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Estimated Effects of Future Atmospheric CO₂ Concentrations on Protein Intake and the Risk of Protein Deficiency by Country and Region

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BACKGROUND: Crops grown under elevated atmospheric CO₂ concentrations (eCO₂) contain less protein. Crops particularly affected include rice and wheat, which are primary sources of dietary protein for many countries.

OBJECTIVES: We aimed to estimate global and country-specific risks of protein deficiency attributable to anthropogenic CO₂ emissions by 2050.

METHODS: To model per capita protein intake in countries around the world under eCO₂, we first established the effect size of eCO₂ on the protein concentration of edible portions of crops by performing a meta-analysis of published literature. We then estimated per-country protein intake under current and anticipated future eCO₂ using global food balance sheets (FBS).

We modeled protein intake distributions within countries using Gini coefficients, and we estimated those at risk of deficiency from estimated average protein requirements (EAR) weighted by population age structure.

RESULTS: Under eCO₂, rice, wheat, barley, and potato protein contents decreased by 7.6%, 7.8%, 14.1%, and 6.4%, respectively. Consequently, 18 countries may lose >5% of their dietary protein, including India (5.3%). By 2050, assuming today's diets and levels of income inequality, an additional 1.6% or 148.4 million of the world's population may be placed at risk of protein deficiency because of eCO₂. In India, an additional 53 million people may become at risk.

CONCLUSIONS: Anthropogenic CO₂ emissions threaten the adequacy of protein intake worldwide. Elevated atmospheric CO₂ may widen the disparity in protein intake within countries, with plant-based diets being the most vulnerable. <https://doi.org/10.1289/EHP41>

Introduction

Globally, 76% of the population derives most of their daily protein from plants (FAO 2014a). With projected population growth to 9.5 billion by 2050 (UN 2013), alongside dietary and demographic changes, future nutritional demands may overwhelm global crop production (Alexandratos 1999). Compounding the strain on food supply, plant nutrient content changes under elevated atmospheric carbon dioxide concentrations (eCO₂) (Myers et al. 2014).

Under the CO₂ concentrations predicted in the next 50 y, crops with C₃ photosynthesis, such as rice and wheat, may experience up to 15% decreases in grain protein content (Myers et al. 2014). The effects of eCO₂ are less on C₄ crops, such as maize and sorghum, and on nitrogen-fixing plants, such as legumes (Myers et al. 2014). Thus, the impacts of eCO₂ on dietary protein intake will depend on which staples a country consumes, their dependence on the staple for protein, and their current risk of protein deficiency.

Protein deficiency usually co-occurs with energy and micronutrient deficiencies (Millward and Jackson 2004). Insufficient protein intake limits growth, tissue repair, and turnover (Groppe and Smith 2008). Few controlled studies investigate protein deficiency syndromes in otherwise energy and nutrient sufficient diets. In renal disease, isocaloric protein reduction decreased lean

body mass and lymphocyte count (Ihle et al 1989; Klahr et al. 1994). In elderly women, these diets reduced cell mass and protein synthesis while impairing muscle function and immune status (Castaneda et al. 1995). Low protein intake contributes to wasting, stunting, intrauterine growth restriction, and low birth weight (Black et al. 2008). Together with protein–energy malnutrition syndromes, this causes an estimated 90.9 million disability-adjusted life years (DALYs) and 2 million deaths annually (Black et al. 2008).

Previous meta-analyses conducted on the effects of eCO₂ on plant nutrient contents (Taub et al. 2008; Loladze 2014) have not assessed eCO₂ impacts on edible protein from a global dietary context, nor did they consider distributional effects within countries. We aimed to estimate eCO₂ impacts on global protein intake, and on the proportion of the population by country at risk of protein deficiency. We aimed to expand on the meta-analysis by Myers et al. (2014), including all available studies reporting eCO₂ impacts on the edible portions of crop plants, including lesser-studied foods and studies in (sub)tropical locations. Then, using published food balance sheets (FBS) and measures of economic inequality within countries, we aimed to estimate dietary protein intake under current and future atmospheric CO₂. We thereby tested the sensitivity of global protein intake and inequality of intake to rising atmospheric CO₂, identifying key regions to target with nutritional interventions.

Methods

Systematic Review and Raw Data

We conducted ISI Web of Knowledge (<https://pcs.webofknowledge.com/>) literature searches in July–September 2014 and in January 2016 for the effects of eCO₂ on the protein content of all plants listed in the FAO FBS. This study supplements the meta-analysis of common European/U.S. staples conducted by Myers et al. (2014). Because estimates of plant protein are commonly derived by multiplying measured plant nitrogen (N) by a conversion factor, we considered published changes in N and protein to be equivalent (Taub et al. 2008). For the full search string and exclusions, see “Part 1” and “Part 2” in the Supplemental

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Material. A total of 119 citations were used. For references, see “Part 3” in the Supplemental Material.

We included raw data from free-air CO₂ enrichment (FACE) and open-top chamber studies, with data from European wheat, barley, and potato Changing Climate and Potential Impacts on Potato Yield and Quality (CHIP) and the European Stress Physiology and Climate Experiment (ESPACE) studies (A. Fangmeier, unpublished data, 1994–1999) and Australian wheat and pea Australian Grains Free Air CO₂ Enrichment (AGFACE), Japanese rice, American soy, corn, and sorghum Soybean Free Air Concentration Enrichment (SoyFACE) and Arizona FACE (data from Myers et al. 2014). Raw data included free-to-air carbon dioxide elevation (FACE) and open-top chamber studies, 41 cultivars, nitrogen fertilizer, watering, and time of sowing treatments over multiple years.

Response ratios (RRs) and standard errors (SEs) for protein response to CO₂ were calculated from each study’s reported error terms. When studies indicated merely significant at $p < 0.05$ or not significant, the SE was calculated from p -values of 0.049 and 0.1, respectively.

Metaregression

Metaregression was performed individually for each commodity where data were available from four or more experiments and for commodity groups listed in the FAO FBS (Table 1). We used the statistical package Metafor (version 1.9-4 Wolfgang Viechtbauer) in R (version 3.0.3; R Development Core Team). For each commodity or group, the difference between ambient (aCO₂) and eCO₂ treatments was tested as a modifier. We used multivariate linear (mixed-effects) models (the function rma.mv) with outcomes being percent decrease in protein, and modifiers being the difference between aCO₂ and eCO₂ in parts per million. Models included variance and were weighted by replicate facilities (e.g., number of FACE rings or growth cabinets) with random effects being year within site, and each cultivar (and unless tested as a modifier, each watering and nitrogen fertilizer treatment) was treated as a separate experiment. We performed Q tests to assess heterogeneity.

Meta-Analysis

Because there was no reliable dose-dependent decrease in protein content with degree of CO₂ elevation, we used meta-analysis to derive average response ratios comparing plants grown in aCO₂

Table 1. Percent change in protein content by commodity class.

Commodity (n)	Estimate [mean (95% CI)]
C ₃ grains (257)	-8.14 (-12.17, -4.1)
Wheat (166)	-7.78 (-13.24, -2.32)
Rice (66)	-7.61 (-11.53, -3.69)
Barley (21)	-14.05 (-20.7, -7.39)
C ₄ grains (12)	2.07 (-3.2, 7.35)
Maize (8)	3.08 (-5.19, 11.35)
Sorghum (4)	0.26 (-6.31, 6.84)
Root vegetable (15)	-3.42 (-8.61, 1.78)
Potato (9)	-6.38 (-10.33, -2.42)
Pulses, legumes (26)	-3.51 (-8.05, 1.04)
Peas (15)	-1.69 (-3.56, 0.18)
Beans (7)	-4.58 (-12.37, 3.2)
Chickpea (4)	-13.47 (-21.36, -5.58)
Oil crops (54)	-0.78 (-5.03, 3.47)
Soy (44)	-0.49 (-2.92, 1.95)
Rapeseed/mustard seed (5)	0.92 (-8.9, 10.74)
C ₃ Vegetables (32)	-17.29 (-30.78, -3.8)
Fruit (5)	-22.9 (-54.04, 8.24)

Note: C₃, crops with C₃ photosynthesis; C₄, crops with C₄ photosynthesis; CI, confidence interval; n , number of experiments, where each treatment/cultivar/experiment was treated as a separate experiment, yet experiments at the same location for the same crop were grouped together.

with plants grown in eCO₂, where eCO₂ was in the range of 500–700 ppm. We used the rma.mv function as for metaregression, but without the modifier term. Both meta-analysis and metaregression tested fixed effects of pot- versus field-grown plants and a qualitative measure of nitrogen fertilizer treatment, categorized as low, adequate, or high, based on descriptions in each study’s experimental design. Neither modifier changed the magnitude of the CO₂ response, and neither was used in subsequent analyses.

We minimized publication bias by including unpublished data. Furthermore, we tested sensitivity to publication bias. For each commodity, we incrementally added experiments with no effect of eCO₂ on protein content (RR 1, variance 0.5) until confidence intervals for RR crossed 1. Some commodities, including rice, were sensitive to null results, but wheat was insensitive to null results (see Table S3).

Food Balance Sheets

The FAO FBS estimate per capita availability of each food-based commodity (including energy and protein contents). We averaged data over 2009–2013 FAO FBS. We assumed that protein availability equals protein intake, corrected for digestibility (FAO 2014a). Per convention, we assumed that plant-based protein was 80% digestible and that animal-based protein was 95% digestible (Millward and Jackson 2004).

The “Vegetables, other” and “Cereals, other” categories were large contributors to protein intake in some countries, and contained both C₃ and C₄ plants, and for vegetables, nitrogen fixers. We produced weighted estimates of the contributions of each these categories, using re-calculated 2009 FBS from the FAOstat classic platform (described fully by Smith et al. 2015). We converted from total grams to grams protein, using food composition tables (Abdel-Aal et al 1997; USDA 2011; FAO 2012; Ballogou et al. 2013; New Zealand Ministry of Health 2014). We assumed that the “Cereals, other, not elsewhere specified” category within the “Cereals, other” category was derived from C₄ grains in sub-Saharan Africa, but from C₃ grains elsewhere.

To estimate the effect of eCO₂ on protein intake in each country, we assumed constant mass-based consumption of each commodity over time, with declining protein content predicted by our meta-analyses. We used commodity-based averages when available, and otherwise applied the averages from the commodity group to each commodity (Table 1). We found no studies on eCO₂ response of tree nuts, thus conservatively assumed no change in their protein content. Likewise, we assumed no eCO₂ effect on animal protein.

Plant-Based Diets

Within a population, the lowest protein consumers also frequently consume the least meat (see World Food Programme household surveys; e.g. Santacroce 2008). For an extreme scenario, we reran the models, removing all animal-sourced foods (including eggs and dairy) from the diet, assuming no other changes in dietary fractional composition.

Intake Distribution

We assumed a lognormal distribution of protein intake within countries (FAO 2014b), a cumulative distribution function, with the mean,

$$\mu = \ln \bar{x} - \frac{\sigma^2}{2}$$

and the standard deviation,

$$\sigma = \sqrt{\ln(1 + CV^2)}$$

where \bar{x} is the national mean protein intake, as estimated above, and CV is its coefficient of variation. Because protein intake is likely to be related to household income, we estimated the CV of protein intake (CV_{protein}) from the Gini coefficient of national household income inequality. The national Gini coefficient for household income describes a Lorenz curve plotting the cumulative percentages of total income against the cumulative number of households from poorest to richest. Using linear regression, we compared per-household CV_{protein} from household surveys across 36 countries (FAO 2014a) with contemporaneous national Gini coefficients (Arneberg and Pedersen 2001; Garcia et al. 2001; Kim and Kim 2007; OECD 2009; Liberati 2013; USAID 2012; CIA 2014; Solt 2014; World Bank 2014). The FAO uses Gini coefficients, gross domestic product (GDP), and food prices to estimate CV for caloric intake (FAO 2015). We then estimated the national CV_{protein} from the country's Gini coefficient in the year closest to 2011. Owing to high uncertainty among future economic projections, we assumed each country's future CV_{protein} would remain constant.

Estimated Average Requirements

We calculated a weighted estimated average requirement (EAR) (grams per day) for absorbed protein from the published EAR for adults (0.66 g/kg/d) and for children by age and sex, using current and mid-range 2050 demographic projections (IOM 2005; UN 2013). For adults, the minimum safe protein intake in grams per day is based on the minimum healthy body weight calculated from the lowest 5th percentile of body mass index (BMI), this being 18.5 kg/m² (WHO 1995). We calculated average height from national surveys (OECD 2009; Hatton and Bray 2010; USAID 2012). Where male height was unavailable, it was calculated as 1.08 × female height, based on the median male-to-female height ratio across all countries. For child weight, the ideal body mass was the 50th percentile by age from growth tables (WHO 2006). We adjusted EAR to include the increased protein requirements of pregnant and lactating women (IOM 2005) with demographics estimated from projected birth rates, 2009 stillbirth rates and infant mortality, and breastfeeding prevalence and duration (McDowell et al. 2008; AIHW 2011; CDC 2011; UN 2013; USAID 2012; Liu et al. 2013).

Risk of Protein Deficiency

From each country's 2050 population, we calculated the proportion and the number of people whose intake fell below the EAR under current and eCO₂ scenarios, with the difference between these populations being our measure of impact.

We used Monte Carlo methods to propagate error from the SE of the meta-analysis results, and for modeled CV_{protein} , through the model, using 10,000 random draws from normal distributions of mean national protein intakes, and again for error around linear regression of CV_{protein} on Gini coefficient. From these two parameters, we calculated the means (μ) and standard deviations (σ) of 10,000 lognormal distributions. These were used to estimate the probability for each country of protein intake being below the calculated EAR.

We summarize data based on regional classifications from the reporting regions of the Global Burden of Disease Study 2010 (Lim et al. 2012), but we present India and the greater China region separately because of their large population sizes.

At each stage of analysis, where country-specific data were unavailable, data were derived from regional estimates, which were in turn derived from weighted means by population size of

each available country represented within the region (see Table S4 for regions).

Protein–Energy Ratio

Assuming all calories lost from declines in food protein contents were replaced as carbohydrates (as supported by the stoichiometry of Loladze 2014), we calculated the ratio of protein to total energy in current diets and projected diets under eCO₂. Because commodity-based digestibility of energy is less easily estimated, digestibility was not included in these estimates.

Results

Our analysis was based on 99 high-CO₂ experiments and 48 crops, and it included 54 field experiments. Of the 64 experimental sites, 37 were elsewhere than Europe or North America (see Table S1).

In maize, peas, and mustard seed, we found a linear dose response when the RR of protein content was compared with the degree of CO₂ elevation above ambient (see Tables S1 and S2). Metaregression for other crops was not significant, partly because of insufficient statistical power. Maize protein content under eCO₂ was not significantly below that under aCO₂ when considered overall from meta-analyses or when predicted for an atmospheric CO₂ increase of 150 ppm from metaregression. Metaregression predicted a decrease in pea protein content of 4.1% (1.6–6.7%) with an atmospheric CO₂ increase of 150 ppm, and overall, meta-analyses showed no significant declines in pea protein. National changes in dietary protein content were on average 0.04% less when modeled for a 150 ppm increase in atmospheric CO₂ based on metaregression results compared with meta-analyses. This difference was small enough to warrant the use of meta-analyses rather than metaregression. Comparisons between field and pot-based experiments, and between nitrogen fertilizer treatments were largely nonsignificant ($p > 0.05$; see Table S2).

Meta-analyses confirmed lower protein content of C₃ grains (including barley, 14.1% lower), tubers (including potato, 6.4% lower), fruit (23.0% lower), and vegetables (17.3% lower) under eCO₂, with no significant change in the protein content of C₄ grains, nitrogen-fixing pulses, or oil crops (Table 1).

When these effect sizes were translated to FBS-standardized commodity intakes, the mean protein intake decreased under eCO₂ by >5% in 18 countries, including India, Bangladesh, Turkey, Egypt, Iran, and Iraq. Particularly large declines are expected through the Middle East and India, where a 5.3% decrease in dietary protein is predicted (Table 2, Figure 1).

Globally, >7% decreases in protein intake are predicted for plant-based diets under eCO₂, with countries dependent on C₃ staples particularly affected (Table 2), including Central Asia, North Africa and the Middle East (7.9%), Central and Eastern Europe (8.2%), and China (8.9%).

A significant positive linear relationship existed between the natural log of CV_{protein} and income-based Gini coefficients (slope 0.026, $p < 0.0001$; Figure 2). Income inequality explained half of within-country variation in protein intake ($r^2 = 0.49$).

Estimates indicated a 12.2% current risk of protein deficiency globally. With constant atmospheric CO₂ concentrations, we predict that globally, 15.1% or 1.4 billion people will be at risk of protein deficiency by 2050 because of demographic changes. This estimate includes 613.6 million people at risk in sub-Saharan Africa, 276.4 million in India, 131.7 million in Eastern and Southeast Asia and the Pacific, 84.4 million in Central Latin America and the Caribbean, and 77.8 million elsewhere in South Asia (Figure 3, Table 3).

Table 2. Change in dietary protein.

Region	Mean change in protein intake (%)	Mean change in protein intake (%), plant-based diet	Difference in protein–energy ratio (aCO ₂ minus eCO ₂ , %)
CALACA	–1.99 (–3.61, –0.36)	–4.03 (–6.64, –1.42)	–0.20 (–0.37, –0.04)
CANAME	–5.04 (–7.29, –2.79)	–7.87 (–10.88, –4.85)	–0.52 (–0.75, –0.29)
CEEAEU	–3.43 (–4.90, –1.97)	–8.19 (–10.6, –5.77)	–0.39 (–0.55, –0.22)
CHINAR	–4.91 (–6.06, –3.75)	–8.86 (–10.4, –7.32)	–0.57 (–0.71, –0.44)
ESEASP	–4.01 (–5.51, –2.52)	–6.78 (–8.96, –4.59)	–0.36 (–0.50, –0.23)
HIGHIN	–2.67 (–3.65, –1.68)	–7.95 (–9.91, –5.98)	–0.32 (–0.43, –0.20)
India	–5.34 (–7.02, –3.66)	–7.04 (–9.02, –5.05)	–0.47 (–0.61, –0.32)
SOASIA	–4.69 (–6.44, –2.94)	–7.11 (–9.40, –4.82)	–0.43 (–0.59, –0.27)
SOTRLA	–2.40 (–3.46, –1.34)	–6.18 (–8.14, –4.22)	–0.27 (–0.38, –0.15)
SUSAAF	–2.03 (–4.05, –0.01)	–2.71 (–5.13, –0.30)	–0.18 (–0.36, 0.00)
World	–3.93 (–5.15, –2.70)	–7.14 (–8.91, –5.37)	–0.41 (–0.53, –0.28)

Note: Figures represent population-weighted averages (and 95% confidence intervals) globally and for each region (2050 populations). Protein–energy ratio is the percentage of dietary energy (calories) that is derived from protein. CALACA, Central and Andean Latin America and the Caribbean; CANAME, Central Asia, North Africa and the Middle East; CEEAEU, Central and Eastern Europe; CHINAR, Greater China; ESEASP, East and Southeast Asia and the Pacific excluding China; HIGHIN, high income countries; SOASIA, South Asia excluding India; SOTRLA, Southern and Tropical Latin America; SUSAAF, sub-Saharan Africa. See Table S4 for country grouping.

With predicted atmospheric CO₂ concentrations >500 ppm by 2050, we estimate an additional 1.57% of the world’s population (148.4 million) will be at risk of protein deficiency, compared with 2050 aCO₂ scenarios. In particular, an additional 53.4 million people in India, 15.9 million elsewhere in South Asia and 24.6 million in sub-Saharan Africa are estimated to become newly at risk (Table 3, Figure 3). An additional 15.9 million people in the China region and 12.0 million in Central Asia, North Africa, and the Middle East are expected to become at risk with eCO₂. The greatest increases in percent at risk of protein deficiency are expected in Tajikistan, Bangladesh, Burundi, Liberia, Occupied Palestinian Territory, Iraq, and Afghanistan (Figure 3B).

Globally, we predict the protein–energy ratio (protein caloric contribution as a percent of total calories) to decrease under eCO₂ by 0.41%; in individual countries and regions, we predict this ratio to decrease by 0.6% in 17 countries including China, Iran, Iraq, Morocco, and Turkey. We expect decreases in China of 0.57% (Table 2).

Discussion

Our study highlights the potential impact of eCO₂ on dietary protein intake globally. Wheat and rice, among the most sensitive crops to eCO₂, are primary protein sources for 71% of the world’s population (FAO 2014a). By 2050, 148.4 million people worldwide may become at risk of protein deficiency from rising CO₂.

In India, expected to be the world’s most populous country (UN 2013), and a country that is highly dependent on rice, 53.4 million people may be newly at risk of protein deficiency. Additionally, the protein deficiency in roughly 1.4 billion people globally (predicted under aCO₂ in 2050) is anticipated to become more severe under eCO₂ scenarios. Although estimates of current protein intake and income inequality highlight the current risk of deficiency in sub-Saharan Africa and South America, their dependence on less-sensitive C₄ crops make these diets less sensitive to eCO₂.

Importantly, we incorporated into the risk assessment different distributions of protein intake in countries based on income inequality from the association of income-based Gini coefficients with variability in protein intake from national dietary surveys. We find it equally plausible that CV_{protein} would decrease or increase by 2050. We therefore provide the most conservative estimate of future protein intake distributions, namely that CV_{protein} within countries will remain unchanged. We also assume unchanged duration and prevalence of breastfeeding, and unchanged adult height.

Although our calculations assume no change in the shape of the intake distribution, we anticipate a worsening of inequality in protein intake within populations because a larger decrease in protein content is observed in plant-based than in omnivore diets under eCO₂ (Table 2). Some changes in meat quality are anticipated owing to increased fat content under lower-protein diets

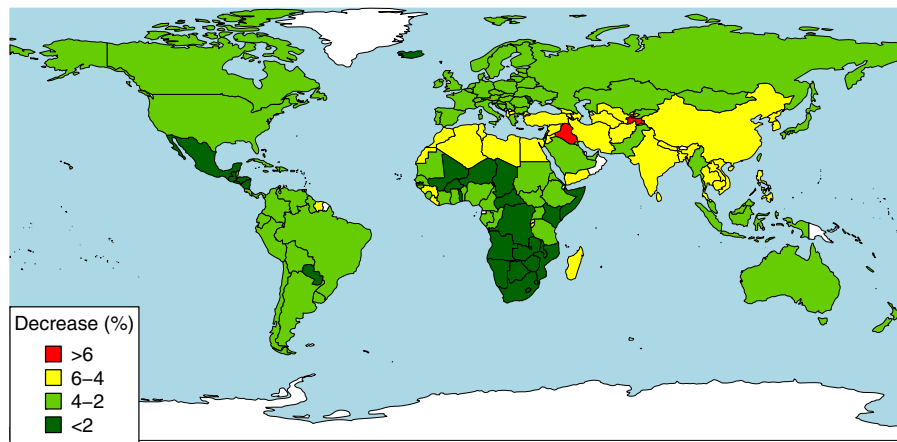


Figure 1. Per-country change in dietary protein intake under elevated carbon dioxide [eCO₂ (%)]. Baseline intake is based on Food and Agriculture Organisation of the United Nations Food Balance Sheets (FAO FBS) estimates, and changes are calculated from decreases in protein content in the edible portions of crops when grown under eCO₂. Data were plotted using the Rworldmap package in R (version 3.2.4; R Development Core Team).

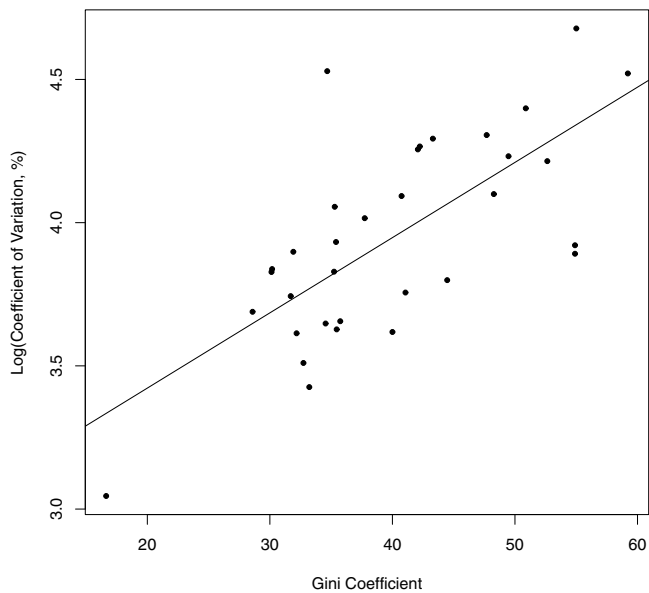


Figure 2. Coefficient of variation in protein intake derived from household surveys plotted against the income-based Gini coefficient for the year closest to the year household surveys were conducted (slope 0.026, $p < 0.0001$).

(Blome et al. 2003), but this is likely to be negligible compared with the effects on plant-based protein sources. Those who consume the least protein have diets more dependent on plant protein, and these people are more vulnerable to eCO_2 effects on plant protein. This is likely to extend the lower tail of the intake distribution, increasing the severity and prevalence of protein inadequacy. Our estimates are worst-case scenarios where no substitution of animal-sourced protein sources for other high-protein foods is allowed. In particular, the predicted large decreases in protein content of plant-based diets in high income countries may be overestimates, where plant-based diets are likely to be supplemented with other protein sources.

The countries that we estimated to be currently most at risk of protein deficiency are also those with the greatest estimated prevalence of undernourishment (FAO 2014b), increasing confidence in our estimates; however, energy balance and nitrogen balance interact (Garza et al. 1976). For simplicity, we modeled overall protein intake and risk of deficiency based on the EAR, which assumes adequate energy intake. Published EARs are defined for zero protein balance, which is a conservative estimate of protein requirements (IOM 2005). Older, sedentary people and those suffering from or recovering from illness are likely to be at greater risk of deficiency in any population (Ghosh 2013). We have not accounted for current or future patterns of illness in our estimates of EAR. Furthermore, we have not considered changes in protein quality; however, several studies have shown that essential amino acids tend to be relatively preserved at the expense of nonessential amino acids under eCO_2 , and degradability may decrease (Högy et al. 2009; Wroblewitz et al. 2013). Bioavailability may change, for example, if meal composition and thus digestibility changes. Furthermore, levels of secondary metabolites, including toxins, tend to increase under elevated CO_2 (Cavagnaro et al. 2011), which could decrease protein bioavailability.

In addition to increasing the risk of protein deficiency, there may be other nutritional consequences of changing the stoichiometry of carbohydrate-to-protein ratios in staple food crops. For example, replacing dietary carbohydrate with protein has been shown in interventional trials and observational studies to 15-y duration, and in diverse countries including Japan, China, the

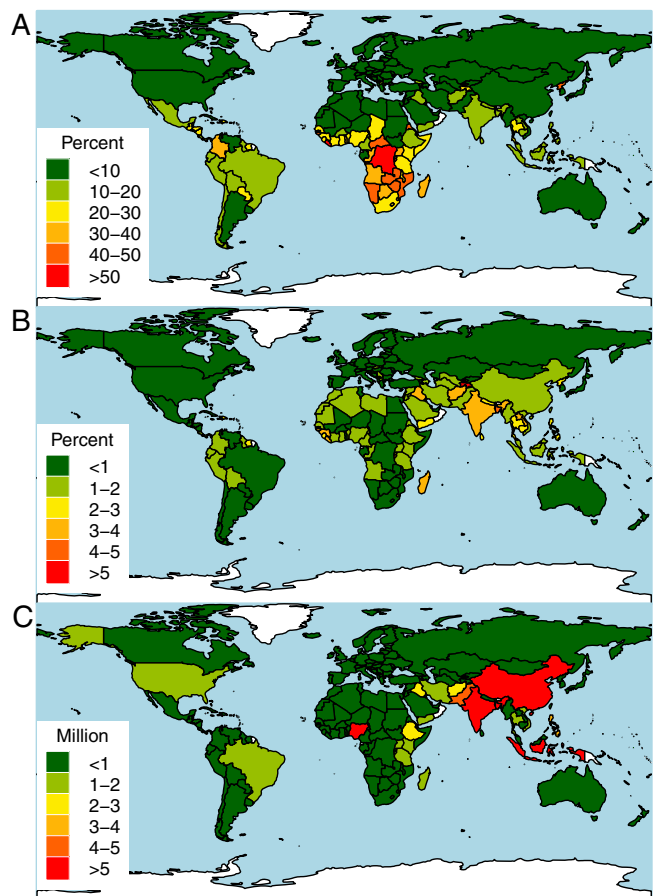


Figure 3. Risk of protein deficiency as defined by protein intake below estimated average protein requirements (EAR). Estimates of (A) current percentage of the population at risk of deficiency, (B) percent of the population newly at risk of deficiency under elevated carbon dioxide (eCO_2), and (C) millions of people estimated to be newly at risk of deficiency under eCO_2 , based on 2050 population projections. Data were plotted using the Rworldmap package in R (version 3.2.4; R Development Core Team).

United States, and Chile, to improve cardiovascular disease risk through lowering blood pressure and changing lipid profiles (Hu et al. 1999; Obarzanek et al. 1996; Appel et al. 2005; Altorf-van der Kuil et al. 2010; Rebolz et al. 2012). Improvements are often greatest with plant-rather than animal-sourced protein (Altorf-van der Kuil et al. 2010). These experiments underscore the need for additional investigation into whether replacing plant-sourced protein with plant-sourced carbohydrate could exacerbate the already concerning pandemic of metabolic disease driving increased cardiovascular morbidity and mortality globally.

It is unclear how trends in dietary quality will be counterbalanced by the effects of population growth and climate change. That is why, for our analysis, we assume no future change to food composition of diets or to per capita food intake and no dietary substitution to compensate for deficits. Agricultural production will need to roughly double to match increasing demand by 2050 (Alexandratos 1999). Climate change may pose the greatest challenge to this need. Climate change-induced reductions in crop yield are expected to be greatest in lower-latitude regions, including developing countries and those dependent on C_4 crops (Rosenzweig et al. 2014). Resulting economic changes may shape future diets, and changes to water, soils, and weather in these areas may affect crops in ways that may overwhelm, or exacerbate, the effects of eCO_2 . For example, decreases in yield

Table 3. Populations at risk of protein deficiency under aCO₂ and eCO₂ (population-weighted averages and 95% confidence intervals).

Region	EAR, 2050 (g/d)	At risk of protein deficiency, aCO ₂ (%)	At risk of deficiency in 2050, aCO ₂ (%)	At risk of deficiency in 2050, aCO ₂ (millions)	Additionally at risk with eCO ₂ : 2050 (%)	Additionally at risk with eCO ₂ : 2050 (millions)
CALACA	30.49	17.05 (11.64, 24.65)	18.4 (12.84, 25.64)	84.37 (58.90, 117.61)	0.86 (0.57, 1.19)	3.94 (2.64, 5.46)
CANAME	31.46	6.22 (4.00, 9.32)	7.32 (4.88, 10.46)	57.2 (38.09, 81.71)	1.53 (1.14, 1.94)	11.97 (8.93, 15.12)
CEEAEU	33.44	3.58 (1.40, 9.84)	3.52 (1.37, 9.79)	9.64 (3.74, 26.77)	0.56 (0.27, 0.95)	1.52 (0.73, 2.61)
CHINAR	31.68	5.25 (0.16, 21.01)	5.38 (0.16, 21.31)	74.96 (2.27, 297)	1.14 (0.11, 2.04)	15.94 (1.47, 28.45)
ESEASP	29.47	15.35 (9.59, 22.78)	15.79 (9.68, 23.56)	131.67 (80.71, 196.44)	1.92 (1.40, 2.43)	15.99 (11.68, 20.28)
HIGHIN	33.05	2.62 (1.01, 6.86)	2.6 (0.99, 7.36)	28.39 (10.83, 80.47)	0.31 (0.16, 0.53)	3.41 (1.75, 5.78)
India	30.06	16.27 (3.73, 32.49)	17.06 (4.46, 33.36)	276.42 (72.32, 540.41)	3.30 (1.93, 4.55)	53.41 (31.22, 73.71)
SOASIA	30.41	13.23 (6.15, 21.98)	13.74 (6.91, 22.59)	77.76 (39.10, 127.88)	2.80 (1.88, 3.74)	15.86 (10.64, 21.20)
SOTRLA	31.35	11.46 (2.80, 27.14)	12.03 (3.25, 27.40)	38.14 (10.30, 86.87)	0.68 (0.26, 1.07)	2.17 (0.81, 3.39)
SUSAAF	30.53	27.12 (23.07, 31.46)	28.89 (24.73, 33.44)	613.56 (525.07, 710.24)	1.16 (0.73, 1.59)	24.64 (15.44, 33.83)
World	30.99	12.18 (9.07, 16.32)	15.06 (12.11, 18.71)	1424.59 (1145.89, 1770.20)	1.57 (1.26, 1.86)	148.37 (119.06, 176.09)

Note: Calculations use 2011 populations and 2050 population projections. aCO₂, ambient atmospheric carbon dioxide; CALACA, Central and Andean Latin America and the Caribbean; CANAME, Central Asia, North Africa and the Middle East; CEEAEU, Central and Eastern Europe; CHINAR, Greater China; EAR, estimated average protein requirement based on 2050 demographic projections; eCO₂ elevated atmospheric carbon dioxide; ESEASP, East and Southeast Asia and the Pacific excluding China; HIGHIN, high income countries; SOASIA, South Asia excluding India; SOTRLA, Southern and Tropical Latin America; SUSAAF, sub-Saharan Africa. See Table S4 for country grouping.

under drought and warming temperatures may counteract the effects of rising CO₂ on protein concentrations (Kimball et al. 2001). Only 37 of 99 study sites in our meta-analysis were in countries outside of Europe and North America, and only just over half of the studies were performed in the field, with only 10% involving watering experiments (see Table S1). Most experiments were undertaken over 1 y only, and effects on crop nutrient content may not match those under the next 50 y of gradual atmospheric CO₂ increase. The consistent decreases in protein contents across C₃ crop cultivars, including 47 wheat cultivars and 27 rice cultivars, reassure us that our results are generalizable to other cultivars. Nevertheless, to better predict the dietary impacts of eCO₂, we need more long-term field-based eCO₂ experiments involving plants and cultivars grown under the climates and farming practices applicable to the developing world.

We also assumed that global population growth and future demographic trends will match UN projections, which include declining fertility rates, and migration from developing to developed countries (UN 2013). However, the greatest population growth is projected to occur in areas most vulnerable to climate change (Watts et al. 2015). Climate, economic, and demographic changes will likely interact, producing a global population distribution that we are not yet able to fully comprehend. In the absence of conclusive projections of future food production, we believe it is the most conservative, albeit perhaps optimistic, assumption that per capita food intake will remain constant despite sharp increases in global demand.

In predicting the nutritional consequences of eCO₂, other nutrients must be considered. Zinc and iron concentrations are greatly decreased in C₃ plants grown under eCO₂ (Myers et al. 2014). Zinc is a cofactor for protein synthesis, and protein inadequacy decreases uptake and availability of other nutrients (Groppe and Smith 2008). A recent analysis predicts strong increases in the risk of global zinc deficiency with eCO₂ (Myers et al. 2015). Identifying the countries most vulnerable to future malnutrition requires a targeted synthesis of crop research on climate and CO₂ responses. This information can then be applied to global climate and atmospheric models.

To our knowledge, this is the first global comparison of dietary protein that estimates a country-specific CV. Like energy consumption, the variability of protein consumption in a population relates to the Gini coefficient (Raubenheimer et al. 2015). Our use of this metric would be expected to produce more accurate estimates than the previously used 25% CV (Ghosh 2013). The WHO continues to refine its models of energy intake

variability based on gross domestic product (GDP), Gini, and food prices, using skew log rather than lognormal distributions. As this methodology becomes available, future work could incorporate these considerations to produce better estimates of protein consumption.

Because added fertilizer did not predictably mitigate the effects of CO₂ on crop protein, and with the production and application of fertilizer being a principal contributor to agricultural greenhouse gas emissions (Vermeulen et al. 2012), we cannot simply add more fertilizer to reduce the protein deficit. As populations increase, and with livestock production being resource-intensive (Vermeulen et al. 2012), eating more meat is not a practical solution. Cultivars could be selected or bred based on their nutritional content under eCO₂. In addition to efforts to mitigate CO₂ emissions, nutritious and resilient crops should be promoted, for example legumes, which will withstand the effects of eCO₂ on protein content. Because eCO₂ may have the greatest effect on the protein intake of those with the poorest diets, more equitable food distribution, and poverty reduction measures should be a focus for minimizing risk of deficiency.

Conclusions

Anthropogenic CO₂ emissions, via their impact on the protein content of C₃ staples, may threaten the adequacy of protein intake for many populations. Although quantifying protein deficiency is notoriously difficult, we have estimated current and future risk of protein deficiency by country and region, suggesting enduring challenges for sub-Saharan Africa and growing challenges for South Asia, including India. For nutritionally sensitive agriculture, the high CO₂ effects on crop nutrient contents must be incorporated into future food security policies.

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