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Rising CO₂ threatens human nutrition

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Dietary deficiencies of zinc and iron are a major global public health problem. An estimated two billion people suffer these deficiencies ¹ causing a loss of 63 million life years annually ^{2,3}. Most of these people depend upon C₃ grains and legumes as their primary dietary source of zinc and iron. We report that C₃ grains and legumes have lower concentrations of zinc and iron when grown under field conditions at the elevated atmospheric CO₂ concentration anticipated for the middle of this century. C₃ crops other than legumes also have lower concentrations of protein, whereas C₄ crops appear to be less affected. Differences among cultivars of a single crop suggest that breeding for reduced sensitivity to atmospheric CO₂ concentration, i.e., [CO₂], could partially address these new challenges to global health.

In the 1990s, several investigators found that elevated [CO₂] decreased the concentrations of zinc, iron, and protein in grains of wheat ^{4–7}, barley ⁵, and rice ⁸ grown in controlled environment chambers. Subsequent studies, however, failed to replicate these results when plants were grown in open top chambers and free air CO₂ enrichment (FACE) experiments. Lieffering *et al.* (2004) ⁹ found no [CO₂] effect on the concentrations of zinc or iron in rice grains grown under FACE and suggested that the earlier findings had been influenced by “pot effects,” whereby a small rooting volume led to nutrient dilution at the root-soil interface. Of the more recent studies [10–13], most have indicated lower elemental concentrations in soybeans ¹⁰, sorghum ¹⁰, potatoes ¹¹, wheat ¹², or barley, ¹³ grown at elevated [CO₂], but with the exception of iron in one wheat study ¹², these results were statistically insignificant, perhaps because of small sample sizes.

Small sample sizes have limited the statistical power of individual studies of many aspects of plant responses to elevated [CO₂], and meta-analyses involving larger samples of genotypes, environmental conditions, and experimental locations have played an important role in resolving which elements of plant function respond reliably to altered [CO₂] ^{14,15}. A recent meta-analysis of published data concluded that only sulfur is decreased in grains grown at elevated [CO₂] ¹⁶.

Here we report findings from meta-analysis of newly acquired data from 143 comparisons of the edible portions of crops grown at ambient and elevated [CO₂] from seven different FACE experimental locations in Japan, Australia, and the United States involving six food crops (see Table 1). We tested the nutrient concentrations of the edible portions of rice (*Oryza sativa*, 18 cultivars), wheat (*Triticum aestivum*, 8 cultivars), maize (*Zea mays*, 2 cultivars), soybeans (*Glycine max*, 7 cultivars), field peas (*Pisum sativum*, 4 cultivars) and sorghum (*Sorghum bicolor*, 1 cultivar). In all, forty genotypes were tested over 1 to 6 growing seasons at ambient and elevated [CO₂], where the latter was in the range of 546–586 ppm across all seven study sites. Collectively, these experiments contribute more than 10-fold greater data regarding both zinc and iron content of the edible portions of crops grown under FACE conditions than is currently available in the literature. Consistent with earlier meta-analyses of other aspects of plant function under FACE conditions ^{14,15}, we considered the response comparisons observed from different species, cultivars, and stress

treatments and from different years to be independent. The natural log of the mean response ratio ($r = \text{response in elevated } [\text{CO}_2] / \text{response in ambient } [\text{CO}_2]$) is used as the metric for all analyses. Meta-analysis is used to estimate the overall effect of elevated $[\text{CO}_2]$ on the concentration of each nutrient in a particular crop and to determine the significance of this effect (see Methods).

We find that elevated $[\text{CO}_2]$ is associated with significant decreases in the concentrations of zinc and iron in all C_3 grasses and legumes (Figure 1, Table E1). For example, wheat grains grown at elevated $[\text{CO}_2]$ have 9.3% (95% CI: -12.7, -5.9) lower zinc and 5.1% (95% CI: -6.5, -3.7) lower iron than those grown at ambient $[\text{CO}_2]$. We also find that elevated $[\text{CO}_2]$ is associated with lower protein in C_3 grasses with a 6.3% (95% CI: -7.5, -5.2) decrease in wheat grains and a 7.8% (95% CI: -8.9, -6.8) decrease in rice grains. Elevated $[\text{CO}_2]$ is associated with a small decrease in protein in field peas and no significant effect in soybeans or C_4 crops (Figure 1, Table E1).

In addition to our own observations, we obtained data from ten of eleven previously published studies investigating nutrient changes in the edible portion of food crops (Table E6) and combined these data with our own observations in a larger meta-analysis. Analysis of our results combined with previously published FACE data (Table E2), or combined with previously published data from both FACE and chamber experiments (Table E3), is consistent with the results obtained using only our new data. Combining our data with previously published data does not alter the significance or substantially alter the effect size of the nutrient changes for any crop or any nutrient.

In addition to nutrient concentrations, we also measured phytate—a phosphate storage molecule present in most plants that inhibits the absorption of dietary zinc in the human gut¹⁷. We had no *a priori* reason to assume phytate concentrations would change in response to rising $[\text{CO}_2]$. However, formulas for calculating absorbed, or bioavailable, zinc depend both on the amount of dietary zinc and dietary phytate consumed,¹⁷ making it important to interpret changes in zinc concentration in the context of possible changes in phytate. Phytate decreased significantly at elevated $[\text{CO}_2]$ only in wheat ($P < 0.01$). This decrease might offset some of the declines in zinc for this particular crop, though the decrease is fractionally less than half of the decrease in zinc. For other crops examined, however, the lack of a concurrent decrease in phytate may further exacerbate problems of zinc deficiency.

The global $[\text{CO}_2]$ in the atmosphere is expected to reach 550 ppm in the next 40–60 years, even if further actions are taken to reduce emissions¹⁸. At these concentrations, we find that the edible portions of many of the key crops for human nutrition have decreased nutritional value when compared with the same plants grown under identical conditions but at present ambient $[\text{CO}_2]$. Analysis of the United Nations' Food and Agriculture Organization food balance sheets reveals that, as of 2010, roughly 2.3 billion people were living in countries whose populations receive at least 60% of their dietary zinc and/or iron from C_3 grains and legumes and 1.9 billion lived in countries that receive at least 70% of one or both of these nutrients from these crops (Table E5). Reductions in the zinc and iron content of the edible

portion of these food crops will increase the risk of zinc and iron deficiencies across these populations and add to the already considerable burden of disease associated with them.

The implications of reduced protein concentrations in non-leguminous C_3 crops are less clear. From a study of adult men and women in the United States, there is strong evidence that the substitution of dietary carbohydrate for dietary protein increased the risk of hypertension, lipid disorders, and 10-year coronary heart disease risk¹⁹. For the developing world, minimum protein requirements for different demographic groups are an area of active research and debate²⁰. For countries like India, however, where up to one third of the rural population is thought to be at risk of not meeting protein requirements²¹ and where most protein comes in the form of C_3 grains²¹, decreased protein in non-leguminous C_3 crops may have serious public health consequences.

Whereas zinc and iron were significantly decreased in all C_3 crops tested, only iron in maize is observed to decrease amongst the C_4 crops. No changes are found in sorghum. That zinc and iron declines are notable in C_3 crops but less so in C_4 crops is consistent with differences in physiology. C_4 crops concentrate CO_2 internally which results in photosynthesis being CO_2 -saturated even under ambient $[CO_2]$ conditions, leading to no stimulation of photosynthetic carbon assimilation at elevated $[CO_2]$ levels under mesic growing conditions²². Our finding that protein is less affected in legumes than other C_3 crops is also physiologically consistent with leguminous crops' general ability to match stimulation of photosynthetic C gain at elevated $[CO_2]$ with greater N_2 fixation in order to maintain tissue C:N ratios²³. In contrast, most temperate, non-legume C_3 crops are generally unable to extract and assimilate sufficient N from soils to maintain tissue C:N ratios^{24,25}.

Little is known about the mechanism(s) responsible for the decline in nutrient concentrations associated with elevated $[CO_2]$. Some authors have proposed "carbohydrate dilution" whereby CO_2 -stimulated carbohydrate production by plants dilutes the rest of the grain components²⁶. To test this hypothesis, we measured concentrations of additional elements for all crops except wheat (Table E4). Our findings are inconsistent with carbohydrate dilution operating alone. If only passive dilution of nutrients were occurring, we would expect to see very similar changes in the concentration of each nutrient tested for a given crop. In contrast, we find elemental changes in each given crop appear distinct from one another. For example, in rice grains (Table E4) the decrease in zinc concentrations associated with elevated $[CO_2]$ was significantly different from the decreases in the concentrations of copper ($P \leq 0.001$), calcium ($P \leq 0.001$), boron ($P \leq 0.001$), or phosphate ($P = 0.010$). This heterogeneous response was also observed in recent analyses reviewing possible mechanisms for nutrient changes in both edible and non-edible plant tissues grown at elevated $[CO_2]$ ²⁷. It also appears that the mechanism(s) causing these changes operate distinctly in different species. In one instance, for example, we find boron to be significantly decreased in soybeans ($P \leq 0.001$), whereas it is significantly elevated in rice grains ($P \leq 0.001$). While these differences may, in part, derive from different environmental conditions, it suggests that the mechanism is more complex than carbohydrate dilution alone. Of all the elements, changes in nitrogen content at elevated $[CO_2]$ are the most studied, and inhibition

of photorespiration and malate production²⁴, carbohydrate dilution²⁶, slower root N uptake²⁵, and decreased transpiration-driven mass flow of N²⁷ may all play a role.

We examined the effects of elevated [CO₂] on zinc, iron, and protein as a function of cultivar when data were available (Figure 2). Whereas most crops show negligible differences across cultivars, concentrations of zinc and iron across rice cultivars substantially vary ($P = 0.04$, and $P = 0.03$ respectively) (Figure 2a, and 2b).

Such cultivar differences suggest a basis for breeding rice cultivars whose micronutrient levels are less vulnerable to rising [CO₂]. Similar effects may hold in other crops given that the statistical power of many of our other inter-cultivar tests is limited by sample size. We note, however, that such breeding programs will not be a panacea for many reasons including affordability of improved seeds and the numerous criteria used by farmers in making planting decisions that include taste, tradition, marketability, growing requirements, and yield. In addition, as has been noted previously, there are likely to be tradeoffs with respect to yield and other performance characteristics when breeding for increased zinc and iron content²⁸.

The public health implications of global climate change are difficult to anticipate, and we expect there will be many surprises. The finding that raising atmospheric [CO₂] lowers the nutritional value of C₃ food crops is one such surprise that we can now anticipate and prepare for. In addition to efforts to retard the elevation of future [CO₂], it may be important to develop breeding programs designed to reduce the vulnerability of key crops to these changes. Nutritional analysis of which human populations are most vulnerable to decreased dietary zinc, iron, and protein from C₃ crops could help target response efforts including breeding reduced sensitivity to elevated [CO₂], biofortification, and supplementation.

Methods

We examine the response of nutrient levels to elevated atmospheric [CO₂] for the edible portions of rice (*Oryza sativa*, 18 cultivars), wheat (*Triticum aestivum*, 8 cultivars), maize (*Zea mays*, 2 cultivars), soybeans (*Glycine max*, 7 cultivars), field peas (*Pisum sativum*, 4 cultivars) and sorghum (*Sorghum bicolor*, 1 cultivar). The six crops are grown under FACE conditions, and, in all six experiments, the elevated [CO₂] is in the range of 546–586 ppm (see the Agricultural Methods section below for details associated with individual trials).

Statistics

In accordance with methods described by Ainsworth and Long¹⁴ and Curtis and Wang¹⁵, the natural log of the response ratio ($r = \text{response in elevated [CO}_2\text{]}/\text{response in ambient [CO}_2\text{]}$) is used as the metric for analyses and is reported as the mean percentage change $[(r-1) \times 100]$ at elevated [CO₂]. Consistent with these earlier analyses of multiple species grown under FACE conditions, the responses of different species, cultivars, and stress treatments and from different years of the FACE experiments are considered to be independent and suited to meta-analytic analysis¹⁴.

The meta-analysis is designed to estimate the overall effect of elevated [CO₂] on the concentration of each nutrient in a particular crop and to determine the significance of this effect relative to a null hypothesis of no change. All tests are conducted as two-sided---not specifying which direction the nutrient concentrations are expected to change under elevated [CO₂]---in order to make the analysis as general as possible. Meta-analysis is conducted using a linear mixed model. A random intercept is included for each comparison, representing nutrient level variability unrelated to [CO₂] that is common to both treatment groups. Additional analyses indicate that the [CO₂] effect on zinc concentration in rice is modified by cultivar and amount of nitrogen application, suggesting systematic variations across the pooled analysis of rice, and for these samples it is shown that the effect on zinc concentration is still significant when including interactions terms for cultivar and nitrogen. No other significant modifications of the [CO₂] effect are identified. We tested whether changes in different nutrients for particular crops were statistically different from each other as has been described³⁰. To address the issue of multiple comparisons when testing for differences among cultivars within a crop, we multiplied the P-value by the number of independent comparisons. This approach follows the so-called Bonferroni correction and is conservative in the sense of biasing the P-values high, but it is nonetheless sufficient in our case to demonstrate that individual test results are significant despite their having been selected from amongst multiple tests.

Parameter estimates are obtained using the restricted maximum likelihood method, a standard approach for analyzing repeated measurement data²⁹ that, in our case, are of nutrient concentrations at time of harvest. Results for all analyses are reported as the best estimate of percent changes in the concentration of nutrients along with the 95% confidence intervals associated with each estimate. Two-tailed P-values are also reported.

Agricultural Methods—Rice (*Oryza sativa*, 18 cultivars), wheat (*Triticum aestivum*, 8 cultivars), maize (*Zea mays*, 2 cultivars), soybeans (*Glycine max*, 7 cultivars), field peas (*Pisum sativum*, 4 cultivars) and sorghum (*Sorghum bicolor*, 1 cultivar) were grown under FACE conditions during daylight hours. The experiments were conducted in Australia, Japan, and the United States between 1998 and 2010. Ambient [CO₂] ranges between 363 and 386 ppm while elevated [CO₂] is between 546 and 584 ppm. With the exception of soybeans, each experiment involves multiple cultivars of each crop and more than one set of growing conditions. Each experiment for each cultivar and set of treatments is replicated four times with the exception of one of the rice sites where three replicates are performed. These data are summarized in Table 1, and additional details of the soil and growing conditions, FACE methods, and experimental designs have been published for rice³¹, wheat³², maize³³, soybeans³⁴, field peas³², and sorghum³⁵.

Laboratory Methods

Minerals Method: Samples were analyzed for minerals by heated closed vessel digestion/dissolution with nitric acid and hydrogen peroxide followed by quantitation using an inductively coupled plasma atomic emission spectrometer³⁶. Nitrogen content was measured using flash combustion of the sample coupled with thermal conductivity/IR detection of the combustion gases (N₂, NO_x, CO₂) using a LECO TruSpec CN Analyzer³⁷.

Protein values are based on measurement of nitrogen and conversion to protein per the equation below where $k=5.36$ ³⁸:

$$\text{Protein (weight \%)} = k * \text{N (weight \%)}.$$

For phytic acid determination, a modified version of the method of Huag and Lantzsch ³⁹ was used. The method's accuracy was monitored by inclusion of tissue standards of known and varying levels of phytic acid ⁴⁰.

Dietary Calculations—The United Nations Food and Agriculture Organization (UNFAO) publishes annual Food Balance Sheets (FBS), which provide country-specific data on the quantities of 95 ‘standardized’ food commodities available for human consumption. Data, expressed in terms of dietary energy (kcal per capita per day) were downloaded for 210 countries and territories with available information for the period from 2003–2007 (Available at <http://faostat.fao.org>). The percentage of dietary energy available from C₃ grasses (wheat, barley, rye, oats, rice, “cereals, other” (excluding teff)) was calculated globally with estimates weighted by national population size (188 countries available; UN 2011. {Available at: <http://esa.un.org/wpp/>}).

Dietary intake data from the UNFAO FBS (through year 2000) and food composition data from the United States Department of Agriculture National Nutrient Database for Standard Reference were used to calculate per capita nutrient intake for 95 food items and shared with us by permission ⁴¹. This dataset was used to calculate the contribution of each food item to total dietary zinc and iron intake, and the proportions of all food items derived from C₃ grains and legumes were summed to identify countries highly dependent on plant sources of iron and zinc (Table E5).

Extended Data

Extended Data Table E1

Percent change in nutrient content at elevated [CO₂] relative to ambient [CO₂]

	N* (number of pairs)	Zn (µg/g)			Fe (µg/g)			Protein (mg/g)			Phytate (g)		
		%	95% CI	P-value	%	95% CI	P-value	%	95% CI	P-value	%	95% CI	
C ₃ grasses													
Wheat	64	-9.3	(-12.7, -5.9)	<.0001	-5.1	(-6.5, -3.7)	<.0001	-6.3	(-7.5, -5.2)	<.0001	-4.2	(-7.5, -0.9)	
Rice	31	-3.3	(-5.0, -1.7)	<.0001	-5.2	(-7.6, -2.9)	<.0001	-7.8	(-8.9, -6.8)	<.0001	1.2	(-4.6, 7.0)	
C ₃ legumes													
Field peas	10	-6.8	(-9.8, -3.8)	0.002	-4.1	(-6.7, -1.4)	0.003	-2.1	(-4.0, -0.1)	0.039	-5.8	(-11.5, 0.0)	
Soybeans	25	-5.1	(-6.4, -3.9)	<.0001	-4.1	(-5.8, -2.5)	<.0001	0.5	(-0.4, 1.3)	0.267	-1.3	(-3.7, 1.1)	
C ₄ grasses													
Maize	4	-5.2	(-10.7, 0.6)	0.077	-5.8	(-10.9, -0.3)	0.038	-4.6	(-13.0, 4.5)	0.312	-6.1	(-15.0, 2.8)	
Sorghum	4	-1.3	(-6.2, 3.8)	0.603	1.6	(-5.8, 9.7)	0.674	0.0	(-4.9, 5.2)	0.993	12.8	(-15.8, 41.4)	

* number of pairs refers to the number of comparisons where replicates of a particular cultivar grown at a specific site under one set of growing conditions in one year at elevated [CO₂] have been pooled and mean nutrient values for these replicates are compared with mean values for identical cultivars under identical growing conditions except grown at ambient [CO₂].

In most instances, data from four replicates were pooled for each value meaning that eight experiments were combined for each comparison (see Table 1 for details of experiments).

Extended Data Table E2

Original data combined with previously published FACE data from studies 3, 4, 6, and 7. (See Extended Data Table E6 for list of experiments). Percent change in nutrient content at elevated [CO₂] relative to ambient [CO₂]

	N* (number of pairs)	Zn (µg/g)			Fe (µg/g)			Protein (mg/g)			
		%	95% CI	P-value	%	95% CI	P-value	%	95% CI	P-value	
C ₃ grasses											
Wheat	70	-8.8	(-11.9, -5.6)	<.0001	-5.5	(-6.8, -4.1)	<.0001	-6.5	(-7.5, -5.4)	<.0001	
Rice	32	-3.1	(-4.8, -1.5)	<.0001	-4.9	(-7.3, -2.6)	<.0001	-8.0	(-9.0, -6.9)	<.0001	
Barley	4	-11.4	(-19.3, -2.7)	0.012	-10.5	(-12.2, -8.7)	<.0001	-11.9	(-13.1, -10.7)	<.0001	
C ₃ legumes											
Field peas	10	-6.8	(-9.8, -3.8)	0.002	-4.1	(-6.7, -1.4)	0.003	-2.1	(-4.0, -0.1)	0.039	
Soybeans	25	-5.1	(-6.4, -3.9)	<.0001	-4.1	(-5.8, -2.5)	<.0001	0.5	(-0.4,1.3)	0.267	
C ₃ Tuber											
Potato	2	-3.9	(-12.9,6.2)	0.440	2.3	(-3.8,8.7)	0.472	-4.6	(-7.7, -1.4)	<.0001	
C ₄ grasses											
Maize	4	-5.2	(-10.7,0.6)	0.077	-5.8	(-10.9, -0.3)	0.038	-4.6	(-13.0,4.5)	0.312	
Sorghum	4	-1.3	(-6.2,3.8)	0.603	1.6	(-5.8,9.7)	0.674	0.0	(-4.9,5.2)	0.993	

* number of pairs refers to the number of comparisons where replicates of a particular cultivar grown at a specific site under one set of growing conditions in one year at elevated [CO₂] have been pooled and mean nutrient values for these replicates are compared with mean values for identical cultivars under identical growing conditions except grown at ambient [CO₂]. In most instances, data from four replicates were pooled for each value meaning that eight experiments were combined for each comparison (see Table 1 for details of experiments).

Extended Data Table E3

Original data combined with previously published FACE and chamber data from studies 1–10. (See extended data Table E6 for list of experiments). Percent change in nutrient content at elevated [CO₂] relative to ambient [CO₂]

	N* (number of pairs)	Zn (µg/g)			Fe (µg/g)			Protein (mg/g)			
		%	95% CI	P-value	%	95% CI	P-value	%	95% CI	P-value	
C ₃ grasses											
Wheat	78	-9.1	(-12.1, -6.1)	<.0001	-5.9	(-7.8, -4.0)	<.0001	-7.2	(-8.6, -5.8)	<.0001	
Rice	32	-3.1	(-4.8, -1.5)	<.0001	-4.9	(-7.3, -2.6)	<.0001	-8.0	(-9.0, -6.9)	<.0001	
Barley	6	-13.6	(-19.3, -7.6)	<.0001	-10.0	(-12.4, -7.4)	<.0001	-15.0	(-19.1, -10.7)	<.0001	
C ₃ legumes											
Field peas	10	-6.8	(-9.8, -3.8)	<.0001	-4.1	(-6.7, -1.4)	0.003	-2.1	(-4.0, -0.1)	0.039	
Soybeans	28	-5.0	(-6.1, -3.9)	<.0001	-5.2	(-7.9, -2.5)	<.0001	0.1	(-0.8,0.9)	0.865	
C ₃ Tuber											
Potato	5	-10.0	(-20.9,2.4)	0.110	-4.1	(-16.6,10.3)	0.555	-9.7	(-15.9, -3.1)	0.005	
C ₄ grasses											
Maize	4	-5.2	(-10.7,0.6)	0.077	-5.8	(-10.9, -0.3)	0.038	-4.6	(-13.0,4.5)	0.312	
Sorghum	7	-0.6	(-4.5,3.4)	0.764	33.8	(-10.2,99.3)	0.153	-5.6	(-12.7,2.1)	0.150	

* number of pairs refers to the number of comparisons where replicates of a particular cultivar grown at a specific site under one set of growing conditions in one year at elevated [CO₂] have been pooled and mean nutrient values for these replicates are compared with mean values for identical cultivars under identical growing conditions except grown at ambient [CO₂]. In most instances, data from four replicates were pooled for each value meaning that eight experiments were combined for each comparison (see Table 1 for details of experiments).

Extended Data Table E4

Percent change in nutrient content at elevated [CO₂] compared with ambient [CO₂] for all nutrients

	C3 grasses						C3 legumes					
	Wheat			Rice			Field Peas			Soybean		
	%	95% CI	P-value	%	95% CI	P-value	%	95% CI	P-value	%	95% CI	P-value
Zinc (ppm)	-9.3	(-12.7, -5.9)	<.0001	-3.3	(-5.0, -1.7)	<.0001	-6.8	(-9.8, -3.8)	<.0001	-5.1	(-6.4, -3.9)	<.0001
Iron (ppm)	-5.1	(-6.5, -3.7)	<.0001	-5.2	(-7.6, -2.9)	<.0001	-4.1	(-6.7, -1.4)	<.0001	-4.1	(-5.8, -2.5)	<.0001
Phytate (mg/g)	-4.2	(-7.5, -0.8)	0.009	1.2	(-4.6, 7.4)	0.70	-5.8	(-11.5, 0.1)	0.055	-1.3	(-3.7, 1.2)	0.005
Protein	-6.3	(-7.5, -5.2)	<.0001	-7.8	(-8.9, -6.8)	<.0001	-2.1	(-4.0, -0.1)	0.039	0.5	(-0.4, 1.3)	0.003
Mn (ppm)				-7.5	(-12.0, -2.8)	0.00	-2.5	(-4.2, -0.8)	0.005	-1.4	(-3.5, 0.8)	0.005
Mg (%)				-0.9	(-2.3, 0.6)	0.24	0.0	(-1.3, 1.4)	0.960	-3.5	(-4.3, -2.8)	0.005
Cu (ppm)				-10.6	(-13.8, -7.1)	<.0001	-2.7	(-5.1, -0.3)	0.025	-5.7	(-8.0, -3.4)	0.005
Ca (%)				2.0	(-0.8, 4.9)	0.16	-0.5	(-4.2, 3.3)	0.787	-5.8	(-7.3, -4.2)	0.005
S (ppm)				-7.8	(-8.8, -6.8)	<.0001	-2.2	(-3.6, -0.7)	0.003	-2.9	(-3.5, -2.2)	0.003
K (%)				1.1	(-0.3, 2.5)	0.13	2.2	(0.6, 3.8)	0.008	0.1	(-0.8, 1.0)	0.008
B (ppm)				5.1	(1.9, 8.4)	0.002	-1.9	(-3.9, 0.1)	0.057	-6.4	(-9.1, -3.6)	0.002
P (%)				-1.0	(-2.4, 0.4)	0.16	-3.7	(-6.8, -0.5)	0.023	-0.7	(-2.2, 0.9)	0.023

Extended Data Table E5

Countries whose populations receive at least 60% of dietary iron and/or zinc from C₃ grains and legumes per United Nations Food and Agriculture Organization food balance sheets and 2010 United Nations estimated population

Country	% Iron from C ₃ grains & legumes	% Zinc from C ₃ grains & legumes	Population (in thousands)
Afghanistan	78%	78%	31,412
Algeria	76%	79%	35,468
Iraq	74%	83%	31,672
Bangladesh	72%	88%	148,692
Iran, Islamic Rep of	72%	77%	73,974
Pakistan	70%	72%	173,593
Tunisia	70%	77%	10,481
Jordan	69%	73%	6,187
Morocco	69%	78%	31,951
Syrian Arab Republic	67%	71%	20,411
Libya	67%	71%	6,355
Yemen	66%	75%	24,053

Country	% Iron from C ₃ grains & legumes	% Zinc from C ₃ grains & legumes	Population (in thousands)
Myanmar	65%	81%	47,963
Tajikistan	62%	56%	6,879
India	59%	71%	1,224,614
Egypt	54%	65%	81,121
Indonesia	52%	65%	239,871
Sierra Leone	51%	70%	5,868
Cambodia	49%	68%	14,138
Sri Lanka	46%	69%	20,860
Laos	44%	66%	6,201
Viet Nam	43%	61%	87,848
Total			2,329,612

Extended Data Table E6

Literature reporting nutrient changes in the edible portion of crops grown at elevated and ambient [CO₂]

Study	Experimental Method	Associated Citations
1	Growth Chambers	Conroy, J., Seneweera, S. P., Basra, A., Rogers, G. & Nissen-Wooler, B. Influence of rising atmospheric CO ₂ concentrations and temperature on growth, yield and grain quality of cereal crops. <i>Australian Journal of Plant Physiology</i> 21, 741–758 (1994).
		Seneweera, S., Milham, P. & Conroy, J. Influence of elevated CO ₂ and phosphorus nutrition on the growth and yield of a short-duration rice. <i>Australian Journal of Plant Physiology</i> 21, 281–292 (1994).
		Seneweera, S. P. & Conroy, J. P. Growth, grain yield and quality of rice (<i>Oryza sativa</i> L.) in response to elevated CO ₂ and phosphorus nutrition (Reprinted from <i>Plant nutrition for sustainable food production and environment</i> , 1997). <i>Soil Sci. Plant Nutr.</i> 43, 1131–1136 (1997).
2	Temperature Gradient Tunnels	De la Puente, L. S., Perez, P. P., Martinez-Carrasco, R., Morcuende, R. M. & Del Molino, I. M. M. Action of elevated CO ₂ and high temperatures on the mineral chemical composition of two varieties of wheat. <i>Agrochimica</i> 44, 221–230 (2000).
3	Open Top Chambers & FACE	De Temmerman L et al. Effect of climatic conditions on tuber yield (<i>Solanum tuberosum</i> L.) in the European ‘CHIP’ experiments. <i>European Journal of Agronomy</i> 17, 243–255 (2002).
		De Temmerman, L., Hacour, A. & Guns, M. Changing climate and potential impacts on potato yields and quality ‘CHIP’: introduction, aims and methodology. <i>European Journal of Agronomy</i> 17, 233–242 (2002).
		Fangmeier, A., De Temmerman, L., Black, C., Persson, K. & Vorne, V. Effects of elevated CO ₂ and/or ozone on nutrient concentrations and nutrient uptake of potatoes. <i>European Journal of Agronomy</i> 17, 353–368 (2002).
		Högy, P. & Fangmeier, A. Atmospheric CO ₂ enrichment affects potatoes: 2. Tuber quality traits. <i>European Journal of Agronomy</i> 30, 85–94 (2009).
4	FACE	Erbs, M. et al. Effects of free-air CO ₂ enrichment and nitrogen supply on grain quality parameters and elemental composition of wheat and barley grown in a crop rotation. <i>Agriculture, Ecosystems and Environment</i> 136, 59–68 (2010).

Study	Experimental Method	Associated Citations
5	Open Top Chambers	Fangmeier, A. et al. Effects of elevated CO ₂ , nitrogen supply and tropospheric ozone on spring wheat. I. Growth and yield. <i>Environmental Pollution</i> 91, 381–390 (1996).
		Fangmeier, A., Grütters, U., Högy, P., Vermehren, B. & Jäger, H.-J. Effects of elevated CO ₂ , nitrogen supply and tropospheric ozone on spring wheat – II. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). <i>Environmental Pollution</i> 96, 43–59 (1997).
		Fangmeier, A. et al. Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO ₂ concentrations and stress conditions in the European, multiple-site experiment 'ESPACE-wheat'. <i>European Journal of Agronomy</i> 10, 215–229 (1999).
		Jäger, H.-J., Hertstein, U. & Fangmeier, A. The European Stress Physiology and Climate Experiment – project 1: wheat (ESPACE-wheat): introduction, aims and methodology. <i>European Journal of Agronomy</i> 10, 155–162 (1999).
6	FACE	Högy, P. & Fangmeier, A. Effects of elevated atmospheric CO ₂ on grain quality of wheat. <i>Journal of Cereal Science</i> 48, 580–591 (2008).
		Högy, P. et al. Does elevated atmospheric CO ₂ allow for sufficient wheat grain quality in the future?. <i>Journal of Applied Botany and Food Quality</i> 82, 114–121 (2009).
		Högy, P. et al. Effects of elevated CO ₂ on grain yield and quality of wheat: results from a 3-year free-air CO ₂ enrichment experiment. <i>Plant Biology</i> 11, 60–69 (2009).
		Högy, P., Zörb, C., Langenkämper, G., Betsche, T. & Fangmeier, A. Atmospheric CO ₂ enrichment changes the wheat grain proteome. <i>Journal of Cereal Science</i> 50, 248–254 (2009).
7	FACE	Kim, H., Liefferring, M., Miura, S., Kobayashi, K. & Okada, M. Growth and nitrogen uptake of CO ₂ -enriched rice under field conditions. <i>New Phytologist</i> 150, 223–229 (2001).
		Kim, H. et al. Effects of free-air CO ₂ enrichment and nitrogen supply on the yield of temperate paddy rice crops. <i>Field Crops Research</i> 83, 261–270 (2003).
		Liefferring, M., Kim, H.-Y., Kobayashi, K. & Okada, M. The impact of elevated CO ₂ on the elemental concentrations of field-grown rice grains. <i>Field Crops Research</i> 88, 279–286 (2004).
8	Open Top Chambers	Pleijel, H. et al. Effects of elevated carbon dioxide, ozone and water availability on spring wheat growth and yield. <i>Physiologia Plantarum</i> 108, 61–70 (2000).
		Pleijel, H. & Danielsson, H. Yield dilution of grain Zn in wheat grown in open-top chamber experiments with elevated CO ₂ and O ₃ exposure. <i>Journal of Cereal Science</i> 50, 278–282 (2009).
9	Open Top Chambers	Prior, S. A., Runion, G. B., Rogers, H. H., Torbert, H. A. Effects of atmospheric CO ₂ enrichment on crop nutrient dynamics under no-till conditions. <i>Journal of Plant Nutrition</i> 31, 758–773 (2008).
10	Open Top Chambers	Weigel, H., Manderscheid, R., Jäger, H.-J. & Mejer, G. Effects of season-long CO ₂ enrichment on cereals. I. Growth performance and yield. <i>Agriculture, Ecosystems and Environment</i> 48, 231–240 (1994).
		Manderscheid, R., Bender, J., Jäger, H., J & Weigel, H., J. Effects of season long CO ₂ enrichment on cereals. II. Nutrient concentrations and grain quality. <i>Agriculture, Ecosystems & Environment</i> 54, 175–185 (1995).
11	FACE	Yang, L., Wang, Y., Dong, G., Gu, H., Huang, J., Zhu, J., Yang, H., Liu, G., Han, Y. The impact of free-air CO ₂ enrichment (FACE) and nitrogen supply on grain quality of rice. <i>Field Crops Research</i> 102, 128–140 (2007).
	Meta-Analyses	Loladze, I. Rising atmospheric CO ₂ and human nutrition: toward globally imbalanced plant stoichiometry? <i>Trends in Ecology and Evolution</i> 17 (10), 457–461 (2002). [Uses data from studies 1, 2, 5, and 10 as well as numerous other studies on non-edible tissues and plants other than food crops].

Study	Experimental Method	Associated Citations
		McGrath, J. M. and Lobell, D. B. Reduction of transpiration and altered nutrient allocation contribute to nutrient decline of crops grown in elevated CO ₂ concentrations. <i>Plant, Cell, & Environment</i> 36, 697–705 (2013). [Uses data from studies 1, 5, and 10 as well as numerous other studies on non-edible tissues and plants other than food crops].
		Duval, B.D., Blankinship, J. C., Dijkstra, P., Hungate, B. A. CO ₂ effects on plant nutrient concentration depend on plant functional group and available nitrogen: a meta-analysis. <i>Plant Ecology</i> 213, 505–521 (2012). [Uses data from studies 1,2, 3, 5, 6, and 9 as well as numerous other studies on non-edible tissues and plants other than food crops].

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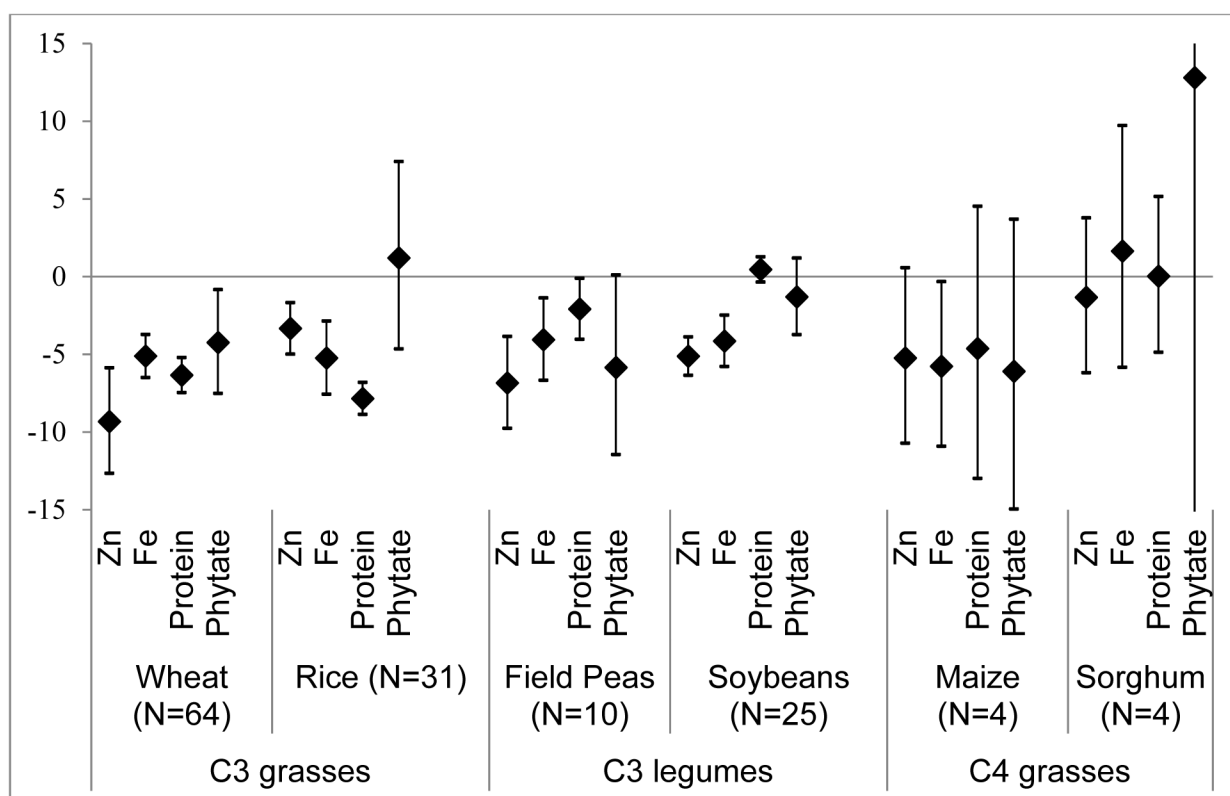
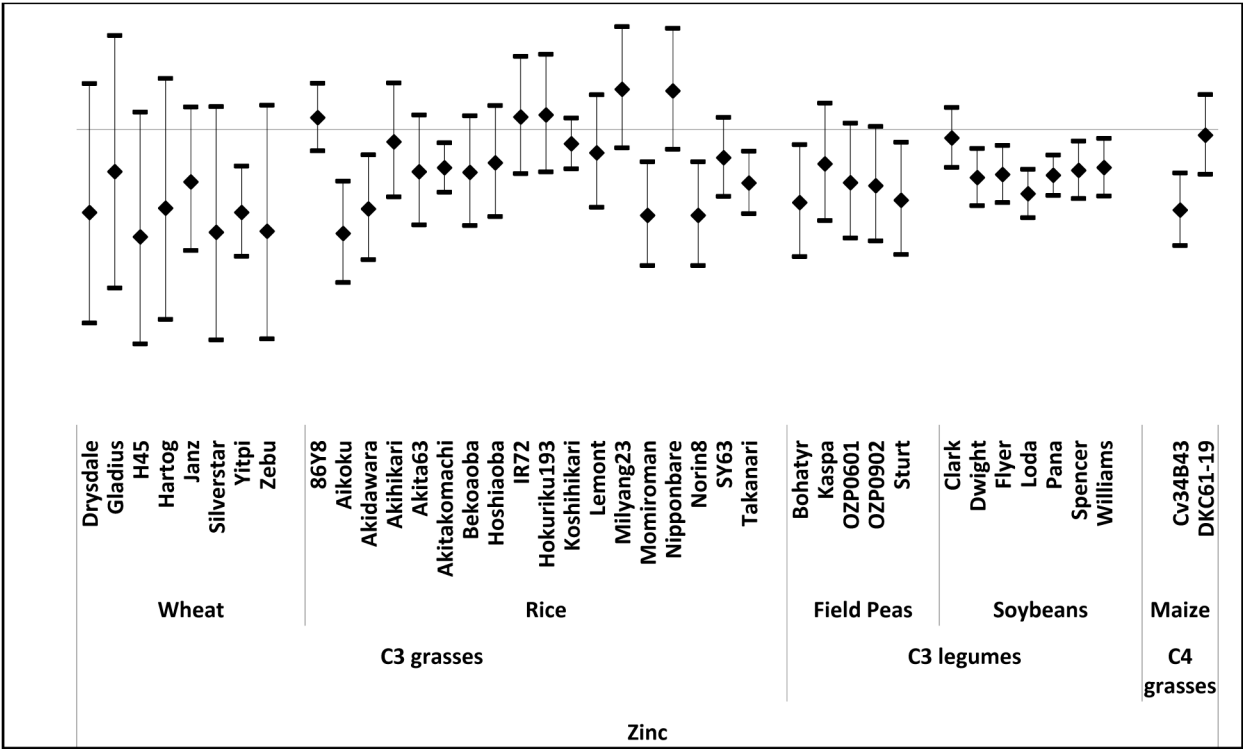
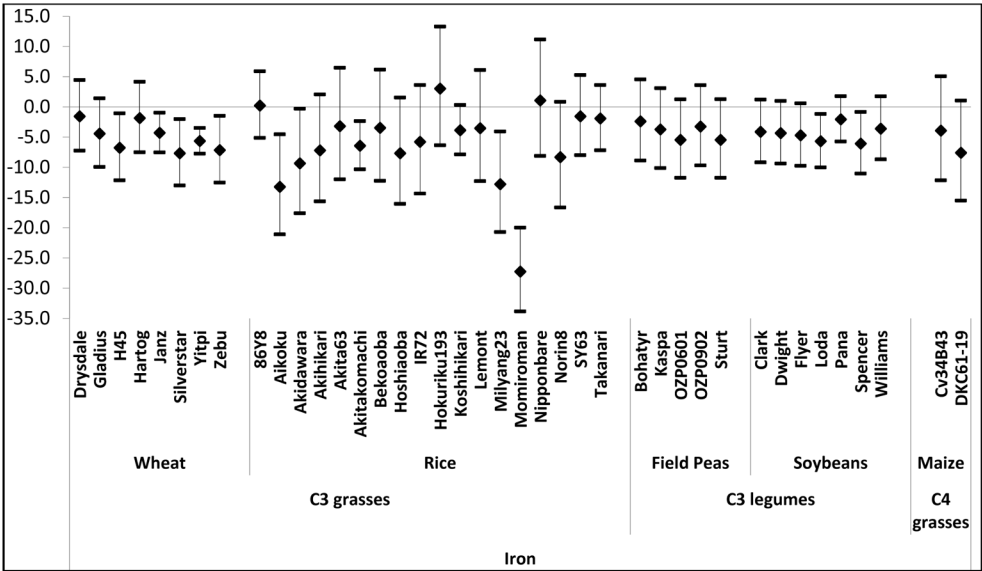


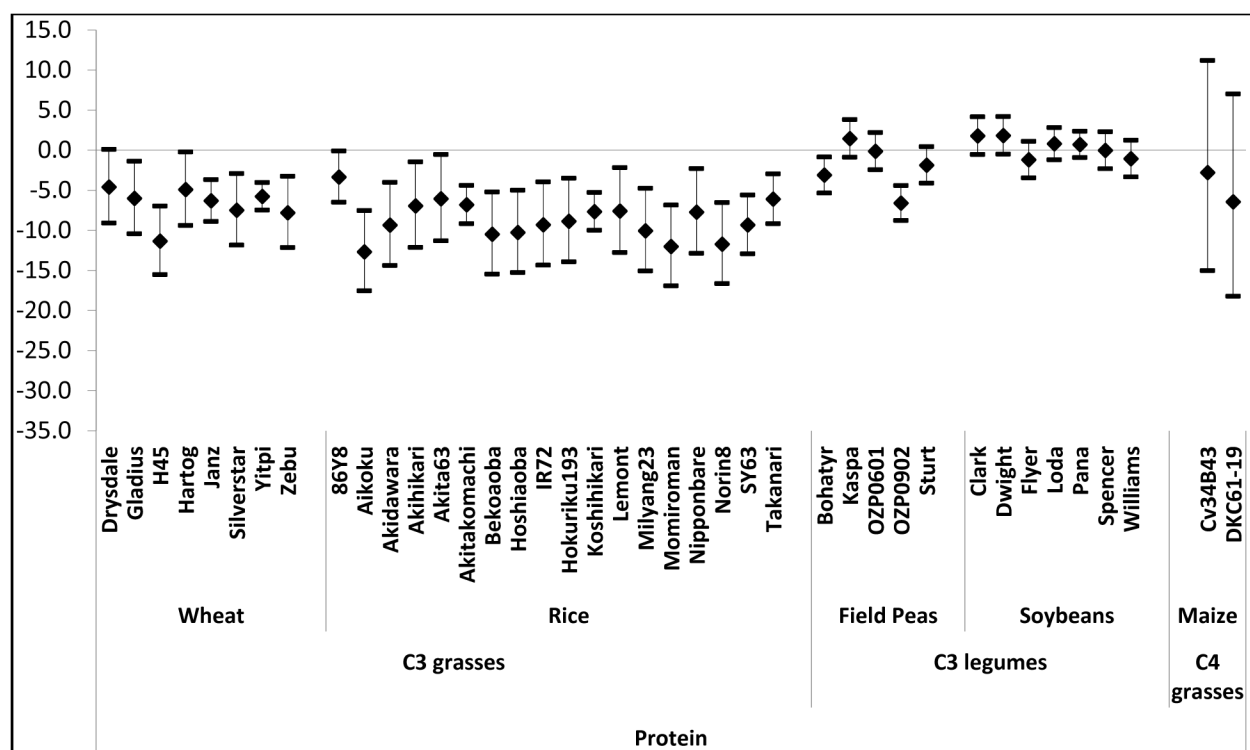
Figure 1. Percent change in nutrient content at elevated $[\text{CO}_2]$ relative to ambient $[\text{CO}_2]$
 Percent change (95% Confidence Intervals) in nutrients at elevated $[\text{CO}_2]$ relative to ambient $[\text{CO}_2]$. N refers to the number of comparisons where replicates of a particular cultivar grown at a specific site under one set of growing conditions in one year at elevated $[\text{CO}_2]$ have been pooled and mean nutrient values for these replicates are compared with mean values for identical cultivars under identical growing conditions except grown at ambient $[\text{CO}_2]$. In most instances, data from four replicates were pooled for each value meaning that eight experiments were combined for each comparison (see Table 1 for details of experiments).



A)



B)



C)

Figure 2. Percent change in nutrient content at elevated $[\text{CO}_2]$ relative to ambient $[\text{CO}_2]$ by cultivar for each of three nutrients

Percent change (95% Confidence Intervals) in zinc (A) iron (B) and protein (C) at elevated $[\text{CO}_2]$ relative to ambient $[\text{CO}_2]$ by cultivar.

Table 1

Characteristics of agricultural experiments

Crops	Country	Treatments used	Years grown	# of Replicates *	# of Cultivars	CO ₂ ambient/elev (ppm)
Wheat	Australia	2 water levels, 2 N treatments, 2 Sowing times	2007–10	4	8	382/546–550
	Australia	1 Water level, 1 N treatment 2 Sowing times	2007–9	4	1	382/546–550
Field Peas	Australia	2 water levels	2010	4	4	382/546–550
Rice	Japan	1 N treatment, 2 warming treatments	2007–8	3	3	376–379/570–576
	Japan	3 N treatments, 2 warming treatments	2010	4	18	386/584
Maize	U.S.	2 N treatments	2008	4	2	385/550
Soybeans	U.S.	1 treatment	2001, 02, 04, 2006–08	4	7	372–385/550
Sorghum	U.S.	2 water levels,	1998–99	4	1	363–373/556–579

* „# of replicates” refers to the number of identical cultivars grown under identical conditions in the same year and location but in separate FACE rings