1983; Strain & Bazzaz, 1983; Cure & Acock, 1986; Strain, 1987) set the stage for a strong emphasis on elevated $[CO_2]$ research in the ecological sciences community. The consensus of these early reviews was that increases in $[CO_2]$ will have direct and relatively immediate effects on two physiological processes in plants: (1) it increases the rate of photosynthetic CO_2 assimilation; and (2) it decreases stomatal conductance. In combination, these effects were thought to substantially increase intrinsic water-use efficiency (WUE; carbon gain per unit water loss) in plants (Morison, 1985). Studies also indicated that plants may produce tissues with lower nitrogen (N) concentration, although it was not known if that was due to a reallocation of N out of leaves or to a dilution effect associated with increased carbohydrate production. These early reviews were also unanimous in articulating great uncertainty about the long-term and whole-ecosystem responses to elevated atmospheric $[CO_2]$ due to a lack of appropriate data and experiments.

Based on these fundamental observations, a conceptual model proposed by Strain & Bazzaz (1983) predicted increased plant growth and ecosystem productivity in response to elevated $[CO_2]$ as water availability decreases or nutrient availability increases. Therefore, ecosystems with ample water and low nutrient availability (e.g. bogs and tropical forests) should be relatively unresponsive to elevated $[CO_2]$; an intermediate response would be observed in systems that are either both water- and nutrient-limited (e.g. upland desert soils and serpentine or calcareous grasslands) or have ample amounts of both water and nutrients (some forests and mesic grasslands); and ecosystems that should respond most strongly would be water-limited yet have adequate nutrients (e.g. alluvial desert soils, fertile dry grasslands). Strain & Bazzaz (1983) thus proposed a testable set of hypotheses that would help guide research on the effects of elevated $[CO_2]$ on plant productivity. These early reviews, citing our uncertainty of plant responses to elevated $[CO_2]$ under a variety of ecological conditions, stimulated a huge amount of research on the physiological responses of plants to elevated $[CO_2]$. For example, the WUE hypothesis, in particular, was the basis for predictive models that simulated changes in global primary production (Melillo *et al.*, 1993) and potential shifts in species composition (Neilson, 1995) as a function of increasing $[CO_2]$.

An area of particular interest to global change scientists has been to derive an estimate of net primary production (NPP) that would (1) widely accommodate differences in vegetation

type, climate and soil nutrient availability, and (2) be useful in regional and global carbon cycle models. One important approach has been the β factor, or 'biotic growth factor' (Bacastow & Keeling, 1973). The β factor has been variously defined as an empirical coefficient that relates a logarithmic response of NPP to increasing [CO_2] (Amthor & Koch, 1996) or as a fractional change in NPP with a fractional change in [CO_2] (Luo & Mooney, 1996). Bacastow &Keeling (1973) gave an initial estimate of β as a likely range of 0.2–0.6 for a recent 10-year increase in [CO_2]. A variety of estimates of the β factor have been put forward, but perhaps the most extensive estimate to date – based on 398 observations from 73 forest tree species – yielded a β factor of 0.43, which translates into an increase in NPP of 32% in response to a doubling (to 700 μmol mol^{-1}) of [CO_2] (Wullschleger *et al.*, 1997). Based on calculations in Amthor & Koch (1996), a β of 0.43 would yield an approximate 20% increase in NPP in response to an increase in [CO_2] to 550 μmol mol^{-1}, the operational set-point of the global FACE network. However, Luo & Mooney (1996) cautioned that there are 'a very wide range of β-values between, and even within, ecosystems'.

Given the potential for strong variation in plant growth to elevated [CO_2] across species and ecosystems, it is not surprising that our predictive capability for ecosystem-level responses such as NPP is much less than for individual physiological responses. Early reviews of ecosystem responses to elevated [CO_2] (Strain, 1987; Bazzaz, 1990; Mooney & Koch, 1994) emphasized this difficulty, and called for larger-scale experiments that specifically examined ecosystem responses to changes in [CO_2] and other global change phenomena. The need for these experiments was further emphasized by evidence of important feedback mechanisms between below-ground carbon inputs and soil microbial processes (Díaz *et al.*, 1993; Zak *et al.*, 1993) and evidence of novel responses in model terrestrial ecosystems (Jones & Thompson, 1998). These considerations, among others, led Körner (2000) to conclude that an ecosystem approach, which uses fully coupled plant–soil systems and considers potential nonlinear responses, was essential if we are to make meaningful predictions about how an integrated biosphere will respond to global change.

A big question has been: How does the ecological research community reach that goal? Although a modeling approach is one way of trying to elucidate the response of complex, interrelated systems to global change, the information base to parameterize models is much more extensive when parameterizing gas exchange responses to elevated [CO_2] than it is for other processes that have important ecosystem-level ramifications, such as carbon partitioning and nutrient uptake (Luo *et al.*, 1999). This disparity in available information is largely a consequence of the methodological history of elevated [CO_2] research. Most early investigations were conducted in controlled environments or glasshouses with herbaceous plants and tree seedlings in pots. These studies had two important limitations (among others): (1) limited rooting volume, and therefore artificial growing conditions, that could influence the [CO_2] response of plants (McConnaughay *et al.*, 1993); and (2) the inability to scale seedling responses to whole trees and forest stands (Strain, 1987; Körner, 1995). This led to an extensive network of open-top chamber (OTC) studies that could be conducted with plants in their natural environment. Although these experiments were constrained by (1) the well known 'chamber effect', in which the chamber itself significantly altered microclimate around the plots being investigated (Leadley & Drake, 1993) and (2) the inability to enclose large plots, they provided valuable information, particularly in short-stature herbaceous communities such as a salt marsh (Drake, 1992) and grassland (Owensby *et al.*, 1999). A number of OTC studies were also conducted with forest seedlings and saplings, and although these studies provided important data on tree responses to elevated [CO_2], they were unable to scale results to closed-canopy forests because they were measuring small trees in the exponential phase of growth (Norby *et al.*, 1999). These limitations with controlled-environment and OTC studies led to the establishment of a new experimental program that utilized free-air CO_2 enrichment (FACE) technology. FACE technology delivers consistent and uniform elevated [CO_2] treatments to large plots of an intact ecosystem without walls and has two key advantages over other technologies. First, FACE experiments often have plot diameters of 25–30 m, a size large enough to encompass the small-scale spatial structure of the ecosystem. Second, alterations of microclimate are minimal when the FACE system is operated properly to avoid night-time temperature effects (Pinter *et al.*, 2000), and disturbance of natural soil and root processes is avoided (Allen, 1992; Hendrey & Kimball, 1994; Hendrey *et al.*, 1999). Thus, FACE systems allow us to examine complex natural ecosystem responses to elevated [CO_2] in the field (McLeod & Long, 1999), particularly with regard to temporal and spatial variations in the natural environment (Saxe *et al.*, 1998; Norby *et al.*, 2001).

Because results from FACE systems are likely to capture representative responses of ecosystems to elevated [CO_2] and given that results from chamber studies have been subject to extensive reviews previously (e.g. Curtis, 1996; Saxe *et al.*, 1998; Medlyn *et al.*, 1999), results from the global network of FACE sites form the basis for this review. We also focus primarily on noncrop systems; Kimball *et al.* (2002) recently summarized results for agricultural crop systems. Our objectives were twofold: (1) to examine whether FACE data support early predictions of plant and ecosystem responses to increasing atmospheric [CO_2] (specifically, responses of assimilation, leaf N content, primary productivity, and functional groups); and (2) to examine if a rational ecological framework accounts for the observed responses. Specific hypotheses, based on early predictions in the literature, were that: (1) acclimatization (i.e. downregulation) of photosynthesis would occur most prevalently in ecological situations where N is limiting; (2) the response of productivity to elevated [CO_2] would be greater in drier ecosystems as well as in dry years within more humid environments; (3) based on

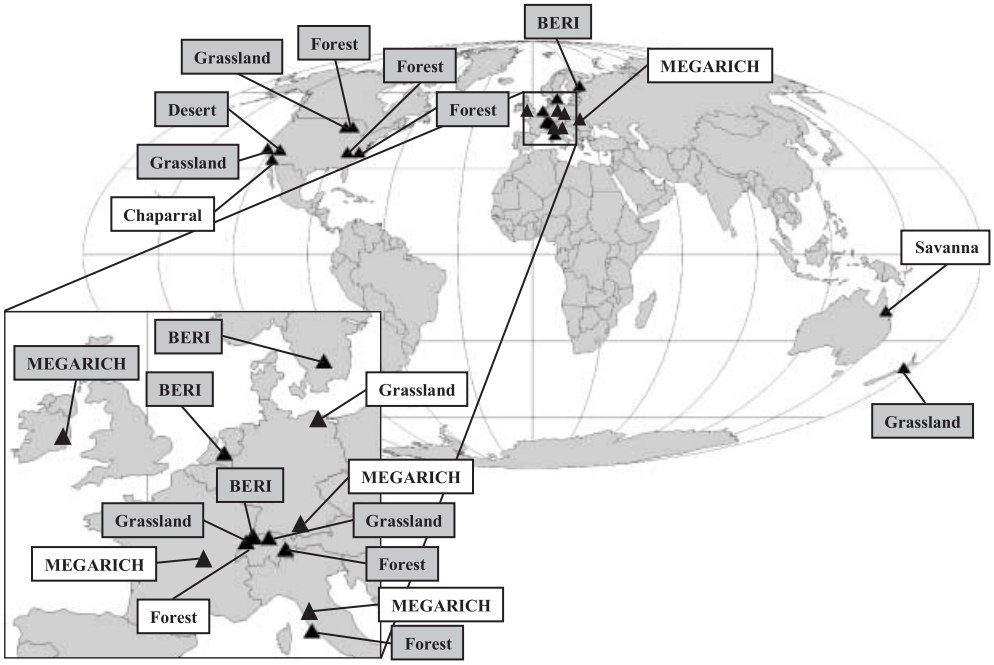

Fig. 1 Geographic distribution of noncrop free-air CO_2 enrichment (FACE) sites with labels indicating the type of global ecosystem represented. Grassland sites include native grasslands and seminative meadows and pastures. Sites whose results are used in this review are shaded grey.

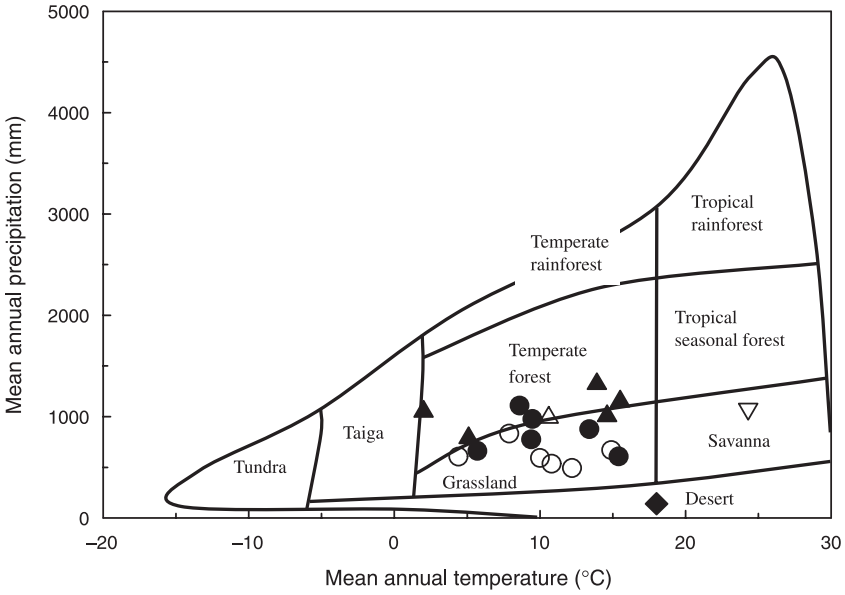

Fig. 2 Mean annual temperature and precipitation of noncrop free-air CO_2 enrichment (FACE) sites, except for the bog (BERI) sites. Closed symbols are sites whose results are used in this review. Triangles, forest FACE sites; circles, grassland sites; inverted triangle, savannah; diamond, desert. Global ecosystem categories and their climatic ranges are after Whittaker (1970).

previous estimates of the β factor, NPP at FACE sites should vary around a mean increase of 20% at 550 μmol mol^{-1} $[CO_2]$; and (4) functional groups such as legumes, C_3 plants, and herbaceous perennials should be more responsive to elevated $[CO_2]$ than woody perennials or C_4 plants.

III. Global network of FACE sites

A total of 24 noncrop FACE sites are situated around the world (Fig. 1). The majority of sites are in Europe, and the majority of the European sites are organized into two multisite networks: four bog sites in the Bog Ecosystem Research Initiative (BERI) and five grassland sites in a project entitled 'Managing European Grasslands as a Sustainable Resource in a Changing Climate' (MEGARICH). Although five different types of global ecosystems are represented in this network (bogs plus the four shown in Fig. 2), 75% of the current sites are either temperate forest or grassland vegetation. Five global ecosystems do not have any FACE sites, although some (e.g. tundra and tropical forests) have been studied in controlled-environment

facilities or *in situ* using OTCs. Only one site is in a tropical climate (mean annual temperature > 18°C), and no sites receive, on average, > 1500 mm of precipitation each year.

For most sites, CO_2 enrichment occurs using either: (1) the Brookhaven National Laboratory design (Lewin *et al.*, 1994; Hendrey *et al.*, 1999), where blowers mix ambient air with pure CO_2 and then distributes the enriched air across the plot through a series of stand pipes (eight sites); or (2) a pure-CO_2 injection technique (Miglietta *et al.*, 2001a, 2001b; Pepin & Körner, 2002), where pure CO_2 is injected through holes under pressure and turbulent mixing distributes the enriched air across the plot (10 sites). Twenty-one sites have an effective $[CO_2]$ within 10% of 550 μmol mol^{-1} during daylight hours; 19 of these control for a set $[CO_2]$, whereas the other two maintain an 'ambient plus 200 μmol mol^{-1}' $[CO_2]$. Of the remaining sites, two sites control for $[CO_2]$ < 495 μmol mol^{-1} and one site controls for *c.* 700 μmol mol^{-1}. It is important to note that the long-term, integrated $[CO_2]$ achieved by these experiments always is less than their target $[CO_2]$ because of programed and unprogramed periods of time when the $[CO_2]$ control is off. Furthermore, ambient $[CO_2]$ also varies among sites, especially at night and in the early morning when plant respiration increases local $[CO_2]$. The Carbon Dioxide Information Analysis Center (http://cdiac.esd.ornl.gov) provides links to individual FACE web sites as well as other useful web sites.

For this review, we primarily extracted results from journal articles that pertain to an individual FACE site. Unfortunately, published data were not available from all sites – the sites used in this review are indicated in Fig. 1 (shaded names). Table 1 lists general information and literature citations on each site whose results we analysed in this review. Although most sites focus solely on $[CO_2]$ treatments, some sites have multifactor experimental designs; for example, complete factorial designs with $[CO_2]$ and one or more other global change factors such as N, precipitation, ozone, or biodiversity. While such interactions are of great interest and offer powerful insights into how other global change factors may modify $[CO_2]$ responses, we did not want to confound the $[CO_2]$ effects with these other factors. Thus, we have generally limited our use of data to only those experimental factors that had all ambient conditions with and without elevated $[CO_2]$; exceptions are noted in Table 1 and the text. In addition, three sites had two different experiments: ETH-Z and SCG had a managed grassland experiment and a second experiment that examined responses of different plant functional types, and FACTS I has an unreplicated prototype experiment that began 3 yr before the replicated main experiment. Results from both experiments are used as appropriate and are treated as independent studies.

Some precautionary thoughts on our data sets follow. First, data are limited in a number of ways, such as coverage of global ecosystems and climates, number of years of operation, and types of data available. These limitations reflect the nature of the global FACE network: the great expense to build and operate a FACE site generally limits them to developed countries, which are primarily in temperate ecosystems, and even these developed countries do not always adequately fund the sites. These limitations also highlight the importance of maintaining the current infrastructure and allocating adequate resources to FACE experiments, especially multifactorial experiments and experiments in nontemperate or extreme climates. Second, individual data points within any of our data sets are not true experimental replicates because all other factors that may affect the vegetation responses (e.g. weather, soil characteristics, vegetation management such as grazing or cutting, etc.) are not the same among all FACE sites. We have partly compensated for this variation among sites by expressing most data as the ratio of the response under elevated $[CO_2]$ to that under ambient $[CO_2]$ (i.e. elevated/ambient or E/A), although this approach is not without limitations (Jasienski & Bazzaz, 1999). Furthermore, given that we expect a greater random error for statistical analyses of the data (Filion *et al.*, 2000), we have also carefully examined statistical results when the *P*-value was between 0.05 and 0.10. Although we typically use '$P \leq 0.05$' as the standard for statistical significance, we also emphasize meaningful results (with the associated *P*-value) when $0.05 < P \leq 0.10$. Third, measurement protocols differed among sites, and in some cases, even among years for a particular site. Again, these differences among protocols potentially confound statistical comparisons of data. To the extent possible, we used results that yielded the most comparable measures of vegetation responses. For example, measurement protocols to determine above-ground production in forests (i.e. allometric measurements of tree size) differ from those in grasslands (i.e. destructive harvests at set time intervals), but both protocols result in comparable measures of above-ground production in units of g m^{-2} yr^{-1}. Fourth is that the actual $[CO_2]$ treatment varies among sites, as discussed above. Finally, our goal in this review was to examine broad patterns of plant and ecosystem $[CO_2]$ responses to elevated $[CO_2]$ across different resource levels characterized by different sites and not necessarily to characterize the response of a specific flora. Thus, many interesting and important results that pertain to an individual site are not discussed here – the literature cited throughout the text as well as listed in Table 1 provide detailed information on particular sites.

IV. Assimilation and leaf N content

The biochemical basis of leaf CO_2 assimilation responses to short-term increases in $[CO_2]$ is well-established (Farquhar *et al.*, 1980). $[CO_2]$ below 600 μmol mol^{-1} is typically insufficient to saturate carboxylation in photosynthesis (Fig. 3). Thus, short-term increases in CO_2 supply at $[CO_2]$ below 600 μmol mol^{-1} tend to increase leaf CO_2 assimilation (A_{net}) because carboxylation by Rubisco increases due to increased substrate availability and the suppression of competitive

Table 1 List of free-air CO_2 enrichment (FACE) sites whose data we analysed in this review, along with some site and operating characteristics, sources for data, and explanatory notes for the sites or data sets

Site name and abbreviation used in text	Vegetation type	Country: latitude, longitude	FACE design[1]	Target $[CO_2]$[2]	Source for data[3]	Notes
Bog Ecosystem Research Initiative (BERI)	Bog	Finland[4], Sweden, Netherlands, Switzerland	Pure CO_2	560 (24 h; season)	*Production*: for specific species – Heijmans *et al*. (2001) Table 2; for ecosystem – Hoosbeek *et al*. (2001) Tables 3 and 4	*Production*: Results are after 3 yr of elevated $[CO_2]$
Oak Ridge National Laboratory: Sweetgum plantation (ORNL)	Forest (deciduous)	USA: 35°54′ N, 84°20′ W	BNL	565 (24 h, season)	*Assimilation*: Gunderson *et al*. (2002) Table 1, Figs 2 and 3 *Precipitation*: NCDC Oak Ridge ATDD (406750) *Production*: Belote *et al*. (2003) Table 1; Norby *et al*. (2002) Table 1; R. J. Norby (unpublished).	*Production*: Results are for sweetgum (*Liquidambar styraciflua*) only; understory < 6% NPP
Forest atmosphere carbon transfer and storage I: Loblolly pine (FACTS I)	Forest (conifer)	USA: 35°59′ N, 79°6′ W	BNL	Ambient + 200 (24 h, 365 d)	*Assimilation*: Herrick & Thomas (2001) Fig. 2; Rogers & Ellsworth (2002) Fig. 2 *Precipitation*: Schäfer *et al*. (2002) Table 5; NCDC Chapel Hill 2 W (311677) *Production*: Full experiment – DeLucia *et al*. (1999) Table 2; Finzi *et al*. (2002) Table 1; D. Moore & E. H. DeLucia (unpublished); Matamala & Schlesinger (2001) Table 1; Pritchard *et al*. (2001) Table 3. Prototype – Oren *et al*. (2001) Fig. 1	Results from both the unreplicated prototype ring and full experiment are used. Prototype APP is woody biomass only. Prototype Target $[CO_2]$ = 550 (d, season)
Poplar plantation (PopFACE)	Forest (deciduous)	Italy: 42°22′ N, 11°48′ E	Pure CO_2	550 (d, season)	*Assimilation*: Bernacchi *et al*. (2003) *Production*: Gielen *et al*. (2001) Fig. 7	Plots were irrigated; thus precipitation data were not relevant *Production*: Used LAI as index for APP, averaged over three poplar varieties
Forest atmosphere carbon transfer and storage II: Aspen plantation (FACTS II)	Forest (deciduous)	USA: 45°36′ N, 89°42′ W	BNL	Ambient + 200 (d, season)	*Assimilation*: Takeuchi *et al*. (2001) Table 3 *Precipitation*: NCDC Rhinelander (477113) *Production*: Isebrands *et al*. (2001) Table 4; King *et al*. (2001) Fig. 1; Percy *et al*. (2002) Fig. 1; D. F. Karnosky & M. E. Kubiske (unpublished).	*Production*: Used yearly increment of wood volume as index of APP. Used live + dead root standing crop after 2 yr elevated $[CO_2]$ as index of BPP

Swiss alpine treeline (SAT)	Forest (conifer)	Switzerland: 46°45′ N, 9°45′ E	Pure CO_2	550 (d, season)	*Precipitation*: Hättenschwiler *et al*. (2002) Table 1 *Production*: Hättenschwiler *et al*. (2002) Fig. 6	*Production*: Used shoot length, averaged over lead and lateral shoots and over two species, as index of APP
Swiss Eschikon grassland (ETH-Z)	Grassland (perennial)	Switzerland: 47°27′ N, 8°41′ E	BNL	600 (d, season)	*Assimilation*: Ainsworth *et al*. (2003) Fig. 5 *Precipitation*: Hebeisen *et al*. (1997) Table 1; Daepp *et al*. (2000) Table 1; WMO Zurich (646066600) *Production*: Managed grassland experiment – Hebeisen *et al*. (1997) Figs 1, 3 and 4; Daepp *et al*. (2000) Fig. 1. Diversity experiment – Lüscher *et al*. (1998) Table 3	Results from both experiments (managed grassland and functional type) are used. *Production*: Excluded partial fumigation year (1993). Managed grassland experiment – averaged over different cutting treatments; averaged monoculture and mixture results if both available; only the low N treatment was used unless otherwise noted
Swiss calcareous grassland (SCG)	Grassland (perennial)	Switzerland: 47°33′ N, 7°34′ E	Screen Aided CO_2 Control	600 (24 h, season)	*Precipitation*: Niklaus *et al*. (2001) Table 1 *Production*: Managed grassland experiment – Leadley *et al*. (1999) Figs 2 and 3. Diversity experiment – Niklaus *et al*. (2001) Figs 1 and 3	Results from both experiments (managed grassland and biodiversity) are used
Irish seminatural grassland (MR-Irish)	Grassland (perennial)	Ireland: 52°48′ N, 6°54′ W	Pure CO_2	600 (d, season)	*Production*: Bryne & Jones (2002) Table 5 *Assimilation*: von Caemmerer *et al*. (2001) Fig. 5 *Precipitation*: P. C. D. Newton (unpublished) *Production*: Morgan *et al*. (2004b) Fig. 2; P. C. D. Newton (unpublished)	
Grazed pasture grassland (NZGraze)	Grassland (perennial)	New Zealand: 40°14′ S, 175°16′ E	BNL	475 (d, 365 d)		
Biodiversity, CO_2, and Nitrogen experiment (BioCON)	Grassland (perennial)	USA: 45°24′ N, 93°12′ W	BNL	550 (d, season)	*Assimilation*: Lee *et al*. (2001) Table 1; Lee *et al*. (2003) Fig. 2 *Precipitation*: NCDC Cedar (211390) *Production*: Reich *et al*. (2001a) Fig. 2; Reich *et al*. (2001b) Table 1; D. S. Ellsworth (unpublished)	Multi-factor experiment *Production*: Results averaged over 2 yr and diversity levels except for functional type results, which were for the low N treatment only

Table 1 *continued*

Site name and abbreviation used in text	Vegetation type	Country: latitude, longitude	FACE design[1]	Target [CO_2][2]	Source for data[3]	Notes
Jasper Ridge Global Change Experiment (JRGCE)	Grassland (annual)	USA: 37°24′ N, 122°14′ W	Pure CO_2	700 (24 h, season)	*Precipitation*: J. S. Dukes (unpublished) *Production*: J. S. Dukes (unpublished); Shaw *et al*. (2002) Table 1; Zavaleta (2001) Chapter 5, Fig. 13	Multi-factor experiment *Production*: Results from only all-ambient and all-ambient except CO_2 treatments are used except for comparisons of functional types, which averaged over both water and N treatments
Nevada Desert FACE Facility (NDFF)	Desert	USA: 36°39′ N, 115°55′ W	BNL	550 (24 h, 365 d)	*Assimilation*: Hamerlynck *et al*. (2000) Table 1, Fig. 1; Housman (2002); Naumburg *et al*. (2003) Fig. 1 *Precipitation*: http://www.unlv.edu/Climate_Change_Research/Data_Bases/data_index.htm *Production*: Housman (2002); DeFalco (2003); D. L. Phillips (unpublished); Smith *et al*. (2000) Figs 1 and 2; S. F. Zitzer (unpublished)	*Production*: As an index of APP in a year, shoot production for three shrub and two perennial grass species was first weighted by plant cover. Then perennial shoot production was averaged with total production of the four dominant annual species using a 2 : 1 weighting to estimate total above-ground production. Root length density used as index of BPP

[1]Citations for different designs are: For Brookhaven National Laboratory (BNL) design, see Lewin *et al*. (1994) and Hendrey *et al*. (1999); for pure CO_2 injection design, see Miglietta *et al*. (2001a, 2001b) and Pepin & Körner (2002); for Screen Aided CO_2 Control design, see Leadley *et al*. (1997). [2]Atmospheric CO_2 concentration (μmol mol^{-1}) that site strived to maintain and the time period (daylight hours only or full 24-h day, during growing season only or 365 d yr^{-1}) that CO_2 control was maintained. [3]For precipitation data, station names and numbers from the US NOAA National Climate Data Center (NCDC) and UN World Meteorological Observatory (WMO) networks are given where off-site climate data was used. [4]Latitudes and longitudes are: Finland 62°47′° N, 30°56′° E; Sweden 57°8′° N, 14°30′° E; Netherlands 51°59′° N, 5°42′° E; Switzerland 47°13′° N, 7°3′° E.

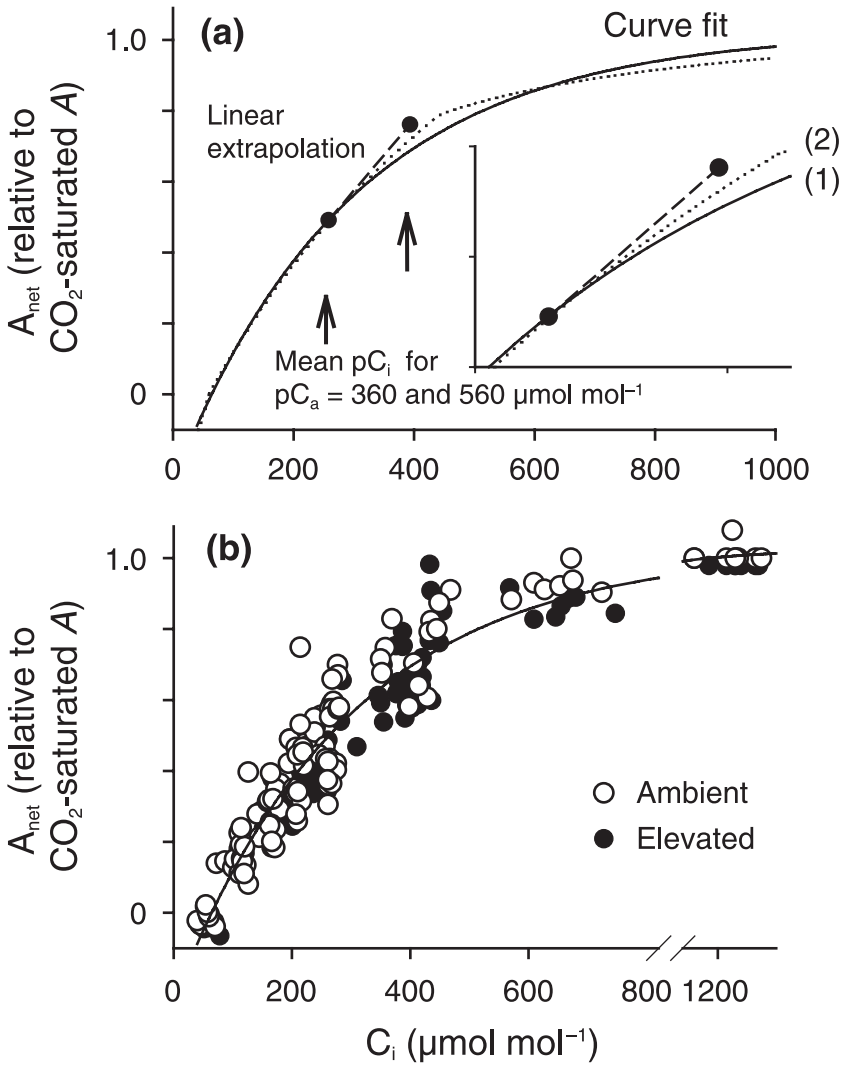

Fig. 3 Relationship between relative leaf CO_2 assimilation (A_{net}) and [CO_2] in the intercellular air spaces (C_i) composited across five woody species at three different free-air CO_2 enrichment (FACE) sites, using data from D. S. Ellsworth *et al*. (unpublished). A_{net} at all CO_2 levels is expressed relative to the CO_2 and light-saturated assimilation rate. (a) The overall relationship and linear extrapolation using C_i/C_a = 0.70 with two different model fits: (1) a hyperbolic fit and (2) fit from the Farquhar *et al*. (1980) model. The inset shows the two model fits in more detail. (b) Nonrectangular hyperbola function fit to all the data across species using measurements at 28°C for these curves. This temperature is used as it is close to the summertime mid-day temperature for FACE sites in North America.

oxygenation. However, a number of questions remain concerning the longer-term responses of A_{net} to increased [CO_2]: (1) what is the magnitude of the A_{net} response for field-grown plants; (2) is downregulation of photosynthetic metabolism significant; and (3) is the long-term A_{net} response sustained under plant resource limitations? In this section, we present some recent progress towards understanding the variability in CO_2 enhancement responses from studies of different plant species in FACE experiments.

The Farquhar *et al.* (1980) photosynthesis model provides a reference point to evaluate the response of A_{net} to elevated [CO_2]. Assuming that carboxylation rate is strictly CO_2-limited, one might expect that enhancements in A_{net} would be linearly proportional to the experimental enhancement in [CO_2] (i.e. the linear extrapolation in Fig. 3a). However, the observed short-term response of A_{net} to intercellular air space [CO_2] (C_i) (commonly called the A_{net}–C_i response curve) is curvilinear, which indicates that strict CO_2-substrate limitation may not extend much higher in C_i than that commonly corresponding with atmospheric [CO_2] (C_a). The two major components of the photosynthetic dark reactions in the Farquhar photosynthesis model (Farquhar *et al.*, 1980), carboxylation capacity under Rubisco-limited conditions ($V_{c\text{-}max}$ prescribed by the Farquhar model) and RuBP regeneration resulting from electron transport (J_{max}), are assumed to virtually always scale with one another, including leaves grown under elevated CO_2 (Leuning, 1997; Medlyn *et al.*, 1999). Therefore, the family of A_{net}–C_i response curves in all C_3 species should collapse to a single characteristic curve if normalized by leaf N-content or light- and CO_2-saturated maximum assimilation (A_{sat}) (Fig. 3b; Ollinger *et al.*, 2002; D. S. Ellsworth *et al.*, unpublished). We used two different curvature assumptions for the A_{net}–C_i curve depicted in Fig. 3a: (1) an empirical rectangular hyperbola function (Hanson *et al.*, 1987; Ellsworth *et al.*, 1995) fit to data for multiple tree species in FACE experiments at 28°C; and (2) the theoretical model of Farquhar *et al.* (1980) fitted to data via the $V_{c\text{-}max}$ and J_{max} parameters, also at 28°C. In both cases, for an enhancement in atmospheric [CO_2]

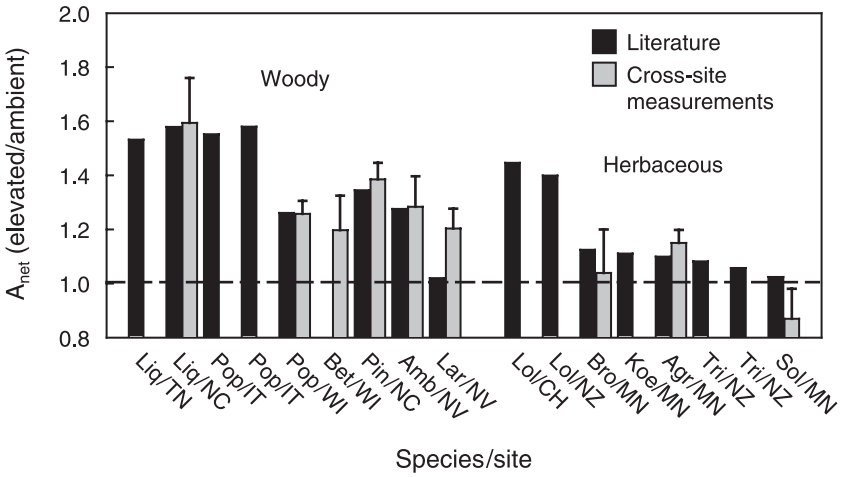

Fig. 4 Enhancement of CO_2 assimilation (A_{net}) for individual species from eight free-air CO_2 enrichment (FACE) sites in response to a 50–55% increase in growth [CO_2]. Cross-site measurements by D. S. Ellsworth *et al*. (unpublished) are grey bars, and measurements collected by specific site studies in the literature (see Table 1) are closed bars. Woody species are grouped on the left; herbaceous species on the right. Potential enhancements in A_{net} are shown as a ratio of A_{net} at elevated [CO_2] divided by A_{net} at ambient [CO_2], with the dashed line indicating no increase in A_{net} at elevated [CO_2] as a reference point. Abbreviations for species: Liq, *Liquidambar*; Pin, *Pinus*; Pop, *Populus*; Bet, *Betula*; Amb, *Ambrosia*; Lar, *Larrea*; Lol, *Lolium*; Bro, *Bromus*; Koe, *Koeleria*; Agr, *Agropyron*; Tri, *Trifolium*; Sol, *Solidago*. Abbreviations for sites: TN, ORNL; NC, FACTS I; IT, PopFACE; WI, FACTS II; NV, NDFF; CH, ETH-Z; MN, BioCON; NZ, NZGraze.

from 365 to 565 μmol mol^{-1}, which is typical for many FACE sites, and assuming a $C_i : C_a$ ratio of 0.70, the response ratio E/A for A_{net} is either (69% of A_{sat})/(49% of A_{sat}) = 1.41 as predicted by (1), or (73% of A_{sat})/(49% of A_{sat}) = 1.49 as predicted by (2) (Fig. 3, inset). D. S. Ellsworth *et al*. (unpublished) observed a mean instantaneous response of 1.51 for photosynthesis in leaves with an instantaneous step change from 360 to 560 μmol mol^{-1}. Thus, theory and empirical measurements delineate the expected short-term enhancement of photosynthesis by elevated [CO_2] as a basis against which the possibility of longer-term changes in photosynthetic enhancement can be evaluated.

A compilation of results for elevated [CO_2] effects on A_{net} for 15 species from eight FACE sites indicates fairly substantial increases in A_{net} in response to a 50–55% increase in [CO_2], particularly for woody plants (Fig. 4). Reviews of earlier studies under controlled-environment and OTC conditions, including several meta-analyses, also indicate enhancement of A_{net} at elevated [CO_2] in herbaceous species and many woody plants (Drake & Leadley, 1991; Curtis, 1996; Medlyn *et al*., 1999, 2001). Mean stimulation in A_{net} at the species level across all FACE literature studies was 26 ± 5% (range 0–60%; Fig. 4). It is important to bear in mind that this enhancement was typically measured under favorable environmental conditions during the growing season, and that diurnal and seasonal integrated enhancements in A_{net} (Ainsworth *et al*., 2003; Naumburg *et al*., 2003) may be different from those for physiological optimum conditions. Nonetheless, stimulation of A_{net} (based on species means, not averaged over the entire leaf area of the community) was variable in FACE experiments, ranging from essentially no stimulation in Minnesota prairie species (Lee *et al*., 2001) to more substantial increases for pine and sweetgum and large (45–60%) increases for *Populus* species on rich, irrigated soils (Fig. 4). Species in a Mojave Desert scrub (Naumburg *et al*., 2003) and Wisconsin hardwood plantation (Noormets *et al*., 2001) had intermediate stimulation values of 22% and 38%, respectively.

The A_{net} enhancement measured under naturally occurring conditions at FACE sites is smaller than that for controlled-environment and OTC studies (e.g. 53% in Saxe *et al*., 1998, 51% in Medlyn *et al*., 1999). However, [CO_2] targets that are commonly used in FACE studies also differ from those in OTC studies. A coarse adjustment of the data presented in Medlyn *et al*. (1999) from model parameters suggests that a +22% response in A_{net} would be anticipated for about +55% elevated [CO_2], which in turn indicates similarities in adjustments of the physiological responses of OTC and FACE plants (i.e. 22 and 26%, respectively) to long-term compared with short-term elevated [CO_2] when considered to the same [CO_2] target level. Note that these modeled A_{net} responses to elevated [CO_2] are instructive for simple, coarse comparisons among different types of studies, but they cannot be used to indicate actual responses because the actual [CO_2] attained is less than the target [CO_2], as discussed above.

Because different sites may collect gas exchange data in slightly different ways, D. S. Ellsworth *et al*. (unpublished) collected A_{net} data across five woody taxa from three FACE sites in a standardized manner. When their data were compared with gas exchange measurements made by site investigators, A_{net} had a mean stimulation of 22 ± 7%, which is similar to the average stimulation from previous literature measurements. In such a comparison, considerations such as measurements at different times of year and that stomatal conductance in particular is highly seasonally variable (Ellsworth, 2000; Nowak

et al., 2001) might explain some of the discrepancies between data sets. However, both sets of studies identified those species that were moderately and highly responsive to elevated [CO_2], such as *Liquidambar*.

For a number of studies, the relative increase in A_{net} for leaves grown under ambient [CO_2] v. leaves grown under elevated [CO_2] was less than the instantaneous response to changes from 360 to 560 μmol mol^{-1} [CO_2] for leaves grown under ambient [CO_2]. The fact that the per cent increase in A_{net} was less than the expected per cent increase based on the Farquhar photosynthesis model suggests that biochemical adjustments in photosynthetic capacity (frequently termed 'down-regulation'; Sage, 1994) are important in governing plant production responses to elevated CO_2. Such a reduction occurs as a result of changes in the operating C_i for gas exchange or down-regulation. Most evidence points to the latter phenomenon rather than the former (Medlyn *et al.*, 2001; von Caemmerer *et al.*, 2001). In fact, Huxman *et al.* (1998), von Caemmerer *et al.* (2001), Rogers & Ellsworth (2002), Ainsworth *et al.* (2003) and Bernacchi *et al.* (2003) all presented statistical evidence of downregulation in selected species in FACE experiments. However, in the majority of these studies, downregulation was observed under particular conditions such as low nutrient conditions (von Caemmerer *et al.*, 2001; Ainsworth *et al.*, 2003), in wet years when N and water are available but not in dry years (Huxman *et al.*, 1998; Naumburg *et al.*, 2003), and in older but not young leaves for evergreen species (Griffin *et al.*, 2000; Rogers & Ellsworth, 2002). By contrast, data for *Liquidambar* (Herrick & Thomas, 2001; Gunderson *et al.*, 2002), for *Populus tremuloides* (Takeuchi *et al.*, 2001) and for two *Populus* species (Bernacchi *et al.*, 2003) do not support an interpretation of photosynthetic downregulation in these species (Table 2). Therefore, the photosynthetic downregulation response appears to be both growth-form and environment specific. Nonetheless, even in experiments where downregulation is observed, A_{net} under elevated [CO_2] is still stimulated in long-term experiments (Medlyn *et al.*, 1999), even after 7–10 yr of treatment (Ainsworth *et al.*, 2003; Crous & Ellsworth, 2004).

The maintenance of leaf enzyme content is critical to the sustainability of photosynthetic responses to elevated [CO_2], and reductions in leaf N-content (Yin, 2002) or the rate of carboxylation per unit N are implicated when photosynthetic downregulation occurs (Medlyn *et al.*, 1999). We used the familiar relationship between A_{net} and leaf N (Reich *et al.*, 1998; Peterson *et al.*, 1999) to provide a framework for understanding the enhancement of A_{net} as a function of changes in leaf N-content, where leaf N-content serves as a proxy for photosynthetic protein content. Overall reductions in leaf N under elevated [CO_2] would tend to reduce A_{net}, and reallocation of leaf N from photosynthetic to nonphotosynthetic leaf constituents would tend to reduce A_{net} and the ratio of A_{net} : N in particular (Peterson *et al.*, 1999). However, the former would indicate a simple dilution

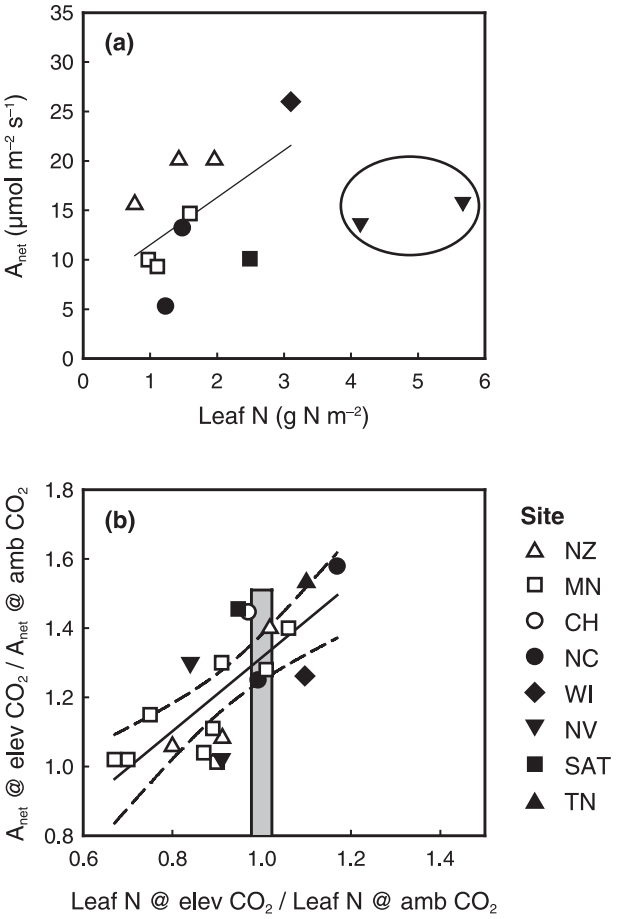

Fig. 5 (a) Relationship between A_{net} and leaf N content for plant species growing under ambient [CO_2] at different free-air CO_2 enrichment (FACE) sites. Each point is a different species, and different symbol shapes are the different FACE sites shown in (b). Solid line is a simple linear regression for data except for the two inverted triangles enclosed by the oval; these represent two species that do not fit the overall relationship. Open symbols are herbaceous species and closed symbols are woody species. (b) Enhancement ratio of A_{net} at elevated [CO_2] as a function of changes in leaf N content (leaf N content at elevated [CO_2] divided by leaf N content at ambient [CO_2]) for species from six FACE sites. Solid line is a simple linear regression for data. Each point is a different species, and different symbol shapes are the different FACE sites. Open symbols are herbaceous species and closed symbols are woody species. FACE sites: open triangle, NZGraze; open square, BioCON; open circles, ETH-Z; closed circles, FACTS I; closed diamond, FACTS II; closed downward-pointing triangle, NDFF; closed square, SAT; closed upward-pointing triangle, ORNL.

effect that might be a result of accumulation of simple carbohydrates in leaves under elevated [CO_2], whereas the latter would indicate biochemical adjustments in leaves, as might occur owing to specific, hypothesized molecular mechanisms (Stitt & Krapp, 1999; Rogers & Ellsworth, 2002; Luomala *et al.*, 2003). A strong overall relationship between A_{net} at current [CO_2] and leaf N-content occurred across four FACE sites (Fig. 5a; $P = 0.001$; $R^2 = 0.532$). However, the desert shrub species were outliers to this relationship because of N

Table 2 Summary of the most-recent published growing season results for light-saturated leaf net CO_2 assimilation (A_{net}) rate of C_3 plant species in free-air CO_2 enrichment (FACE) experiments

FACE site	Species	Exposure duration (yr)	Sampling date[1]	Measurement temperature (°C)[2]	Mean (SE) ambient A_{net}[3]	E/A for A_{net}[4]	Response ratio N_{elev} : N_{amb}	Reference
NZGraze	*Trifolium subterraneum*	2	November 1999	20	20.1 (1.4)	1.08	0.912	von Caemmerer *et al*. (2001)
NZGraze	*Trifolium repens*	2	November 1999	20	20.1 (1.2)	1.06	0.8	von Caemmerer *et al*. (2001)
NZGraze	*Lolium perenne*	2	November 1999	20	15.6 (1.7)	1.40	1.018	von Caemmerer *et al*. (2001)
FACTS I	*Pinus taeda*	2.75	May 1999	28	5.3 (0.4)	1.25	0.99	Rogers & Ellsworth (2002)
FACTS I	*Liquidambar styraciflua*	3	September 1999	30 ± 0.5	13.2 (0.4)	1.58	1.17	Herrick & Thomas (2001)
BioCON	*Achillea millefolium*	1	August 1999	27.3	15.9 (0.7)	1.01	–	Lee *et al*. (2003)
BioCON	*Agropyron repens*	1	August 1999	27.3	9.0 (1.6)	1.03	1.14	Lee *et al*. (2003)
BioCON	*Bromus inermis*	1–2	July 1999	26.6	9.3 (1.9)	1.12	0.75	Lee *et al*. (2001)
BioCON	*Koeleria cristata*	1–2	July 1999	26.6	14.7 (1.6)	1.11	0.89	Lee *et al*. (2001)
FACTS II	*Populus tremuloides*	1.5	July 1999	Ambient ± 2	26	1.26	1.09	Takeuchi *et al*. (2001)
ORNL	*Liquidambar styraciflua*	2	July 2000	26 ± 2	12.4 (1.9)	1.53	1.1	Gunderson *et al*. (2002)
ETH-Z	*Lolium perenne*	9	May 2002	15 (air temp.)	16.8 (0.9)	1.45	–	Ainsworth *et al*. (2003)
NDFF	*Larrea tridentata*	4	April 2001	20	12.1 (1.1)	1.02	0.93	Naumburg *et al*. (2003)
NDFF	*Ambrosia dumosa*	4	April 2001	20	16.4 (4.2)	1.27	0.84	Naumburg *et al*. (2003)
SAT	*Larix decidua*	0.25	August 2001	21.1	10.1 (0.3)	1.46	0.95	Hättenschwiler *et al*. (2002)
PopFACE	*Populus alba*	3	July 2001	25–30	18.5 (2.5)	1.55	–	Bernacchi *et al*. (2003)
PopFACE	*Populus nigra*	3	July 2001	25–30	18.6 (2.7)	1.58	–	Bernacchi *et al*. (2003)
PopFACE	*Populus* × *euramericana*	3	July 2001	25–30	18.9 (1.4)	1.44	–	Bernacchi *et al*. (2003)

[1]A mid- to late growing season sampling date was selected in cases where multiple measurements were made across a season. [2]Measurement temperature is leaf temperature unless noted. [3]Means (SE) of A_{net} for plants grown at ambient [CO_2]. [4]The response of A_{net} to elevated [CO_2] treatment is defined as the ratio of leaf A_{net} in elevated [CO_2]-grown plants to A_{net} in ambient [CO_2]-grown plants.

stacking in thick leaves and lower photosynthetic nutrient-use efficiency. Of greater interest, however, is the relationship between the long-term [CO_2] responses of A_{net} and leaf N-content (both area-based) across six FACE sites (Fig. 5b; $P < 0.001$; $R^2 = 0.568$). Species that showed the greatest reductions in leaf N-content at elevated [CO_2] also tended to show reduced enhancement in A_{net} (Fig. 5b). This A_{net}–leaf N relationship would, of course, be expected, but it is indeed encouraging to see that data across multiple growth forms and sites support this expectation. Given that A_{net}–C_i curves in diverse species collapse to a single relative response function that predicts a common enhancement of A_{net} (Fig. 3) and that variation in A_{sat} represents a range of leaf N contents, the correlation of the A_{net} response to elevated CO_2 with the leaf N response (Fig. 5) strongly suggests that resource availability mediates leaf N content and how it is maintained in ecosystems at elevated CO_2, consistent with the original hypothesis of Strain & Bazzaz (1983).

Of additional importance is the clear dichotomy between herbaceous and woody species. Realizing that they are from different sites, most herbaceous species (except *Lolium*) show a reduction in leaf N content (mean reduction of 14%) and thus a modest mean enhancement in A_{net} of 12% at elevated [CO_2], whereas woody species show a stronger enhancement in A_{net} of 38% but virtually no mean change in leaf N content over all species (Fig. 5b). Herbaceous species may indeed be more functionally plastic to a change in [CO_2], as exemplified by a strong response in leaf N content, whereas woody species tend to exhibit a more conservative response.

V. Primary productivity

1. Datasets and statistical analyses

Measurements of production used in our datasets were from either destructive harvest of plant biomass or derived through allometric techniques; details on how data were collected and sources of the data are noted in the references in Table 1. We treated each measurement of above-ground, below-ground, or net (i.e. total above-ground plus below-ground) primary production for 1 yr at a site (abbreviated as APP, BPP and NPP, respectively) as an observation or replicate for our statistical analyses. Results from each of the two experiments at FACTS I and SCG were used as two independent studies. It is important to note that the [CO_2] effect was not always significant for each year at each site, which raises the issue of how one treats data when the [CO_2] effect is not significant. One approach is to set E/A equal to 1.0 when the [CO_2] effect is not significant. However, this approach ignores the problems of high, naturally occurring variation and low replication that are typical for field experiments, both of which lead to an inherently low statistical power. Furthermore, this approach masks the real variation that occurs in natural systems and precludes any analyses that try to tease out underlying causes of that variation, which is a goal of our review. Another approach is to use only those results that are significant. However, this approach yields a biased result that overestimates the true effect. A third approach, and the one that we use in this review, is to use all raw data without any alterations. The underlying assumption of this approach is that each data point is an estimate of the treatment effect. Although we have explicitly recognized limitations of the data sets (end of Section III above), each FACE experiment has been carefully designed to minimize potentially confounding effects. Thus, the raw data without any alterations represent the best available estimates of the [CO_2] effect.

To statistically analyse the production data, we used a general linear model that included both discrete and continuous variables. Because we were interested in potential differences among vegetation types, vegetation type was the discrete, indicator variable in the regression model. Because we anticipated that production may vary with annual precipitation and that production may decrease through time, annual precipitation and years of CO_2 treatment were included in the regression model as continuous, predictor variables. Finally, we anticipated that the effects of precipitation or years of CO_2 treatment on production might differ among the vegetation types, so the interactions between vegetation type and each predictor variable were included in the model. Data were analysed with the PROC GLM procedure in SAS V8.02 (SAS, 2001) using the REGDIAG macro (Fernandez, 2003a).

Statistical output includes a typical ANOVA table and typical regression statistics (Table 3a). The ANOVA table indicates which variables in the linear model are significant, and interpretation of the significant model variables depends on if the variable is an indicator or predictor variable. A significant 'vegetation type' variable indicates a significant difference among vegetation types after linear relationships with the two predictor variables, annual precipitation and years of CO_2 treatment, are accounted for. Significant predictor variables indicate that a significant linear relationship occurred between production and the predictor variable across all vegetation types. A significant interaction between vegetation type and one of the predictor variables indicates that the linear relationship between production and the predictor variable differed among vegetation types. In addition to these statistical assessments, the *P*-value from the *F*-test of the overall linear model and the R^2 for the overall model are also reported.

We also ran 'reduced model' statistical analyses when the main effect of a predictor variable was not significant (Table 3b,c). For example, the main effect for the predictor variable 'years of CO_2 treatment' was not significant in the full model analysis of APP (Table 3a). Thus, this term and its interaction with vegetation type were dropped from the linear model, and data reanalysed with a reduced model where precipitation was the only predictor variable (Table 3b).

During examination of the results, we observed that this linear model over all data did not accurately characterize the

Table 3 Results from statistical analyses of above-ground (APP), below-ground (BPP) and net (NPP) primary production data from ecosystem free-air CO_2 enrichment (FACE) experiments

	APP		BPP		NPP	
Variable	df	P	df	*P*	df	P
(a) Full model[1]						
Vegetation type	2	0.238	1	0.464	1	0.012
Precipitation	1	0.011	1	0.405	1	0.060
Year CO_2	1	0.366	1	0.258	1	0.347
Vegetation × precipitation	2	0.022	1	0.281	1	0.008
Vegetation × year CO_2	2	0.428	1	0.336	1	0.016
Error	44		14		19	
Regression model *P*	0.003		0.069		0.001	
Regression R^2	0.414		0.582		0.675	
(b) Reduced model: annual precipitation only						
Vegetation type	2	0.169	2	0.457	1	0.248
Precipitation	1	0.003	1	0.792	1	0.047
Vegetation × precipitation	2	0.003	2	0.693	1	0.073
Error	47		16		21	
Regression model *P*	< 0.001		0.114		0.002	
Regression R^2	0.391		0.438		0.546	
(c) Reduced model: year CO_2 only						
Vegetation type			2	0.710	1	0.972
Year CO_2			1	0.833	1	0.359
Vegetation × year CO_2			2	0.194	1	0.078
Error			16		21	
Regression model *P*			0.041		0.005	
Regression R^2			0.522		0.497	

[1]Data were analysed with the general linear model procedure in SAS V8.02 (SAS, 2001) using the REGDIAG macro (Fernandez, 2003a) with the full model of vegetation type as a discrete (i.e. indicator or classification) variable and both annual precipitation and years of CO_2 treatment as continuous (i.e. predictor) variables (a), or with reduced model of vegetation type and only one of the continuous, predictor variables (b and c). *F*-tests were based on Type III sums of squares.

subset of data for APP of the forest sites. The linear relationships between APP and annual precipitation appeared to vary among the different forest sites, and the site-specific relationships differed from that across all forest sites. Thus, we also conducted 'reduced data set' analyses where we analysed APP data from only the forest sites in a separate general linear model (Table 4a). This statistical model was similar to that above except that FACE site was used as the discrete, indicator variable rather than vegetation type. As with the complete data set analyses, we also ran reduced model analyses that dropped nonsignificant variables from the linear model (Table 4b). For completeness, we also analysed APP data from only the grassland sites in a similar manner, but neither the site factor nor the site interaction terms were significant (results not shown).

Skewness, kurtosis, heteroscedasticity and normality of the data sets were examined for each statistical analysis. For all analyses except one, none of these ANOVA criteria were significant ($P \leq 0.05$). The only data set that failed these criteria was the NPP data. In 1994, NPP for the natural experiment at the SCG site was much lower than any other reported values, and this data point was highly influential on the statistical analyses (as measured by its DFFITS statistic of −3.55) and appeared to be an outlier (as measured by its studentized residual of −3.78). We first tried several transformations of the data (ln, squared, etc.) to normalize the data set, but no transformation resulted in the data set passing the criteria. However, once this data point was removed from the NPP data set, skewness, kurtosis, heteroscedasticity and normality were no longer significant. Thus, we assumed that this data point was an outlier, and the statistical results given in this review exclude this data point. For completeness, we have shown the data point as an 'x' in Figs 6, 7, and 10.

2. Comparisons of ecosystems

As measured by either direct harvest or allometry-based techniques (Table 1), APP was almost always greater under elevated [CO_2] than under ambient [CO_2] (Fig. 6, top graph). Averaged over all 56 observations among 18 experiments at 16 FACE sites, APP under elevated [CO_2] was *c.* 19% greater than that under ambient [CO_2]. The greatest single-year increase in APP occurred in a desert ecosystem (E/A = 1.82, or 82% increase averaged over three shrub, two perennial grass, and

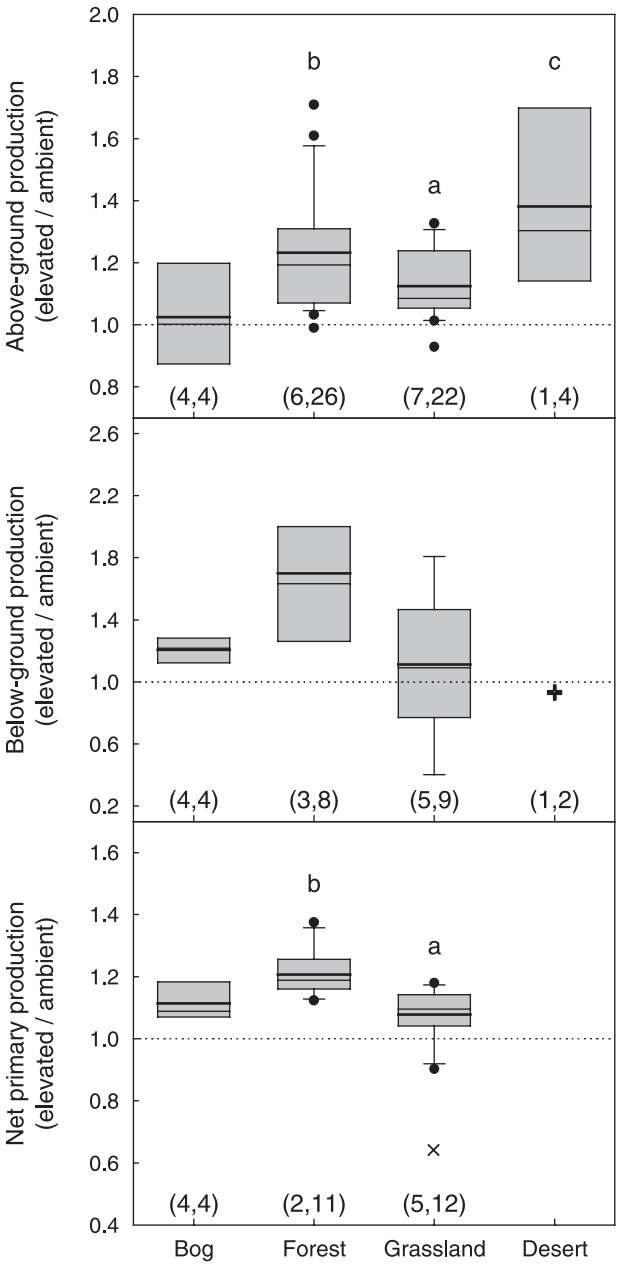

Fig. 6 Box plots of annual primary production, expressed as an enhancement ratio of production under elevated [CO_2] to that under ambient [CO_2], from 18 experiments at 16 free-air CO_2 enrichment (FACE) sites grouped by vegetation type. The thick line is the mean of the observed values, the thin line is the median value, the upper and lower lines of the box are the 75th and 25th percentiles, the upper and lower whisker lines are the 90th and 10th percentiles, and circles are potential outliers. Sample sizes are given in parentheses above the lower *x*-axis of each graph; the first number is the number of experiments with measurements and the second number is the total number of observations (an observation is 1 yr of production from an experiment, except for BioCON, where an average over 2 yr was the only result available). The '+' in below-ground primary production (BPP) of deserts indicates the actual observations (insufficient data were available to create a box plot), and '×' in net primary production (NPP) of grasslands indicates a statistical outlier. Preplanned, least-squared comparisons among the forest, grassland, and desert vegetation types were made based on the general linear model analysis in Table 3; note that the bog vegetation type could not be compared statistically with other vegetation types using this model because bogs did not have comparable precipitation data. Mean comparison within each graph are shown by the lower-case letters above each box; vegetation types within a graph with different letters were significantly different ($P < 0.05$). Note differences in ranges and scales for the *y*-axes among the production measurements. Dotted line across each graph shows ratio of response under elevated [CO_2] to that under ambient [CO_2] (E/A) = 1.0 for reference. Sources for data are given in Table 1.

four annual species; Smith *et al.*, 2000; Housman, 2002), followed by a forest plantation (E/A = 1.71 for leaf area index of poplar seedlings during their first year of growth; Gielen *et al.*, 2001). Pre-planned comparisons of ecosystems showed significant differences among desert, grassland, and forest ecosystems. On average, and when corrected for precipitation effects, increases in APP with elevated [CO_2] were significantly greater in desert than in forest and grassland ecosystems ($P < 0.001$ for both comparisons) and greater in forest than in grassland ecosystems ($P = 0.055$), but the variation in E/A was also high for all ecosystems. Note that least-squared comparisons could not be made between the bog FACE sites and other ecosystems based on the general linear model (Table 3) because precipitation data for the bog ecosystems were not comparable to that of the other ecosystems. Using a simple one-way ANOVA of the data set and least significant difference comparison of means, mean APP of bogs was significantly less than that of deserts and forests ($P < 0.05$), but not different from that of grasslands (results not shown).

Not all sites measured BPP (Fig. 6, middle graph), and for those sites that did, the data have not been published for all years at all sites. It is very difficult to quantify BPP accurately (Böhm, 1979), and different techniques were used to estimate it among sites. Thus, the larger variation in E/A for BPP than for APP may be partly related to these measurement difficulties and differences. Forests generally had greater increases in BPP under elevated [CO_2] than the other ecosystems (average E/A of 1.70 for forests vs 1.21, 1.11 and 0.93 for bog, grassland, and desert, respectively), but vegetation type was not significant in any of our statistical analyses (Table 3). The greatest increase in BPP (174%) was for a *Liquidambar* forest at the ORNL site during the fifth year of elevated [CO_2] treatment (R. J. Norby, unpublished), whereas the greatest decrease in BPP (60%) was noted in an infertile, calcareous grassland during the first full year of treatment (Leadley *et al.*, 1999). The magnitude of this decrease may be inflated by random error, as subsequent years of results for the same site showed small (4–9%) increases in BPP at elevated [CO_2]. Nonetheless, decreased BPP was observed in another experiment at the same site (Niklaus *et al.*, 2001) as well as in an annual grassland (Shaw *et al.*, 2002).

Most ecosystems have greater NPP under elevated [CO_2] (Fig. 6, bottom graph). Averaged over all 27 observations among 11 FACE sites that reported NPP, NPP was increased

by almost 12% under elevated [CO_2]. Vegetation type was significant in the statistical analysis of NPP (Table 3a), and forests had a significantly greater increase in NPP with elevated [CO_2] than did grasslands ($P < 0.05$). As with APP, bog ecosystems could not be compared with the other ecosystems using the general linear model. Using a simple one-way ANOVA of the data set and least significant difference comparison of means, mean E/A for NPP of bogs was significantly less than that of forests, but not different from that of grasslands. The maximum reported increase in NPP in any one year was approx. 38% in a forest ecosystem (R. J. Norby, unpublished). Decreased NPP under elevated [CO_2] only occurred in grasslands, with three different experiments reporting E/A < 1.0 in one year each. The minimum E/A was 0.64 (i.e. a decrease in NPP by 36%) (Leadley *et al.*, 1999), and as discussed above, this point appeared to be a statistical outlier.

These results for the four different ecosystem types provide limited support for the early prediction that the response of productivity to elevated [CO_2] would be greater in drier ecosystems (Strain & Bazzaz, 1983). The APP enhancement in elevated [CO_2] was lowest in bogs and greatest in deserts, with forest and grasslands intermediate, which is consistent with the predictions of Strain & Bazzaz (1983). However, APP is only part of the carbon assimilated by plants, and results for NPP are contrary to the Strain & Bazzaz (1983) predictions. Although the results for BPP were not significantly different among ecosystems, E/A for BPP tended to decrease from mesic forest to xeric desert ecosystems. Phillips *et al.* (2002) speculated that higher water-use efficiency associated with elevated [CO_2] and decreased stomatal conductance may allow sufficient water uptake with slightly smaller amounts of fine roots for plants growing under elevated [CO_2] in deserts. Thus, plants in more water-limited environments may not need to invest as much carbon in their root systems to maintain water uptake and hence growth and productivity.

Interestingly, these overall increases in above-ground production for ecosystem FACE experiments are similar to those observed in crop FACE experiments (Kimball *et al.*, 2002). Excluding the results from the ETH-Z FACE site from Kimball *et al.*'s (2002) data set (ETH-Z results are also included in our data sets), crops with an ample supply of both water and N had an overall mean E/A for APP of 1.16, which is similar to the 1.19 value for all ecosystem studies. The elevated [CO_2] effect on BPP for crops was substantially higher than that observed in ecosystems (average E/A for root biomass accumulation of grains and cotton and for potato tuber yield was 1.45, whereas BPP enhancement averaged over all available ecosystem data was 1.32).

3. Influence of water on enhancing production

A more rigorous test of the prediction that the relative effect of elevated [CO_2] on growth increases as water availability decreases is to determine if [CO_2]-induced changes in primary production is related to annual precipitation. Results from our general linear model analyses show that both APP and NPP are significantly correlated with annual precipitation, but these relationships differ among vegetation types (Table 3, Fig. 7). For forest ecosystems, the E/A for APP increases with increasing annual precipitation, but the relationship differs among FACE sites (Table 4; Fig. 7, top left panel). The E/A for APP also increases with increased precipitation for deserts, but it decreases for grasslands. The decreasing relationship for grasslands is consistent across all sites, with one regression fitting the data for all grassland sites. For NPP, E/A increases with increasing precipitation for both forests and grasslands (Table 3), but the slope of the relationship in forests is greater than that in grasslands. For all FACE sites, E/A for BPP is not significantly related to annual precipitation (Table 3). Thus, the only data set from ecosystem FACE experiments that is consistent with the prediction that the [CO_2] enhancement of productivity will be greater in dry years is APP of grasslands; all other data sets either show the opposing trend or are not significantly related to precipitation. Interestingly, crops also show increased above-ground production under low water (but ample N) growth conditions, with E/A increasing from 1.16 for ample water conditions to 1.20 for low water conditions (Kimball *et al.*, 2002).

Table 4 Results from statistical analyses of above-ground production (APP) data for the reduced data set of only forest free-air CO_2 enrichment (FACE) sites

	APP	
Variable	df	*P*
(a) Full model[1]		
Site	3	0.418
Precipitation	1	0.042
Year CO_2	1	0.712
Site × precipitation	3	0.702
Site × year CO_2	3	0.024
Error	11	
Regression model *P*	< 0.001	
Regression R^2	0.903	
(b) Reduced Model: Annual precipitation only		
Site	3	0.178
Precipitation	1	0.002
Site × precipitation	3	0.039
Error	15	
Regression model *P*	0.004	
Regression R^2	0.704	

[1]Data were analysed with SAS V8.02 (SAS, 2001) using the REGDIAG macro (Fernandez, 2003a) with Site as an indicator (i.e. classification) variable and both annual precipitation and years of CO_2 treatment as predictor (i.e. continuous) variables in a general linear model (a) or for the reduced model that only had precipitation as the predictor variable (b). *F*-tests were based on Type III sums of squares.

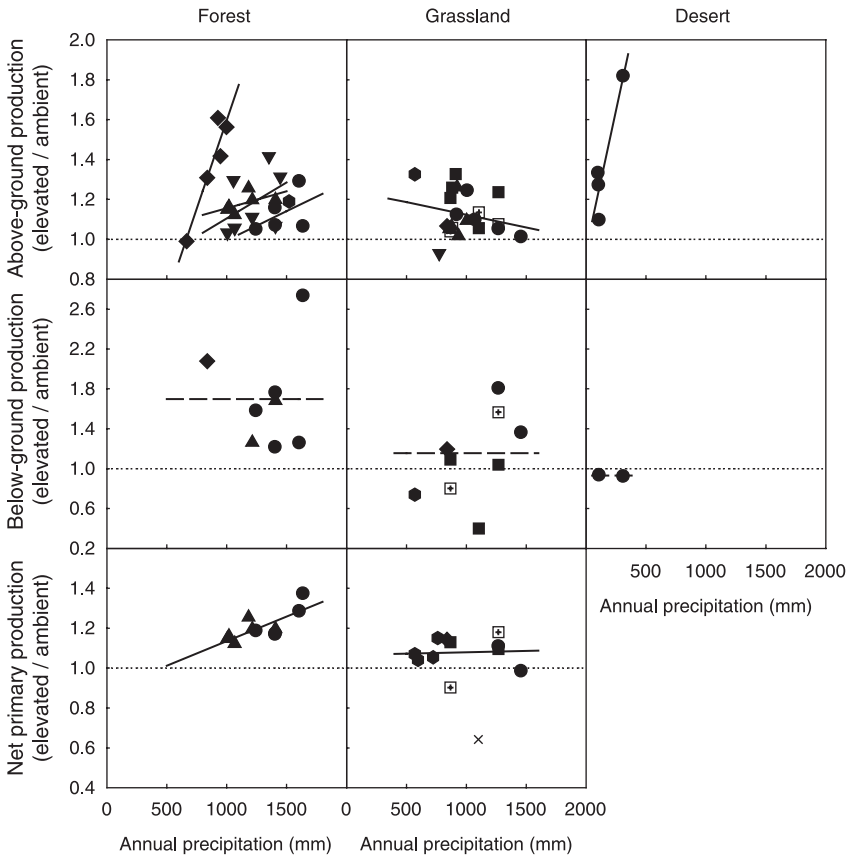

Fig. 7 Relationship between enhancement ratio of primary production and annual precipitation for forest (left three graphs), grassland (central three graphs), and desert (right two graphs) free-air CO_2 enrichment (FACE) sites. Top three graphs are above-ground, middle three are below-ground, and bottom two are net primary production; note differences in range and scaling for the *y*-axis among the production measurements. Each symbol represents the ratio of response under elevated [CO_2] to that under ambient [CO_2] (E/A) of production for 1 yr along with the corresponding precipitation for that year. Within each vegetation type, different symbol shapes represent different FACE experiments; the '×' in the net primary production (NPP) of grasslands graph is a statistical outlier that was excluded from the statistical analyses (see text). Solid lines represent significant linear relationships between production and precipitation for all data within a graph, except for the upper left (above-ground primary production (APP) of forest) graph; for this graph, individual lines are regressions for four forest FACE experiments with > 3 yr of measurements (significant site × precipitation term in the statistical analysis of the above-ground production data for the forest vegetation type; see Table 4b). The *P* and R^2 values for the linear regressions are shown in Tables 3 and 4. For data sets that did not have a significant linear relationship, the mean value of all observations is indicated by a dashed line. A dotted line across each graph shows E/A = 1.0 for reference. Sources for data are given in Table 1.

Results for APP data from grassland OTC experiments agree well with the ecosystem FACE data (Fig. 8, top graph). The solid lines in Fig. 8 are the same as those shown in the top panels of Fig. 7 and are color coded for the different vegetation types. The open green symbols are data from a short-grass (squares, Morgan *et al.*, 2003) and a tall-grass prairie (hexagons; Owensby *et al.*, 1999), and except for the driest year of OTC data, the regression line between APP E/A and annual precipitation for the OTC data is not significantly different from that for the grassland FACE data. Interestingly, the driest year of OTC data falls within the 95% confidence intervals around the regression line for the desert FACE site.

Comparisons between OTC and FACE results for forests are more difficult to make because the relationship between E/A for APP and precipitation is site-specific for the FACE sites. When annual precipitation is near 1500 mm, OTC data fall well above the regression lines for the FACE data. However, these OTC data are for rapidly growing seedlings, whereas the FACE data are for older trees nearing or past canopy closure. In addition, the FACE site with the steepest slope consists of rapidly growing seedlings (FACTS II). Thus, the greater E/A from the OTC experiments may simply be related to differences in tree age and their accompanying developmental stage (Norby *et al.*, 1999).

Taken together, these results do not provide strong support for predictions that the response of productivity to elevated [CO_2] would be greater in drier ecosystems or in dry years within an ecosystem. The difference in the APP-annual precipitation relationship between grassland and desert ecosystems is especially surprising because one would expect that these primarily water-limited ecosystems would have similar responses to elevated [CO_2]. Despite this apparent

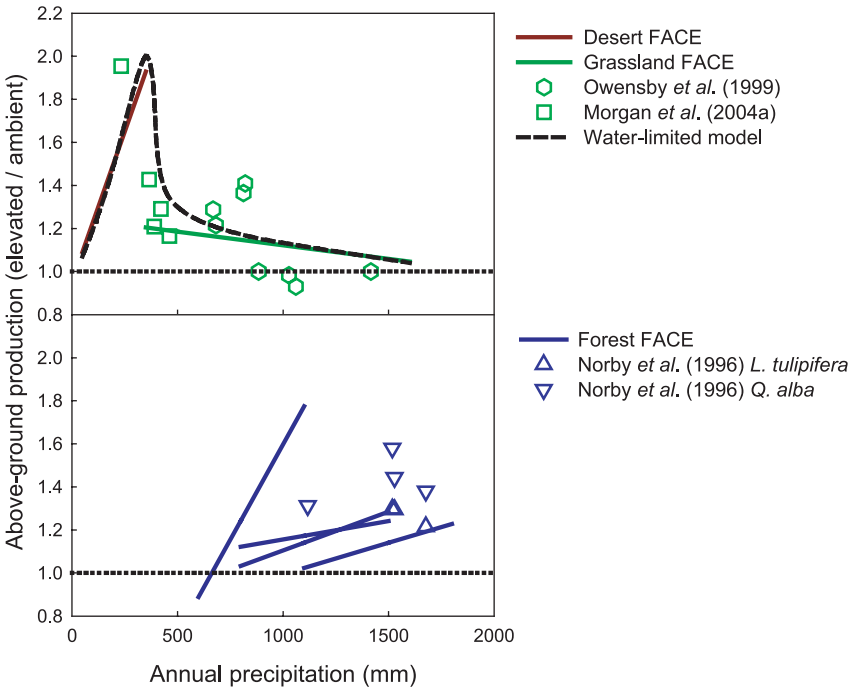

Fig. 8 Comparison of above-ground production enhancements as related to annual precipitation between free-air CO_2 enrichment (FACE, solid lines) and open-top chamber (OTC, open symbols) experiments. Results for FACE experiments are the same regression lines shown in Fig. 7 except color-coded here (dark red, deserts; dark green, grasslands; dark blue, forests). Results for OTC experiments are from tall-grass prairie (light-green hexagons), short-grass-prairie (light-green squares), *Liriodendron tulipifera* (light-blue triangles) and *Quercus alba* (light-blue inverted triangles). Black dashed line is a conceptual model to explain the relationship between the ratio of response under elevated [CO_2] to that under ambient [CO_2] (E/A) for above-ground primary production (APP) and annual precipitation in ecosystems that are primarily water-limited.

discrepancy, we suspect that a more complex conceptual model fits the APP results for water-limited systems. This conceptual model, which is represented by the black dashed line in Fig. 8, top graph, has two components. First is the benefits of increasing water-use efficiency (WUE) from elevated [CO_2] that underlies the predictions from Strain & Bazzaz (1983) – as exhibited by grasslands, the increasing benefits of increased WUE under elevated [CO_2] results in a greater enhancement of APP as annual precipitation decreases. However, just as high WUE is not sufficient for survival of desert plants, the benefits of increased WUE from elevated [CO_2] has only limited effects on APP as precipitation continues to decrease. As demonstrated by desert vegetation, the response of APP to elevated [CO_2] is constrained at very low precipitation by the need for plants to cope with severe drought. Thus, the enhancements of APP by elevated [CO_2] peaks at some intermediate precipitation (the empirical results from the FACE and OTC experiments suggest that the maximum E/A for APP occurs between 300 mm and 500 mm annual precipitation).

Results for forest ecosystems clearly do not fit predictions that enhancements of productivity increase with decreased water availability. The relationship of increased E/A with increased annual precipitation (Fig. 7) was highly significant and well correlated for both APP (Table 4b) and NPP (Table 3a). Although differences among sites in steepness of the slope for APP appear to be related to stand age, as discussed above, we still need to account for why E/A increases with increased precipitation, contrary to the early conceptual model of Strain & Bazzaz (1983). One explanation might be that annual precipitation is not the best index of water availability for forest production. For example, even though the growth of large trees in wet years is greater than that in dry years, seasonal timing of rainfall has a large impact on their growth (Hanson *et al.*, 2001). Thus, if short-term drought at critical growth periods is accompanied by wet periods at other, noncritical times during the year, then the short-term drought will be masked in the annual precipitation measurements. A second explanation may be that nutrient availability increases with increased precipitation, which then drives the increased productivity response to elevated [CO_2]. However, recent studies of the N cycle at three forest FACE sites did not find any significant effects of elevated [CO_2] on microbial N cycling (Zak *et al.*, 2003). Another possibility would be that some other climatic factor, such as growing season temperature or length of the growing season, covaries with annual precipitation. For example, photosynthetic enhancement by elevated [CO_2] increased with increased leaf temperature for loblolly pine at FACTS I (Myers *et al.*, 1999).

4. Influence of nitrogen on enhancing production

Although fewer data are available, an enhanced [CO_2]-effect on production typically occurs when ecosystem N is increased (Fig. 9), a response that is consistent with earlier predictions. The results, shown as wide, dark-colored bars in Fig. 9, are from three grassland, one forest, and one desert FACE site where soil N varied either by adding additional N (BioCON, ETH-Z, FACTS I Prototype, MEGARICH) or by natural variation among different microsites (NDFF). Note that for

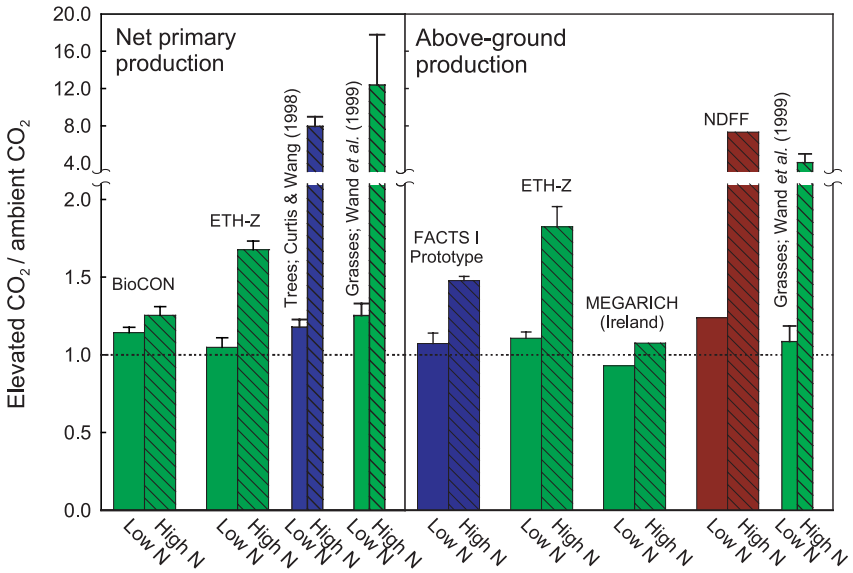

Fig. 9 Effects of increased nitrogen availability on the enhancement of primary production by elevated [CO_2]. Wide, dark-colored bars are results from ecosystem free-air CO_2 enrichment (FACE) experiments whereas narrow, light-colored bars are from meta-analysis of controlled-environment and open-top chamber (OTC) experiments. The ratio of response under elevated [CO_2] to that under ambient [CO_2] (E/A) for low nitrogen (N) availability (closed bars) are production under elevated [CO_2] and low N availability divided by production under ambient [CO_2] and low N. The E/A ratio for high N availability (hatched bars) are production under elevated CO_2 and high N availability divided by production under ambient [CO_2] and low N. Except for NDFF, results for ecosystem FACE experiments are means and standard errors, averaged over all years of observation at a site; only 1 yr of data from the NDFF was available. For the meta-analysis studies, results are recalculated using all controlled-environment and OTC experiments in the databases of the meta-analyses and are means and standard errors. A dotted line across each graph shows E/A = 1.0 for reference. Sources for ecosystem FACE data are given in Table 1.

the three sites where N was added, the N additions were within generally accepted management practices. The low N values in Fig. 9 represent the ratio of production under the combined treatments of elevated [CO_2] and low N to that under the combined treatments of ambient [CO_2] and low N, i.e. the same N treatment but different [CO_2] treatments. To directly determine if increased N availability further increases the [CO_2] effect, we need to use the same reference point for production under high N (i.e. we need to use the same denominator – combined treatments of ambient [CO_2] and low N – but the numerator is now the combined treatments of elevated [CO_2] and high N). Thus, if the [CO_2] effect increases when additional N is available, then the height of the bars should increase from low to high N availability, which occurs without exception for the ecosystem FACE experiments.

To compare these ecosystem FACE results with controlled-environment and OTC experiments, we recalculated similar E/A ratios for low and high N studies using the databases from meta-analyses of trees (Curtis & Wang, 1998) and grasses (Wand *et al.*, 1999). Results from the controlled-environment and OTC studies show a similar pattern to the ecosystem FACE experiments, although the enhancement of NPP when N is more readily available is much greater for the controlled-environment and OTC studies than for the ecosystem FACE experiments. This much greater enhancement of E/A for NPP in controlled-environment experiments is likely caused by the optimal growing conditions that plants experience during the experiments, the short periods during which the experiments are conducted and the fact that most experiments use seedlings that are rapidly growing. Results from other OTC experiments that are not included in these meta-analyses (Norby *et al.*, 1999; Joel *et al.*, 2001) show increased enhancements of productivity when nutrients are more available that are more similar to those of FACE experiments. For example, the E/A values for APP under ambient N were 1.32 and 1.07 for sandstone and serpentine communities, respectively, and the enhancement ratios, expressed as APP under elevated CO_2 and high N vs APP under ambient CO_2 and ambient N, increased to 2.22 for sandstone and 1.55 for serpentine communities (Joel *et al.*, 2001). Further support for this greater enhancement of the [CO_2] effect comes from crops: the E/A for APP of rice grown under high N was greater than that under ample N (Kimball *et al.*, 2002), although the E/A for BPP was less under high N.

Related to the prediction that increased N will increase the [CO_2] effect is that ecosystem responses to a step-change in [CO_2] are transient because ecosystems quickly develop N limitations (Luo & Reynolds, 1999), which in turn will decrease E/A over time. For the 10 FACE experiments that have at least 3 yr of results, neither the E/A for APP nor that for BPP significantly changed over time when precipitation

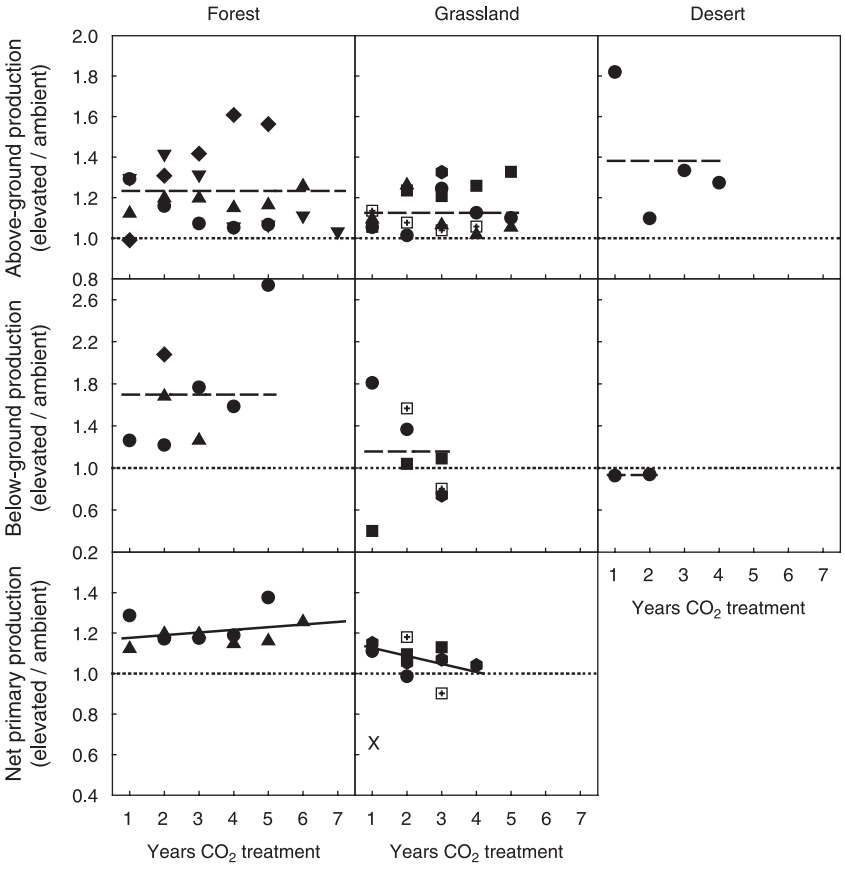

Fig. 10 Relationship between primary production and the number of years of CO_2 treatment for free-air CO_2 enrichment (FACE) experiments that have reported three or more years of above-ground production results. Top three graphs are above-ground, middle three are below-ground and bottom two are net primary production; left three graphs are for forest, center three for grassland, and right two are desert FACE sites. Note differences in range and scaling among the production measurements. Each point is production for the first, second, third, etc., year of CO_2 treatment. Within each vegetation type, different symbol shapes represent different FACE experiments; the 'X' in the net primary production (NPP) of grasslands graph is a statistical outlier that was excluded from the statistical analysis (see text). Solid lines represent significant linear relationships between production and years of CO_2 treatment for all data within a graph; the P and R^2 values for the linear regression are shown in Table 3. For data sets that did not have a significant linear relationship between production and years of CO_2 treatment, the mean value of all observations is indicated by a dashed line. A dotted line across each graph shows ratio of response under elevated [CO_2] to that under ambient [CO_2] (E/A) = 1.0 for reference. Sources for data are given in Table 1.

effects were also accounted for (Table 3a; Fig. 10 top and middle panels). For the E/A of NPP, the vegetation type × years of CO_2 interaction term was significant (Table 3a), indicating that the relationship between the NPP enhancement and years of CO_2 treatment for forests sites differed from that for grassland sites. For forests, the E/A for NPP significantly increased with time, whereas that for grasslands decreases (Fig. 10 bottom panels). Although the [CO_2] effect on production does not appear to be dampened over time, except for NPP of grasslands, these results must be interpreted cautiously; results from models suggest that the decrease in E/A with time likely occurs on a time-scale of > 10 yr (Luo & Reynolds, 1999). Thus, it is critically important that the current FACE experiments be continued.

VI. Response of plant functional types

Free-air CO_2 enrichment studies, most of which use intact vegetation that is not highly manipulated experimentally, are not well suited for explicitly examining community diversity responses to elevated [CO_2], especially given the long lifespan of perennial dominants relative to the length of time that the experiments have been occurring. However, an examination of the relative responses of different plant functional groups can serve as a proxy for how changing [CO_2] may influence the relative abundance of these functional types over longer periods.

The data set to determine if the effects of elevated [CO_2] differed among plant functional types consists of measurements of APP for individual species at different FACE experiments. In most cases, data are reported for an individual species, but we also used data reported for a group of species. When the data set for a functional type included a single mean reported for a group of species, we represented that result as a single data point in the data set (as opposed to replicating the mean a number of times in our data set to match the number of species that went into that mean). To indicate that a particular data set had data that included a single mean for a group of species, '>' is placed before the number of species in Fig. 11, i.e. the sample size for the number of species is actually greater than the number of means in the data set. For many species, two or more years of observations are reported, and a replicate is considered to be an individual year of results for an individual species (or a group if that was the only reported data) for an individual experiment.

Statistical analysis to compare E/A for APP among plant functional types was complicated by three factors. First, not all sites have representatives of all functional types. Second, no one species was common among all sites. Third, measurements for most species were not made or reported in all years of

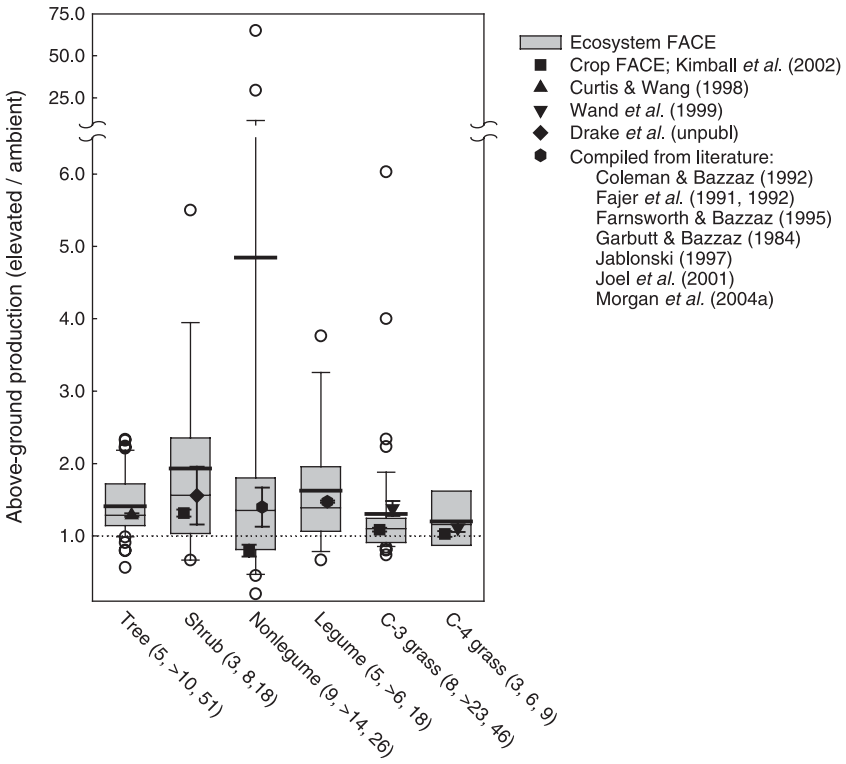

Fig. 11 Enhancement ratios of above-ground production for different plant functional types. Results from the ecosystem experiments in this review are shown as box plots where the thick line is the mean of the observed values, the thin line is the median value, the upper and lower lines of the box are the 75th and 25th percentiles, the upper and lower whisker lines are the 90th and 10th percentiles, and circles are potential outliers. Sample sizes for the box plots are given in parentheses after the plant functional type name; the first number is the number of free-air CO_2 enrichment (FACE) experiments with measurements, the second number is number of species with observations (note that '>' indicates that results used from the literature were averaged over more than one species), and the total number of observations (an observation is 1 yr of production for a species at a site). Preplanned, least-squared comparisons among the plant functional types for the ecosystem FACE experiments were not significant. Corresponding results for crop plants from FACE experiments as well as data from controlled-environment and open-top chamber (OTC) studies are shown as closed symbols. Dotted line across graph shows ratio of response under elevated [CO_2] to that under ambient [CO_2] (E/A) = 1.0 for reference.

the experiment. Thus, a simple repeated measures factorial ANOVA could not be used to examine the data because of the large number of missing cells in the data set. To overcome these issues, we first constructed a dummy variable called 'SiteType' that combined the specific site information with the plant functional type information (e.g. ShrubORNL would be results for shrub species at ORNL). Next, APP was ln-transformed so that the data set met skewness, kurtosis, heteroscedasticity, and normality criteria. Then, SiteTypes were compared using a Qualitative X Qualitative Repeated Measures ANOVA (Fernandez, 2003b) where SiteType and Species were the two qualitative factors and Year was the repeated measures factor; this analysis utilized PROC MIXED in SAS. Because the SiteType main effect was significant in this ANOVA (Table 5a), we then conducted a series of planned contrasts to examine if plant functional types differed from each other, where all sites with one functional type were compared with those for another functional type (Table 5b). One nonlegume, *Solidago canadensis* at ORNL, had E/A > 25 for each of the two years of measurements (Belote *et al.*, 2003), which results in the relatively high mean and 90th percentile for the nonlegumes. Although we emphasize that the ln-transformed data met all four assumptions of ANOVA's, we also analysed the data set without these two data points. Again, data had to be ln-transformed to meet the ANOVA criteria, but the SiteType main effect was not significant in this ANOVA ($P = 0.206$). Thus, we conclude that the data set with the two *Solidago* data points does not bias the statistical analyses.

Because legumes fix N and hence potentially avoid severe N limitations, and because increased A_{net} under elevated [CO_2] could alleviate some of the carbon limitations for N-fixation, legumes have been predicted to have greater responses to elevated [CO_2] than other plant functional types (Tissue *et al.*, 1997; Grünzweig & Körner, 2001). Although the effects of elevated [CO_2] on APP of legumes tended to be greater than those reported for some other plant functional types (Fig. 11), the planned contrasts between legumes and all other functional types across all FACE sites was not significant (Table 5b). The four FACE experiments that had legumes also had nonleguminous herbs, and although the E/A ratio of the legumes was numerically greater than that of the nonlegumes for three of the experiments, the difference between legumes and nonlegumes was not significant for any one experiment (Lüscher *et al.*, 1998; Leadley *et al.*, 1999; Niklaus *et al.*, 2001; Reich *et al.*, 2001b). Thus, although legumes tended to have the expected greater response to elevated [CO_2], the variation in responses among sites (Fig. 11) as well as among species within each site suggest that the N-fixation trait is not sufficient to predict how leguminous and nonleguminous herbs will respond to elevated [CO_2].

Other comparisons of interest are those between C_3 and C_4 plants and between woody and nonwoody plants, where C_3 (and nonwoody) plants have been predicted to have a greater

Table 5 Results from statistical analyses of ln-transformed above-ground production (APP) for different plant functional types from ecosystem free-air CO_2 enrichment (FACE) experiments

Variable	Numerator df	Denominator df	*P*
(a) ANOVA[1]			
SiteType	32	36	< 0.001
Species	8	35	0.303
Year	4	80	0.696
(b) Planned contrasts			
C_3 vs C_4	1	37	0.770
C_3 vs Legume	1	41	0.738
C_3 vs Nonlegume	1	39	0.352
C_3 vs Shrub	1	41	0.282
C_3 vs Tree	1	34	0.929
C_4 vs Legume	1	38	0.601
C_4 vs Nonlegume	1	36	0.341
C_4 vs Shrub	1	38	0.288
C_4 vs Tree	1	34	0.824
Legume vs Nonlegume	1	41	0.639
Legume vs Shrub	1	42	0.510
Legume vs Tree	1	37	0.685
Nonlegume vs Shrub	1	40	0.786
Nonlegume vs Tree	1	34	0.324
Shrub vs Tree	1	36	0.262

[1]Data were analysed with SAS V8.02 (SAS, 2001) using a 'Ql × Ql repeated' routine (Fernandez, 2003b). *F*-tests were based on Type III sums of squares. Numerator and denominator degrees of freedom are shown for each *F*-test.

response than C_4 (and woody) plants (Strain & Bazzaz, 1983). The C_3 grass functional type had a slightly greater mean response to elevated [CO_2] than C_4 grasses (Fig. 11), but this difference, as well as those between C_4's and all other functional types, was not significant (Table 5B). Similarly, comparisons between woody functional groups (trees and shrubs) and the other functional groups were also not significant. Taken together, these results for different functional types suggest 'that current trait-based functional classifications might be useful, but not sufficient, for understanding plant and ecosystem responses to elevated CO_2' (Reich *et al.*, 2001b) and that environmental factors interact with plant functional type to influence plant responses to elevated [CO_2].

Results from controlled-environment and OTC experiments were near the mean or median of data from the ecosystem FACE experiments (Fig. 11). The controlled-environment and OTC data are from meta-analyses of woody plants (primarily trees; Fig. 11, closed triangles) or C_3 and C_4 grasses (closed, inverted triangles), from a shrub-oak OTC experiment (closed diamonds), or was compiled from various literature (closed hexagons). However, results for crops when grouped by functional types (closed squares) did not always match those for plants from ecosystem studies (Fig. 11). We compared data for crops, which are from Kimball *et al.* (2002), with ecosystems as follows: cotton and grapes (woody perennials) are compared with shrubs; potato (broadleaf forb) with nonlegumes; wheat and rice (C_3 grains) with C_3 grasses; and sorghum (C_4 grain) with C_4 grasses. Mean E/A for crop functional types were numerically less than those for ecosystem functional types, but the data overlapped extensively. However, crops are not bred for APP, but for their agricultural yield, and E/A of agricultural yields typically are greater than those for APP, especially under water or N limitation (Kimball *et al.*, 2002).

Several lines of evidence suggest that elevated [CO_2] may preferentially increase the abundance of another group of plants – invasive species (Dukes & Mooney, 1999; Weltzin *et al.*, 2003). For example, results from a controlled-environment experiment with six common invasive species found that these plants were more responsive to [CO_2] increases that have occurred in the past century than to the rise in [CO_2] anticipated in the next century, suggesting that changes in [CO_2] have already played a stimulatory role in plant invasions (Ziska, 2003). The most responsive species to elevated [CO_2] in the desert was an invasive C_3 annual grass (Smith *et al.*, 2000), while production of another invasive species, a C_3 woody vine, increased threefold in a forested ecosystem at ORNL (Belote *et al.*, 2003). However, not all invasive species respond favorably to elevated [CO_2]: an invasive C_4 annual grass showed reduced production under elevated [CO_2] in the same ORNL experiment. However, this reduced production for the C_4 annual is not unexpected when compared with the responses of other C_4 plants (Fig. 11). Thus, the available results provide support for the prediction that elevated [CO_2] favors at least C_3 invasive species. Furthermore, when invasive species have a potentially disruptive role through a stimulation of anomalous change in the ecosystem, they could have a major impact on subsequent community structure and diversity. For example, *Bromus* spp. are known to stimulate a fire cycle (Sage, 1996) and to alter N-cycling (Evans *et al.*, 2001) in arid and semiarid ecosystems in the western USA. The differential stimulation of growth and seed production in *Bromus* by elevated [CO_2] could therefore result in a marked change in community structure and function of the ecosystems they are currently invading (Smith *et al.*, 2000).

More diverse plant communities are predicted to be more responsive to elevated [CO_2] (Bolker *et al.*, 1995). As demonstrated by the results above, along with others (Hooper & Vitousek, 1997; Tilman *et al.*, 1997), all plants are not equal in their responses to environmental perturbations, even those within a functional group. Thus, the prediction that communities with greater biodiversity will have a greater [CO_2] response may or may not be due to some inherent characteristic of biodiversity. For example, more diverse communities are more likely to have more species that respond more strongly to elevated [CO_2], which can be interpreted as a 'sampling' effect (Loreau, 2000; Niklaus *et al.*, 2001). Two FACE sites have explicitly examined the biodiversity hypothesis:

BioCON and SCG. Both studies showed significantly increased production for more diverse species assemblages. The elevated [CO_2] effect changed from +7% to +22% as the number of species increased from 1 to 16 at BioCON (Reich *et al.*, 2001a). For the biodiversity experiment at the Swiss calcareous grassland, the [CO_2] effect varied through time, but E/A ratios of total community biomass at final harvest were 0.80, 1.08 and 1.41 for communities that initially had 5, 12 or 31 species (Niklaus *et al.*, 2001). Some functional group effects were evident (Craine *et al.*, 2003), but in both experiments, the effects of biodiversity on [CO_2] responses were largely caused by a subset of the species that were used in the experiments, which is consistent with the 'sampling effect' concept. Interestingly, biodiversity of a California grassland that is dominated by annual grasses decreased with elevated [CO_2], primarily because of decreased forb diversity (Zavaleta *et al.*, 2003). Clearly, the influence of biodiversity, plant functional type composition, and species identity all play a role in ecosystem-level responses to elevated [CO_2].

VII. Conclusions

Results from FACE sites (i.e. for plants growing in a competitive matrix under natural conditions) have largely substantiated predictions of how elevated [CO_2] affects leaf CO_2 assimilation. As expected, almost all the C_3 species examined at different FACE sites have increased photosynthesis under elevated [CO_2]. Also as expected, the increase in A_{net} with elevated [CO_2] when averaged over all species (26%) was less than the increase in [CO_2] (50–55%), and the increase in ecosystem primary production (19% for APP, 32% for BPP, and 12% for NPP) was less than both. The enhancement of A_{net} for field-grown plants was roughly similar to that for plants in controlled-environment and OTC studies after adjusting for differences in experimental [CO_2]. Finally, downregulation of photosynthesis occurred in a number of FACE experiments, but not in all species and only under certain conditions for other species.

Although the effects of elevated [CO_2] on A_{net} varied among species, two relationships were consistent. First, the enhancement of photosynthesis by elevated [CO_2] was positively related to the relative change in leaf N content: smaller increases in A_{net} under elevated [CO_2] occurred for plants that had reduced leaf N under elevated [CO_2], whereas plants that showed no or small increases in leaf N had larger increases in A_{net}. Second, herbaceous species consistently had reduced leaf N-content under elevated [CO_2], and hence smaller enhancements of A_{net}, than woody species. Thus, herbaceous species may be more functionally plastic than woody species under elevated [CO_2]. This assimilation–leaf N relationship also implies that the effects of elevated [CO_2] on A_{net} is responsive to fertility or increased N deposition, and downregulation of photosynthesis may occur more prevalently under N-limited conditions, as earlier predicted. Interestingly, the ecosystems that had the greatest enhancements of A_{net} (i.e. woody-dominated ecosystems such as forests and deserts) had the greatest enhancements in APP, suggesting that A_{net} may scale to the ecosystem level, although the form and value of the scaling factor is not currently known. Nonetheless, results for BPP and NPP suggest that the scaling factor must also include an allocation component, as responses of BPP to elevated [CO_2] differ between forests and deserts.

Results for predictions of the effects of elevated [CO_2] on primary production are more mixed, but are generally less than a 20% increase in NPP based on the β-factor approach. The results from FACE sites suggest that a single β is not feasible, at least for global predictive purposes, given differences among ecosystems types and differences in plant responses to elevated [CO_2] in combination with other environmental parameters such as water and N availability. Early predictions that are based on resource limitations generally are valid for N availability, but less so for water availability. The significantly greater enhancement of APP for deserts compared with other ecosystems is consistent with predictions that enhancement of productivity would be greater in drier ecosystems, but the result that forests have significantly greater enhancements of APP and NPP than grasslands is not. Furthermore, only APP for grasslands had greater productivity enhancements in drier years – relationships between the enhancement of APP and annual precipitation for forests and deserts and those between BPP or NPP and annual precipitation were either not significant or increasing. By contrast, the predicted increase in productivity enhancement with increased N availability is well supported by the FACE results as well as by controlled-environment and OTC studies. Although the water availability effects are counter to initial predictions of Strain & Bazzaz (1983) made 20 yr ago, their initial conceptual model based on the importance of increased WUE under elevated [CO_2] coupled with the concept of an over-riding importance of drought survival mechanisms at very low precipitation is consistent with an empirical fit to data from water-limited ecosystems (Fig. 8).

Results for plant functional type also do not generally fit predictions that certain groups of plants such as legumes and C_3 plants will have greater enhancements of productivity than woody and C_4 plants. Two factors are important in this assessment of plant functional types. First, predictions based on the [CO_2] enhancement of productivity from single, isolated plants are not good predictors of how well those same plants do under interspecific competition (Poorter & Navas, 2003). Second, the identity of individual species is important, i.e. not all species within a functional type are necessarily similar. The presence or absence of individual species and functional groups can significantly influence responses of native ecosystems to elevated [CO_2] and their feedbacks with other global change factors (Reich *et al.*, 2001a; Zavaleta *et al.*, 2003), and we anticipate greater attention to this topic in current and future experiments.

We have focused almost exclusively on plant processes in this review, primarily because the majority of results from FACE sites that have been reported to date concern plant processes and hence they form the most comprehensive data set. Fortunately, results from other trophic levels are beginning to emerge. For example, increases in soil microbial biomass (Schortemeyer *et al.*, 1996) and changes in N cycling (Billings *et al.*, 2002) are evident in some ecosystems, as postulated by Zak *et al.* (1993), although changes in soil microbial biomass or composition do not always change with elevated [CO_2] (Allen *et al.*, 2000; Zak *et al.*, 2000, 2003; Niklaus *et al.*, 2003). Changes in leaf quality with elevated [CO_2] have also been noted, although these changes had either no or only subtle affects on insect herbivores for aspen (Percy *et al.*, 2002; Kopper & Lindroth, 2003). Effects on plant fungal pathogens are also variable, with no effects noted for aspen (Percy *et al.*, 2002) but increased pathogen loads on C_3 grasses under elevated [CO_2] (Mitchell *et al.*, 2003). These variable, and sometimes surprising, results further emphasize Körner's (2000) conclusion that only a fully coupled ecosystem approach will yield meaningful information on how the biosphere may respond to global change. We contend that integrated studies at FACE sites are currently our best method to achieve this approach.

This review also has focused primarily on an elevated [CO_2] effect and largely ignored other environmental factors that are likely to change as [CO_2] continues to increase. With the exception of N availability (Fig. 9), multifactor FACE experiments are rare. Realistic, multifactor experiments are difficult and costly to achieve in some ecosystems such as forests and deserts, but the importance of factor interaction is evident from the studies in the annual grassland community at JRGCE (Shaw *et al.*, 2002). Although elevated [CO_2] alone increased NPP by *c.* 8%, the interactive effects of elevated [CO_2] with temperature, N, and precipitation on NPP were less than those of ambient [CO_2] with those factors. These results clearly point to the need for multifactor experiments, and they also strengthen the argument that both resource availability and species composition are important. Thus, an integrative approach, such as that proposed by Field *et al.* (1992), is needed to predict the impacts of a suite of global changes on ecosystem attributes.

Clearly, results from the FACE sites that are summarized in this review have greatly advanced our knowledge of plant and ecosystem responses to elevated [CO_2] for specific ecosystems as well as across multiple ecosystems. But the utility of these experiments goes well beyond simply predicting global change effects. These FACE experiments are often designed to investigate fundamental mechanisms that drive ecosystem structure and function, issues that are at the heart of ecology. Thus, the importance of these FACE sites is not only how well they can predict the impacts of elevated [CO_2], but also how well they test ecological concepts.

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