Potential impact of climate change on world food supply

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A global assessment of the potential impact of climate change on world food supply suggests that doubling of the atmospheric carbon dioxide concentration will lead to only a small decrease in global crop production. But developing countries are likely to bear the brunt of the problem, and simulations of the effect of adaptive measures by farmers imply that these will do little to reduce the disparity between developed and developing countries.

RECENT research assessing the potential effects of climate change on agriculture has focused on regional and national evaluations[1–3]. These efforts have, for the most part, treated each region or nation in isolation, without relation to changes in agricultural production elsewhere. Recent work[4,5] emphasizes the important role of international trade in the adjustment of the world food system to climate change-induced changes in crop yields. Crop growth models have been used in an extensive international collaboration[6] to determine the effect of various climate change scenarios on crop yields for individual countries and geographical regions (Fig. 1). In this article we combine the data from these individual studies to obtain a global picture of the simulated change in crop yield associated with the different climate change scenarios. We then use a world food trade model to simulate the economic consequences of these potential changes in crop yields; we estimate changes in world food prices, and in the number of people at risk of hunger (defined as a measure of food energy availability—which depends on income and food price levels—relative to nutritional requirements) in developing countries.

The major finding of the study is that there appears to be a large disparity in agricultural vulnerability to climate change between developed and developing countries. This occurs even though simulated global agricultural production of major grain crop declines are only small to moderate under the climate change conditions tested. The analysis included the combined effects of climate change and increasing CO_2 on crop yields and water use. Although projected temperature change in low latitudes (where many developing countries are located) tends to be lower than the global average in the general circulation model (GCM) scenarios tested, modelled yield changes are primarily negative there, in contrast to predominantly positive yield changes in middle and high latitudes where many developed countries are located. This result has significant implications for potential future distributional aspects of the world food system.

Studies such as this explore the sensitivity of important human systems (in this case world food supply), as currently understood, to projected levels of global climate change. Such studies are initial demonstrations of the comprehensive, interdisciplinary research needed to improve understanding of the interactive biophysical and socio-economic effects that may result from global environmental change.

Climate change scenarios

Scenarios were developed from climate conditions predicted by three GCMs for doubled atmospheric CO_2 levels (Table 1). The temperature changes of these GCM scenarios (4.0–5.2 °C) are near the upper end of the range (1.5–4.5 °C) projected for doubled CO_2 warming by the IPCC[7,8]. Mean monthly changes in temperature, precipitation and solar radiation from the appropriate GCM gridbox were applied to observed daily climate records (1951–80, or as many years of daily climate records as available) to create climate change scenarios for each study site.

Because atmospheric concentrations of other greenhouse gases besides CO_2 (for example, methane (CH_4), nitrous oxide (N_2O) and the chlorofluorocarbons (CFCs)) are also increasing, an 'effective CO_2 doubling' has been defined as the combined radiative forcing of all greenhouse gases having the same forcing as doubled CO_2, usually taken to be ~600 p.p.m. CO_2 level is important when estimating potential impact on crops because crop growth and water use have been shown to benefit from increased levels of CO_2 (refs 9, 10). For the crop model simulations, climate changes from the doubled CO_2 GCM simulations were used with an associated level of 555 p.p.m. CO_2; these conditions are assumed to occur in AD2060. The 555 p.p.m. level is based on the GISS GCM trace gas scenario A (ref. 11), in which the simulated climate had warmed to the effective doubled CO_2 level of ~4 °C by AD2060.

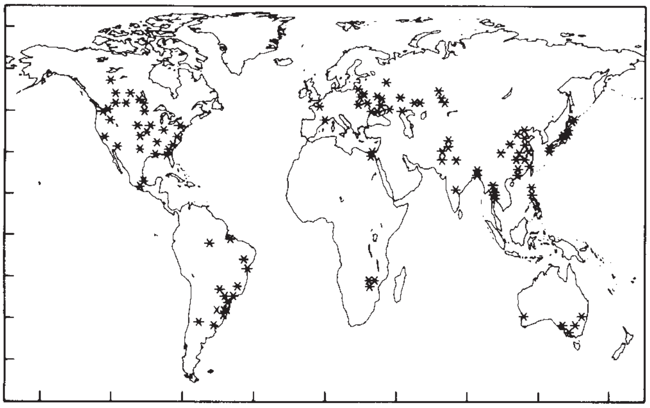

FIG. 1 Crop model sites[6]. Countries and participants were as follows: Argentina, O. E. Sala and J. M. Paruelo; Australia, B. D. Baer, W. S. Meyer and D. Erskine; Bangladesh, Z. Karim, M. Ahmed, S. G. Hussain and Kh. B. Rashid; Brazil, O. J. F. de Siqueira, J. R. B. Farias and L. M. A. Sans. Canada, M. Brklacich, R. Stewart, V. Kirkwood and R. Muma; China, Z. Jin, D. Ge, H. Chen, J. Fang and X. Zheng; Egypt, H. M. Eid; France, R. Delécolle, D. Ripoche, F. Ruget and G. Gosse; India, D. G. Rao; Japan, H. Seino; Mexico, D. Liverman, M. Dilley, K. O'Brien and L. Menchaca; Pakistan, A. Qureshi and A. Iglesias; Philippines, C. R. Escaño and L. Buendia; Thailand, M. L. C. Tongyai; Russia, G. Menzhulin, L. Koval and A. Badenko; USA, C. Rosenzweig, B. Curry, T.-Y. Chou, J. Ritchie, J. Jones and R. Peart; Uruguay, W. E. Baethgen; Zimbabwe, P. Muchena.

TABLE 1 GCM doubled-CO_2 climate change scenarios

GCM	Year*	Resolution (lat. × long.)	CO_2 (p.p.m.)	Change in average global temperature (°C)	Change in average global precipitation (%)
GISS†	1982	7.83° × 10°	630	4.2	11
GFDL‡	1988	4.4° × 7.5°	600	4.0	8
UKMO§	1986	5.0° × 7.5°	640	5.2	15

* When calculated.
† Goddard Institute for Space Studies[20].
‡ Geophysical Fluid Dynamics Laboratory[21].
§ United Kingdom Meteorological Office[22].

Crop yield change methods

Agricultural scientists in 18 countries estimated potential changes in national grain crop yields using compatible crop models and the GCM scenarios at 112 sites (Fig. 1). The crop model linkages were developed by the US Agency for International Development[12]. Simulations were carried out in regions representing 70–75% of the current world production of wheat, maize and soybean; rice production was less well represented (48% of current world production).

Site-specific estimates of yield changes were aggregated to national levels based on current regional production. The regional yield estimates represent the current mix of rainfed and irrigated production, and today's crop varieties, nitrogen management and agricultural soils. The national crop yield changes were then extrapolated to provide estimates of yield changes for the other countries and crops included in the world food trade model. National yield changes of other crops and commodity groups and regions not simulated were estimated based on three criteria: (1) similarities to modelled crops and growing conditions; (2) results from ~50 previously published and unpublished regional climate change impact studies; and (3) projected temperature and precipitation changes from the GCM scenarios. The primary sources of uncertainty in the estimates lies in the sparseness of the crop modelling sites and the lack of explicitly modelled yield changes for subsistence crops such as millet and cassava, which may respond differently to both climate change and increases in CO_2.

Estimates were made of yield changes with and without the direct physiological effects of CO_2 on crop growth, that is increased rates of net photosynthesis and reduced stomatal openings as reported from experimental results[13]. The photosynthesis ratios (555/330 p.p.m. CO_2) for soybean, wheat and rice, and maize were 1.21, 1.17, and 1.06, respectively. Changes in stomatal resistance were based on experimental results[14] (49.7/34.4 s m^{-1} for C3 crops, 87.4/55.8 s m^{-1} for C4 crops). This method of simulating the physiological CO_2 effects on crops may provide a positive bias to yield estimates, as plants grown in experimental settings are often subject to fewer environmental and competitive stresses than are likely to be encountered in farmers' fields.

GCM scenarios and direct CO_2 effects

Figure 2 shows estimated potential changes in average national grain crop yields for the GISS GFDL and UKMO doubled-CO_2 climate change scenarios (Table 1) with and without physiological (direct) CO_2 effects on plant growth. The maps are created from nationally averaged yield changes for wheat, rice, coarse grains and protein feed estimated for each country or group of countries. When climate change is considered without direct CO_2 effects on crop growth and water use, averaged national crop yields declined everywhere, although reductions were less at middle and high latitudes. In the simulations with direct CO_2 effects, yields were positive at middle and high latitudes, and negative at low latitudes for the GISS and GFDL scenarios which produced yield changes ranging from +30 to −30%. The UKMO scenario caused average national crop yields to decline almost everywhere (up to −50% in Pakistan).

Several factors contributed to the latitudinal differences in simulated yields. At some sites near the high-latitude boundaries of current agricultural production, increased temperatures benefited crops otherwise limited by cold temperatures and short growing seasons. In many middle and high latitude areas, where current temperature regimes tend to be cooler, increased temperatures exerted a negative influence on yields through shortening of crop development stages, but did not significantly increase heat or water stress levels. In these regions beneficial CO_2 effects dominated. The climate-change-induced warming at low latitudes brought not only accelerated growing periods for crops, but also greater heat and water stress, resulting in greater yield decreases than at higher latitudes, despite beneficial CO_2 direct effects.

Farm-level adaptations

In each participating country, the agricultural scientists used the crop models to test possible responses to the worst climate-change scenario (this was usually, but not always, the UKMO scenario; adaptation simulations were done with all three GCMs at some sites). These adaptations included changes in planting date, variety and crop, and applications of irrigation and fertilizer. Irrigation simulations assumed automatic irrigation to field capacity when plant available water dropped to 50% and 100% irrigation efficiency. These optimistic assumptions imply that water supply for irrigation would be fully available at all locations under climate change conditions. All adaptation possibilit-

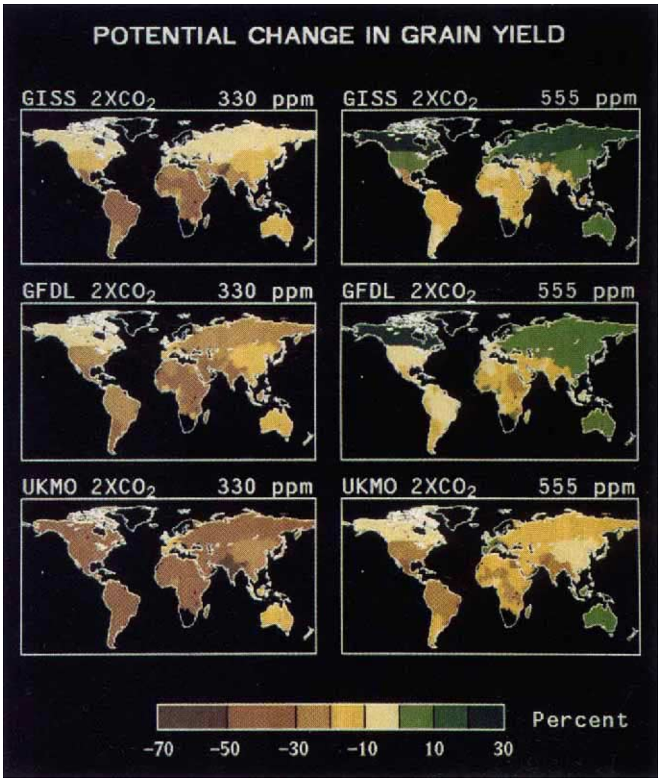

FIG. 2 Estimated change in average national grain yield (wheat, rice, coarse grains, and protein feed) for the GISS, GFDL, and UKMO climate change scenarios. The left-hand column shows the direct physiological effect on grain yield of current (330 p.p.m.) CO_2 concentration. The right-hand column shows the direct physiological effect of 555 p.p.m. Results shown are averages for countries and groups of countries in the Basic Linked System (BLS) world food trade model; regional variations within countries are not reflected.

ies were not simulated at every site and country: choices of adaptations to be tested were made by the participating scientists, based on their knowledge of current agricultural systems.

For the economic analysis, crop model adaptation results were grouped into two levels of adaptation. Level 1 implies little change to existing agricultural systems, reflecting responses to a changing climate that should be easily available to individual farmers. Level 1 adaptations included shifts in planting date (±1 month) that do not imply major changes in crop calendar, additional application of irrigation water to crops already under irrigation, and changes in crop variety to currently available varieties more adapted to the altered climate.

Adaptation level 2 implies more substantial change to agricultural systems, possibly requiring resources beyond the farmers' means, investment in regional and national agricultural infrastructure, and policy changes, although these types of changes were beyond the scope of the analysis. Level 2 adaptations included large shifts in planting date (>1 month), increased fertilizer application (included here because of implied costs for farmers in developing countries), installation of irrigation systems, and development of new varieties (tested by manipulation of genetic coefficients in crop models). Level 2 represents a fairly optimistic assessment of world agriculture's response to the changed climate conditions tested.

To extend the adaptation site results to national yield change estimates for all the countries in the world food trade model and to the other GCM scenarios, a simplifying assumption was made based on the crop modelling results to halve the negative impact if adaptations partially compensated for the negative effects of climate change, and to set yield changes to zero if compensation was full. If yield changes were positive, adaptation to produce even greater yield increases was not included, with the assumption that farmers would lack incentive to adapt further. This unrealistic assumption tends to underestimate potential disparities between countries able to improve productivity under the climate change scenarios and countries that cannot fully adapt. The adaptation estimates were developed only for the scenarios that included direct physiological CO_2 effects as these were judged to be most realistic.

improves realism, but many critical uncertainties remain. Although crop models allow testing of some potential improvements in agricultural production, they do not include yield-enhancing technological developments induced by negative climate change impacts. Level of adoption and efficacy of adaptive practices are also uncertain. There may be social or economic reasons why farmers are reluctant to implement adaptation measures, for example, increased fertilizer application and improved seed stocks may be capital-intensive and/or not suited to indigenous agricultural strategies. Furthermore, such measures may not necessarily result in sustainable production increases (for example, irrigation may eventually lead to soil salinization).

Yield estimates for the two adaptation levels are shown in Fig. 3. Level 1 adaptation compensated incompletely for the climate change scenarios, particularly in the developing countries. For the GISS and GFDL scenarios, level 2 adaptation compensated almost fully for negative climate change impacts. With the high level of global warming projected by the UKMO climate change scenario, neither level 1 nor level 2 adaptation fully overcame the negative climate change effects on crop yields in most countries, even when direct CO_2 effects are taken into account.

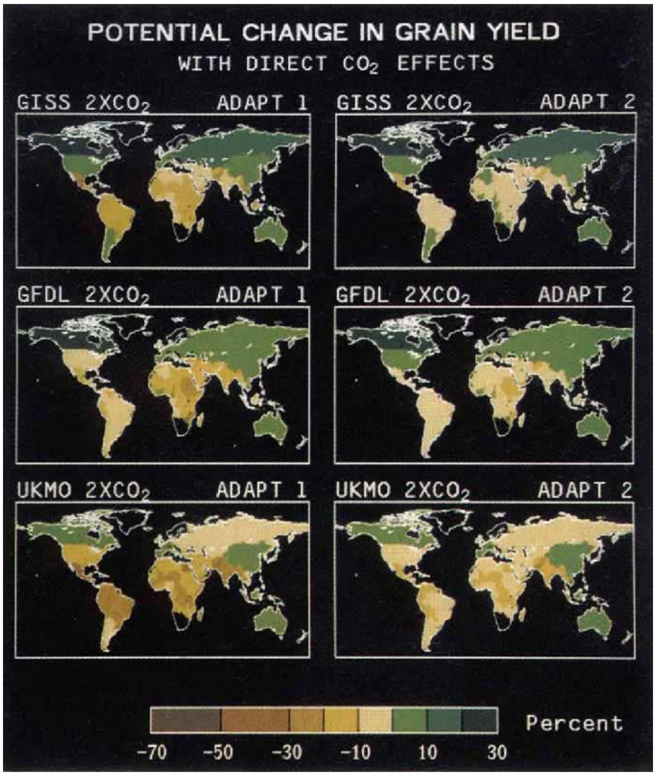

FIG. 3 Estimated changes in average national grain yield (wheat, rice, coarse grains, and protein feed with direct 555 p.p.m. CO_2 effects) under two levels of adaptation for the GISS, GFDL and UKMO doubled-CO_2 climate change scenarios[8]. Adaptation level 1 signifies minor changes to existing agricultural systems; adaptation level 2 signifies major changes. Results shown are averages for countries and groups of countries in the BLS world food trade model; regional variations within countries are not reflected.

World food trade model

The basic linked system (BLS) consists of a set of linked national agricultural sector models[15]. It is comprised of 16 national (including the EU) models with a common structure, 4 models with country-specific structure and 14 regional group models. The political changes as well as changes in national boundaries of the very recent past are not in the BLS, although the model formulation has been adjusted, away from centrally planned economies to more market-oriented behaviour. The 20 models in the first two groups cover ~80% of world agricultural production; the remaining 20% is covered by 14 regional models for countries which have broadly similar attributes (for example African oil-exporting countries, Latin American high-income exporting countries, Asian low-income countries). The BLS is a general equilibrium model system, with representation of all economic sectors, empirically estimated parameters and no unaccounted supply sources or demand sinks. Countries are linked through trade, world market prices and financial flows.

The BLS does not incorporate any climate relationships *per se*. Effects of changes in climate were introduced to the model as changes in the average national or regional yield per commodity as described above. Internal economic adjustments occur as increased agricultural investment, reallocation of agricultural resources according to economic returns (including crop switching), and reclamation of additional arable land as a response to higher commodity prices. Improvements in agricultural technology are represented by annual yield trends for developed and developing countries based on historical trends. The BLS contains yield–fertilizer production functions to capture the effects that changes in fertilizer prices and subsequent changes in fertilizer applications may have on yields at the national level. The economic adjustments to climate change simulated by the BLS are assumed not to alter the basic structure of yield–fertilizer functions, even though some of these relationships (for example, yield responses to nitrogen fertilization) may be altered in a changed climatic regime and under elevated CO_2 conditions.

Summary indicators of the world food system's sensitivity to the climate change scenarios include world cereal production, world cereal prices and population in developing countries (excluding China) at risk of hunger. The 'risk of hunger' indicator in the BLS was developed from estimates of the number of undernourished people in developing countries made by the FAO[16]; a cross-country regression was estimated, explaining the number of people at risk of hunger by a measure of food energy availability relative to nutritional requirements[15]. Food availability, in turn, depends on income and price levels. Average and marginal budget shares of consumption categories besides food (for example, housing and clothing) are included in the analysis. We include the risk of hunger indicator to show the possible trends in future food security, realizing that more comprehensive measures incorporating other socioeconomic variables may be devised.

Here we limit our analysis to results relating to the major cereal food crops, even though the BLS explicitly represents efficiency of feed use and trends in production and consumption of alternative livestock commodities. Thus, the reference case simulates the shift to higher-efficiency feed conversion (poultry over beef) occurring in some developed countries. Beyond the indirect effects of changes in feed costs, livestock production is a significant component of the global food system that is potentially sensitive to climatic change because of changes in rangeland and animal productivity.

World food trade model scenarios

The reference scenario (a future without climate change). The reference scenario projects the agricultural system to the year 2060 with no climate change and no major changes in the political or economic context of world food trade (Table 2). Population growth rates were exogenously specified from the medium projections of the United Nations to 2025, and from World Bank projections thereafter, resulting in ~10.3 billion people by 2060 (refs 17, 18).

Economic growth rates in the BLS are endogenously determined in most of the national models, yielding a moderate projection of world economic growth for the reference scenario. A 50% trade liberalization in agriculture (for example, removal of import restrictions) is introduced gradually by 2020. The analysis of trade liberalization is restricted to removal of distortions between trade prices and domestic prices at the level of agricultural raw materials.

Technology is projected to increase yields over time, but at a slowing rate based on historical trends. The rate of exogenous technical progress starts from historical values (1.3% in the 1980s) and for cereal crops approaches 0.5% per annum by 2060. Availability of arable land for expansion of crop production is based on FAO[19] data.

TABLE 2 World growth rates in the BLS reference scenario

Growth rate %	1980–2000	2000–2020	2020–2040	2040–2060
Population	1.7	1.3	0.8	0.5
GDP	2.9	2.0	1.5	1.1
Cereal yield	1.2	0.7	0.5	0.4
Agricultural production	1.8	1.3	1.0	0.7

All growth rates refer to world average annual per cent growth during the indicated period.

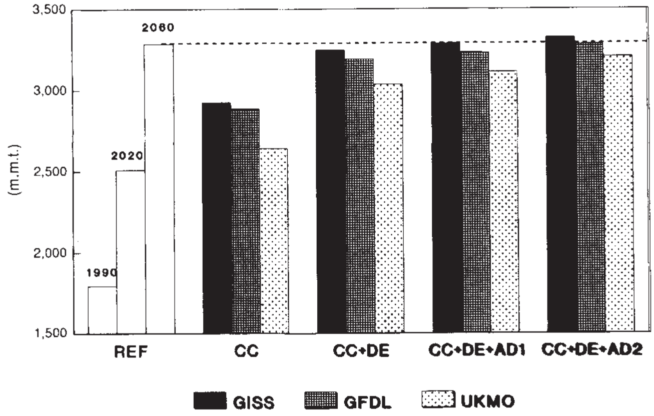

FIG. 4 World cereal production projected by the BLS for the reference, GISS, GFDL and UKMO doubled-CO_2 climate change scenarios, with (CC + DE) and without (CC) direct CO_2 effects on crop yields, and with adaptation levels 1 and 2 (AD1 and AD2). Adaptation level 1 implies minor changes to existing agricultural systems; adaptation level 2 implies major changes. (m.m.t., million metric tons).

Climate change scenarios. The food trade simulations for the three GCM scenarios were started in 1990. The yield changes estimated from the crop model simulations were applied linearly up to 2060 to the yields simulated by the BLS, which include the effect of technological improvement. Although the testing of climate change impacts without farm-level adaptation is unrealistic, it is done for the purpose of establishing a baseline with which to compare the effects of farmer response.

Scenarios including the effects of farm-level adaptations. The next step in the analysis involved adjusting the climate-induced yield changes assuming adaptation levels 1 and 2 described above. We can safely assume that at least some farm-level adaptations will be adopted, especially techniques similar to those tested in adaptation level 1. Policy, cost and water resource availability were assumed not to be barriers to adaptation.

World food trade results

The reference scenario. Assuming that population growth, economic growth, technological progress and trade liberalization proceed as specified above without climate change, world cereal production (wheat, rice, maize, millet, sorghum and minor grains) is estimated to grow to 3,286 million metric tons (m.m.t.) in year 2060 (compared with 1,795 m.m.t. in 1990). Cereal production in developing countries grows to exceed production in developed countries by 2020. Despite slowing gains in yield increases, food production (measured as net calories produced) is projected to exceed population growth throughout the simulation period of the reference scenario.

Cereal prices are estimated at an index of 121 (1970 value, 100) for the year 2060, reversing the falling trend of real cereal prices over the past 100 years. The standard reference scenario has two phases of price development. During 1980 to 2020, while trade barriers and protection are still in place but are being reduced, there are increases in relative prices. This occurs in the short-to-medium term because a removal of subsidies leads to lower farm-gate prices and therefore disincentives to production, while consumers benefit from somewhat lower retail prices, an incentive to demand. In the longer term, price decreases follow due to efficiency gains and technical progress. The number of people at risk of hunger is estimated at ~640 million or ~6% of total population in 2060 (compared with 530 million in 1990, ~10% of total current population).

Climate change scenarios. Without direct CO_2 effects on crop yields, world cereal production is reduced by 11 to 20%, and their inclusion brings yield decreases to between 1 and 8% (Fig. 4). The world production changes mask a disparity in response to climate change between developed and developing countries (Fig. 5). The largest negative changes occur in developing regions, though the extent of decreased production varies greatly by country depending on the projected climate. By contrast, in developed countries, production is estimated to increase under all but the UKMO scenario.

Price increases resulting from climate-induced decreases in yield are estimated to range between ~24–145% (Fig. 5). These increases in price affect the number of people at risk of hunger. Their estimated number increases ~1% for each 2–2.5% increase in prices (depending on climate change scenario). People at risk of hunger increase by 10% to almost 60% in the scenarios tested, resulting in an estimated increase of between 60 million and 350 million people in this condition (above the reference scenario projection of 640 million) by 2060.

Scenarios including the effects of farm-level adaptations. Globally, both minor and major levels of adaptation help restore world production levels (when CO_2 effects are included), compared to the climate change scenarios with no adaptation (Fig. 4). Averaged global cereal production decreases by up to ~160 m.m.t. (0 to −5%) from the reference scenario projection of 3,286 m.m.t. with minor level 1 adaptations. With adaptations implying major changes, global cereal production responses range from a slight increase of 30 m.m.t. to a slight decrease of ~80 m.m.t. (+1% to −2.5%).

Level 1 adaptation largely offsets the negative climate change yield effects in developed countries, improving their comparative advantage in world markets (Fig. 5). In these regions, cereal production increases by 4 to 14% over the reference scenario. However, developing countries are estimated to benefit little from this level of adaptation (−9 to −12% change in cereal production). More extensive adaptation virtually eliminates global negative cereal yield impacts derived under the GISS and GFDL climate scenarios, and reduces impacts under the UKMO scenario to one third.

Under adaptation level 1, price increases range from 10 to 100% (Fig. 5). Under adaptation level 2, cereal price responses range from a decline of ~5% to an increase of 35%. As a consequence of climate change and adaptation level 1, the number of people at risk of hunger increases by ~40 million to 300 million (6–50%) from the reference scenario of 641 million (Fig. 5). With a more significant amount of adaptation by farmers, the number of people at risk of hunger is altered by between −12 million for the GISS scenario and 120 million for the UKMO scenario (−2% and +20%). These results indicate that, except for the GISS scenario under adaptation level 2, the simulated farm-level adaptations did not mitigate entirely the negative effects of climate change on the number of people at risk of hunger, even when economic adjustment, that is, the production and price responses of the world food system, are taken into account.

Discussion

Several major points emerge from this study. Climate change scenarios near the high end of the IPCC range of doubled-CO_2 warming exerted (in most cases) a slight-to-moderate negative effect on simulated world cereal production, even when the beneficial direct effects of CO_2, farm-level adaptations and future technological yield improvements were taken into account. The only scenario that increased global cereal production was one involving major, and possible costly, changes in current agricul-

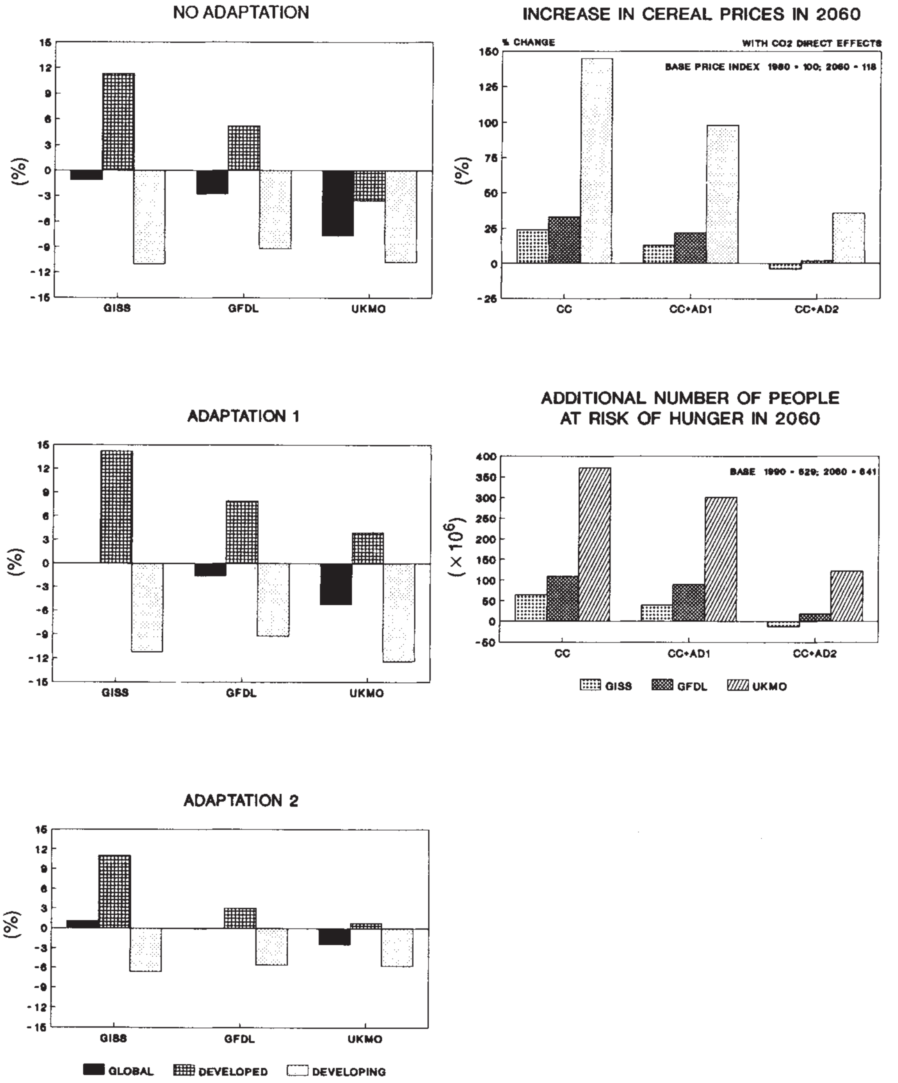

FIG. 5 Change in global, developed country, and developing country cereal production (with direct CO_2 effects), cereal prices, and people at risk of hunger in 2060 for climate change scenarios (CC), and with adaptation levels 1 and 2 (AD1 and AD2). Reference scenario for 2060 assumes no climate change, and projects global cereal production to be 3,286 m.m.t., developed country production to be 1,449 m.m.t., and developing country production to be 1,836 m.m.t.

tural systems, for example, installation of irrigation. Availability of irrigation water, however, was not included explicitly in the study; supplies may be limited under climate change conditions not only for expanding irrigation but for maintaining the current extent of irrigation in some areas. Although the overall results of the study are relatively benign, they depend strongly on the full realization in the field of beneficial direct physiological CO_2 effects on crop growth and water use as currently measured in experimental settings.

Climate change was found to increase the disparities in cereal production between developed and developing countries. Whereas production in the developed world benefited from climate change, production in developing nations declined. Adaptation at the farm-level did little to reduce the disparities, with the developing world suffering the losses. Cereal prices, and thus the population at risk of hunger, increased despite adaptation. Even a high level of farm-level adaptation in the agricultural sector did not entirely prevent such negative effects. Thus, while some countries in the temperate zones may reap some benefit from climate change, many countries in the tropical and subtropical zones appear more vulnerable to the potential impacts of global warming. □

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1. Parry, M. L., Carter, T. R. & Konijn, N. T. (eds) *The Impact of Climatic Variations on Agriculture* Vols 1 & ((Kluwer, Dordrecht, 1988).
2. Adams, R. M. *et al. Nature* **345,** 219–224 (1990).
3. Intergovernmental Panel on Climate Change *Climate Change: The IPCC Impacts Assessment* (eds Tegart, W. J. McG., Sheldon, G. W. & Griffiths, D.C.) (Aust. Govt Publishing Serv., Canberra, 1990).
4. Kane, S., Reilly, J. & Tobey, J. Report AER-No. 647 (US Dept of Agric. Econ. Res. Serv., Washington DC, 1991).
5. Reilly, J. & Hohmann, N. *Am. econ. Ass. Pap. Proc.* **83,** 306–312 (1993).
6. Rosenzweig, C. & Iglesias, A. (eds) *Implications of Climate Change for International Agriculture: Crop Modeling Study* (US Environmental Protection Agency, Washington DC, in the press).
7. *Climate Change: The IPCC Scientific Assessment* (eds Houghton, J. T., Jenkins, G. J. & Ephraums, J. J.) (Cambridge Univ. Press, 1990).
8. IPCC *Climate Change 1992* (eds Houghton, J. T., Callander, B. A. & Varney, S. K.) (Cambridge Univ. Press, 1992).
9. Acock, B. & Allen, L. H. Jr in *Direct Effects of Increasing Carbon Dioxide on Vegetation* (eds Strain, B. R. & Cure, J. D.) 33–97 (US Dept. of Energy DOE/ER-0238, Washington DC, 1985).
10. Cure, J. D. & Acock, B. *Agric. For. Met.* **38,** 127–145 (1986).
11. Hansen, J., *J. geophys. Res.* **93,** 9341–9364 (1988).
12. International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT) *Decision Support System for Agrotechnology Transfer Version 2.1* (*DSSAT V2.1*) (Dept Agron. & Soil Sci., Coll. Trop. Agric. & Hum. Resources, Univ. Hawaii, Honolulu, 1989).
13. Peart, R. M., Jones, J. W., Curry, R. B., Boote, K. & Allen, L. H. Jr. in *The Potential Effects of Global Climate Change on the United States*. Appendix C Vol. 1 (eds Smith, J. B. & Tirpak, D. A.) (US Envir. Protection Ag., Washington DC, 1989).
14. Rogers, H. H., Bingham, G. E., Cure, J. D., Smith, J. M. & Surano, K. A. *J. envir. Qual.* **12,** 569–574 (1983).
15. Fischer, G., Frohberg, K., Keyzer, M. A. & Parikh, K. S. *Linked National Models: A Tool for International Food Policy Analysis* (Kluwer, Dordrecht, 1988).
16. Food and Agriculture Organization *Fourth World Food Survey*. (UN, Rome, 1984); *Fifth World Food Survey* (UN, Rome, 1987).
17. United Nations *World Population Prospects 1988* (UN, New York, 1989).
18. International Bank for Reconstruction and Development/World Bank *World Population Projections* (Johns Hopkins Univ. Press, Baltimore, 1990).
19. *AGROSTAT/PC* (Food and Agricultural Organization, United Nations, Rome, 1991).
20. Hansen, J. *et al. Mon. Weath. Rev.* **111(4),** 609–662 (1983).
21. Manabe, S. & Wetherald, R. T. *J. atmos. Sci.* **44,** 1211–1235 (1987).
22. Wilson, C. A. & Mitchell, J. F. B. *J. geophys. Res.* **92(13),** 315–343 (1987).

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Three-dimensional structure of the 67K N-terminal fragment of *E. coli* DNA topoisomerase I

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The three-dimensional structure of the 67K amino-terminal fragment of *Escherichia coli* DNA topoisomerase I has been determined to 2.2 Å resolution. The polypeptide folds in an unusual way to give four distinct domains enclosing a hole large enough to accommodate a double-stranded DNA. The active-site tyrosyl residue, which is involved in the transient breakage of a DNA strand and the formation of a covalent enzyme–DNA intermediate, is present at the interface of two domains. The structure suggests a plausible mechanism by which *E. coli* DNA topoisomerase I and other members of the same DNA topoisomerase subfamily could catalyse the passage of one DNA strand through a transient break in another strand.

THE DNA topoisomerases are ubiquitous enzymes that can alter the topology of DNA by transiently breaking one or two strands of DNA, passing a single- or double-stranded DNA through the break, and finally resealing the break (for reviews, see refs 1–3). These enzymes are involved in a number of crucial cellular processes, including replication, transcription and recombination, and members of the DNA topoisomerase family have been identified as the targets of antimicrobial and anticancer therapeutics[4–6].

Escherichia coli DNA topoisomerase I, the first topoisomerase identified[7], is the most widely studied member of a subfamily of type-I DNA topoisomerases which includes *E. coli* DNA topoisomerase III (refs 8, 9), *Saccharomyces cerevisiae* topoisomerase III (refs 10, 11), and the archaebacterium *Sulfolobus acidocaldarius* reverse gyrase[12,13]. The enzyme catalyses the following reactions: relaxation of negatively supercoiled DNA, interconversion of unknotted and knotted single-stranded DNA rings, catenation and knotting of double-stranded DNA (provided that a gap or nick is present in at least one of the rings) and linking of two complementary single-stranded DNA rings into a double-stranded ring[2,14]. All these reactions occur as a result of the transient breakage of one DNA strand to allow passage of

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