

All about FACE – plants in a high-[CO₂] world

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The potential effects on plant performance of increases in [CO₂] to levels predicted for later in this century have been intensively studied and analyzed [1]. The controversial results have been passionately debated. Short-time exposure to high [CO₂] in controlled environments showed substantial increases in CO₂-assimilation rates, but prolonged exposures often led to ‘acclimation’ [2], resulting in decreased functioning of the photosynthetic machinery [3–5], correlated with downscaling of Rubisco transcripts, less Rubisco protein, and a general decline of photosynthesis [5,6]. This decline in photosynthesis is accompanied by increases in leaf carbohydrate content, which has long been known to inhibit photosynthesis [7,8]. A strong relationship between nitrogen status and photosynthetic acclimation has been observed [9,10] but the universality and mechanistic basis of this phenomenon remain unknown. The consequences for the physiology and metabolism of plants growing in increased [CO₂] have been rationalized in the context of long-distance source–sink relations, the function of Rubisco as a nitrogen sink, altered signaling between carbon and nitrogen assimilation pathways, and multiple control points for the expression of photosynthetic genes and proteins, partially through sugar sensing, or sucrose cycling [11,12].

Models based on plant responses to elevated [CO₂] in controlled environments, with neither sink nor nutrient limitations, predict that, theoretically, productivity would increase by >30% [13]. However, a different picture has been suggested by data compiled from physiological studies in fields using a variety of species in FACE (Free Air CO₂ Enrichment) facilities in temperate climate zones with [CO₂] enriched to levels expected in 2050 or 2100 [14]. These FACE studies showed that the gains in biomass and yield were lower than had been predicted [1]. Trees show the greatest long-term [CO₂]-dependent increases in biomass and yield, increases in legumes are smaller, those in other C3 species are smaller still and are negligible in C4 plants. However, high [CO₂] appears to exert beneficial effects under water deficit conditions based on lower stomatal conductance prompted by elevated [CO₂] [15]. The responses of C3 plants, overall, exceed those of C4 plants, possibly implicating photorespiration as one mechanism affected by changes in high [CO₂] [16]. A projected depression of photorespiration caused by elevated [CO₂] can be correlated with a disruption of nitrate assimilation and a

depression of nitrate reductase transcripts and activity [17]. Although much has been learned, it might be time to embrace different concepts and tools.

We argue that attention should be focused on genetic, molecular and genomics studies, to reveal underlying mechanisms that give rise to the well-documented physiology, using the power provided by model species, ecotypes, mutants and breeding lines, as the next logical step. *Arabidopsis thaliana* is the organism of choice. Bringing the formidable resources of this model plant into play for a comprehensive view in the context of a whole genome, should refine our understanding of the molecular events that underlie plant reactions in [CO₂]-enriched environments and improve the accuracy of modeling. The typical C3 plant responses to persistently higher [CO₂] – accumulation of excess carbon – can then be modeled into a molecular framework of sensing, signaling and responding.

Arabidopsis ecotype diversity, arising from adaptive evolution [18], is reflected in transcript and metabolite profiles from plants in elevated [CO₂] in FACE [19]. A baseline has already been established by comparing *Arabidopsis* (Col-0) gene expression in a growth chamber with that under field conditions [20], revealing massive increases in the expression of stress-related genes in the field compared with the number expressed in greenhouse-grown plants. Transcript expression profiles of *Arabidopsis* ecotypes, grown in SoyFACE (Soybean Free Air Concentration Enrichment) (<http://www.soyFACE.uiuc.edu>) with [CO₂] at 550 ppm, were compared with those of plants simultaneously grown in ambient air in adjacent FACE structures. Eliminating local weather as a parameter, and choosing ecotypes of different evolutionary adaptations, has provided information about acclimation, ecotype differences and common responses during the short-term growth of the plants in FACE. Decreases in the expression of transcripts related to chloroplast functioning were often observed and characterized all lines while revealing subtly distinct strategies in dealing with high [CO₂] with respect to the regulation of carbohydrate partitioning, N-allocation, cell wall biosynthesis and hormone responses. Irrespective of ecotype differences, a common response to elevated [CO₂] emerged in all lines (Table 1). Many transcripts and processes that distinguish plants grown in high [CO₂]-FACE from plants grown in ambient air highlight a functional association with stress-responsiveness. [20] Furthermore, transcripts regulated in response to N-deficiency also respond in FACE [21], and stimulation of

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Table 1. Significantly up- and down-regulated genes arranged by functional categories in elevated [CO₂] in FACE^a

Category	Percentage of total up-regulated genes	Percentage of total down-regulated genes
Carbon metabolism	8.0	3.0
Cell division and cell organization	2.3	1.1
Cell wall biosynthesis and modification	6.2	0.8
Chlorophyll metabolism	0.1	0.9
Defense/redox	5.7	5.1
Development	1.0	1.1
DNA metabolism and chromatin structure	0.7	0.6
Hormone related	1.7	3.0
Lipid metabolism	3.4	2.1
Mitochondrial electron transport	0.6	0.4
Nitrogen metabolism	1.1	2.1
Protein synthesis, degradation and modification	11.9	13.3
Photosynthesis	0.3	5.8
RNA metabolism and transcription	7.9	6.6
Secondary metabolism	3.2	1.1
Signaling	5.2	1.9
Transport	7.0	1.5
Vesicle transport	2.5	0.0
Other metabolism	1.7	2.6
Unknown	29.7	47.0
Total	100.0	100.0

^aPercentage for a given functional category calculated based on significantly ($p=0.01$) up-regulated (total 725) or down-regulated (total 532) transcripts in *Arabidopsis* ecotypes exposed to elevated [CO₂] at the UIUC SoyFACE facility (<http://www.soyface.uiuc.edu>). Functional categorization according to Mapman [21] and GO annotations. Significant differences in regulation in major functional categories are highlighted in bold. The category 'defense/redox' includes many genes that are regulated either way [18] (P. Li and H.J. Bohnert, unpublished).

organic acid biosynthesis, and the enhancement of pathways that use the resulting carbon burden are observed.

The apparent nitrogen deficient state, or, rather, carbon glut, might be the reason that soybean (*Glycine max*), a nitrogen fixing species, has shown greater yield increases than other C3 species in FACE studies [1]. Nitrate assimilation and metabolism might, therefore, be important sites of sensing mechanisms – cross-referencing to carbon metabolism – that are set in motion in elevated [CO₂].

As a result of studies on the stimulation of stress- and defense-responsive pathways, in particular those downstream from ROS-generating and signaling functions, and the apparent disturbance of C:N homeostasis, we now have a good understanding of the physiological consequences of plant exposure to elevated [CO₂]. What is lacking is an understanding of the sensing and signaling pathways that determine the physiology. Because we can monitor the entire *Arabidopsis* genome, *Arabidopsis* can show us the genes and pathways that underlie the nature of the biochemical changes. The use of *Arabidopsis* is justified by the observation of similar responses in soybean and poplar [22,23], and the resources available for *Arabidopsis* enable a more complete analysis of transcriptome responses. Breeding lines, populations or mutants of crop species can then be scored for genetic traits that determine the differences and susceptibilities first gleaned from differences in the responses of *Arabidopsis* ecotypes to elevated [CO₂]. The behavior of C3 species in FACE predicted by physiology-based modeling should be explained by molecular genetics and genomics approaches because the underlying causes are based on sensing and command circuits.

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