pearance of the corresponding gene product is comparable to that in the SCN. Moreover, the homozygous inactivation of one or both *mCry* genes—known to accelerate, retard, or even abolish the biological clock in the SCN (*18, 20, 23*)—affects the peripheral oscillator to a similar extent. Thus, the peripheral oscillator in immortalized cultured fibroblasts constitutes a bona fide in vitro model for the molecular oscillator in the SCN, and could potentially allow the use of skin fibroblasts as a means of identifying clock gene defects in patients with circadian disorders.

Although peripheral clocks in the intact mouse possess some degree of autonomy, as is evident from the uncoupling of entrainment of peripheral and master clocks by glucocorticoid administration or restricted feeding (*6–8*), they differ from the master clock in the SCN in one important aspect. Unlike in cultured SCN slices, rhythmic clock gene expression in cultured peripheral organs/tissues and fibroblasts is dampened after a number of days (*9*). Because, as we have shown, the molecular makeup of the core oscillator of master and peripheral clocks is identical, the mechanism that allows the master clock to keep on ticking remains to be identified.

References and Notes
1. J. Dunlap, *Cell* **96**, 271 (1999).
2. M. W. Young, *Science* **288**, 451 (2000).
3. N. Cermakian, P. Sassone-Corsi, *Nature Rev. Mol. Cell Biol.* **1**, 59 (2000).
4. L. P. Shearman *et al.*, *Science* **288**, 1013 (2000).
5. R. G. Foster, *Neuron* **20**, 829 (1998).
6. A. Balsalobre *et al.*, *Science* **289**, 2344 (2000).
7. F. Damiola *et al.*, *Genes Dev.* **14**, 2950 (2000).
8. K. A. Stokkan *et al.*, *Science* **291**, 490 (2001).
9. S. Yamazaki *et al.*, *Science* **288**, 682 (2000).
10. A. Balsalobre, F. Damiola, U. Schibler, *Cell* **93**, 929 (1998).
11. K. Yagita and H. Okamura, *FEBS Lett.* **465**, 79 (2000).
12. M. Akashi and E. Nishida, *Genes Dev.* **14**, 645 (2000).
13. Rat-1 fibroblasts were cultured as described (*10*). Before stimulation, cells were cultured for 3 to 4 days in medium containing 5% fetal bovine serum. Cells were stimulated by brief treatment (2 hours) with medium containing either endothelin-1 (final concentration 30 nM, Sigma), after which medium was replaced by serum-free Dulbecco's modified Eagle's medium (Nacalai Tesque, Kyoto, Japan).
14. M. Yanagisawa *et al.*, *Nature* **332**, 411 (1988).
15. T. Kuwaki *et al.*, *Prog. Neurobiol.* **51**, 545 (1997).
16. See *Science* Online (www.sciencemag.org/cgi/content/full/292/5515/278/DC1).
17. Northern blot analysis was performed as described (*11*). Probes of *Per1*, *Per2*, and *dbp* were prepared as described (*11*). For *Clock* and *Bmal1*, full-length cDNAs of *hClock* and *hBmal1* (*27*) were digested by Xba I and Sma I, respectively. Fragments of *hClock* (base pairs 364 to 1084 of *hClock* cDNA) and *hBmal1* (base pairs 687 to 1506 of *hBmal1* cDNA) were used for the templates. G3PDH (Clontech) was used as a control. Probes were labeled with [^{32}P]deoxycytidine triphosphate using a TaKaRa random primer labeling kit (TaKaRa, Tokyo, Japan). Hybridization was performed at 42°C for 16 hours, and membranes were washed twice in 0.2× SSC/0.1% SDS at 60°C for 30 min. Membranes were exposed to an imaging plate and analyzed by BAS 5000 (Fuji Film, Tokyo, Japan). For rehybridization purposes, old probes were removed by treatment of membranes with a preheated (80°C) solution containing 1% SDS/0.1× SSC for 3 min.
18. H. Okamura *et al.*, *Science* **286**, 2531 (1999).
19. Y. Ishida *et al.*, *J. Neurosci. Res.*, in press.
20. M. H. Vitaterna *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 12114 (1999).
21. M. D. Field *et al.*, *Neuron* **25**, 437 (2000).
22. Immunofluorescence was performed as described (*28*). Rabbit polyclonal antibodies to mPER1 (*28*) (affinity purified, 1:200) and mPER2 (affinity purified, 1:200; ADI, San Antonio, TX) were used as primary antibodies. Cy3-conjugated antibody to rabbit IgG (1:2000; Amersham) was used as a secondary antibody. Nuclear staining was performed with 4′,6′-diamidino-2-phenylindole (DAPI).
23. G. T. J. van der Horst *et al.*, *Nature* **398**, 627 (1999).
24. Spontaneously immortalized MEFs from *mCry1*$^{-/-}$, *mCry2*$^{-/-}$, and *mCry1*$^{-/-}$*mCry2*$^{-/-}$ mice were cultured as described (*28*). Stimulation procedures using ET-1 (final concentration 30 nM) or 50% horse serum (Gibco BRL) were as described (*14*).
25. K. Yagita, F. Tamanini, G. T. J. van der Horst, H. Okamura, data not shown.
26. Immunofluorescence was performed as described (*28*). Rabbit polyclonal antibody to DBP (1:2500) and p62 mouse monoclonal antibody (mAb; 1:3000) were used as primary antibodies. Fluorescein isothiocyanate–conjugated antibody to rabbit IgG (1:2000; Amersham) and Cy3-conjugated antibody to mouse IgG (1:800; Jackson ImmunoResearch) were used as secondary antibodies.
27. S. Yamaguchi *et al.*, *Mol. Cell. Biol.* **20**, 4773 (2000).
28. K. Yagita *et al.*, *Genes Dev.* **14**, 1353 (2000).
29. We thank U. Schibler, J. Ripperger, and J. M. Egly for antibodies, and M. Yasuda for technical support. Supported in part by grants from the Special Coordination Funds of the Science and Technology Agency of Japan, a Grant-in-Aid for Scientific Research on Priority Areas of the Ministry of Education, Science, Sports and Culture of Japan, Ministry of Welfare of Japan, Mitsubishi Foundation, and a Spinoza premium from the Netherlands Organization for Scientific Research.

Forecasting Agriculturally Driven Global Environmental Change

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During the next 50 years, which is likely to be the final period of rapid agricultural expansion, demand for food by a wealthier and 50% larger global population will be a major driver of global environmental change. Should past dependences of the global environmental impacts of agriculture on human population and consumption continue, 10^9 hectares of natural ecosystems would be converted to agriculture by 2050. This would be accompanied by 2.4- to 2.7-fold increases in nitrogen- and phosphorus-driven eutrophication of terrestrial, freshwater, and near-shore marine ecosystems, and comparable increases in pesticide use. This eutrophication and habitat destruction would cause unprecedented ecosystem simplification, loss of ecosystem services, and species extinctions. Significant scientific advances and regulatory, technological, and policy changes are needed to control the environmental impacts of agricultural expansion.

During the first 35 years of the Green Revolution, global grain production doubled, greatly reducing food shortages, but at high environmental cost (*1–5*). In addition to its effects on greenhouse gases (*1, 6, 7*), agriculture affects

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ecosystems by the use and release of limiting resources that influence ecosystem functioning (nitrogen, phosphorus, and water), release of pesticides, and conversion of natural ecosystems to agriculture. These sources of global change may rival climate change in environmental and societal impacts (*2, 8*). Population size and per capita consumption are assumed to be the two greatest drivers of global environmental change. Humans currently appropriate more than a third of the production of terrestrial ecosystems and about half of usable freshwaters, have doubled terrestrial nitrogen supply and phosphorus liberation, have manufactured and released globally significant quantities of pesticides, and have initiated a major extinction event (*2–4, 8–10*). Global population, which increased 3.7-fold during the 20th century, to 6 billion people (*11*), is forecast to increase to 7.5 billion by the year 2020 and to about 9 billion by 2050 (*12*). Constant-dollar global per capita

gross domestic product (GDP) increased 4.6-fold in the 20th century (*13*) and is projected to be 1.3 times current levels by 2020 and 2.4 times current levels by 2050 (*14, 15*). How might projected increases in population and wealth influence the global environment? The prospects of climate change are widely recognized (*16*). Here, we explore the nonclimatic global environmental impacts of agricultural expansion during the coming 20 to 50 years. We use past global trends and their dependence on global population and GDP to empirically forecast the potential global environmental impacts of agriculture. Like economic forecasting, ecological forecasting is notoriously difficult and imprecise. Our forecasts are not predictions, but rather are estimates of environmental impacts should agriculture continue on the tra-

jectories of the past 35 or more years. Because these trajectories include in them the impacts of past technological developments, changes in consumer choices, and environmental regulations, our forecasts implicitly assume similar technological, regulatory, and behavioral changes in the future. Shifts in these could cause major deviations from our forecasts.

We use univariate and multiple regressions to forecast future global trends for each of seven environmental variables related to agriculture (Table 1). Because of the exponential nature of past global population and economic growth, we had anticipated exponential temporal trends for these variables. Surprisingly, each was a linear, and almost equally strong, function of time, population, and GDP (Fig. 1 and Table 1). We thus use linear fits in our forecasts, while rec-

ognizing that substantial changes in future population and economic growth, agricultural policies, climate, and other factors would affect our results. Detailed regional forecasts and forecasts based on mechanistic models that couple regional economies, agriculture, and the environment are also needed and would complement our simpler global approach.

Four forecasts were made for each variable: by a linear fit to its temporal trend (Fig. 1), extrapolated to the years 2020 and 2050; by the fitted dependence of each variable on population size (*13, 17, 18*), combined with the global population size projected (*12*) for 2020 and 2050; by the linear dependence of each variable on GDP (*13, 17*), combined with global GDP projections (*14, 15*) for 2020 and 2050; and by multiple regression fitting each variable to year,

Fig. 1. (**A**) Trends in annual rates of application of nitrogenous fertilizer (N) expressed as mass of N, and of phosphate fertilizer (P) expressed as mass of P_2O_5, for all nations of the world except the former USSR (*18, 19*), and trends in global total area of irrigated crop land (H_2O) (*18*). (**B**) Trends in global total area of land in pasture or crops (*18*). (**C**) Trend in global pesticide production rates, measured as millions of metric tons per year (*30*). (**D**) Trend in expenditures on pesticide imports (*18*) summed across all nations of the world, transformed to constant 1996 U.S. dollars. All trends are as dependent on global population and GDP as on time (Table 1).
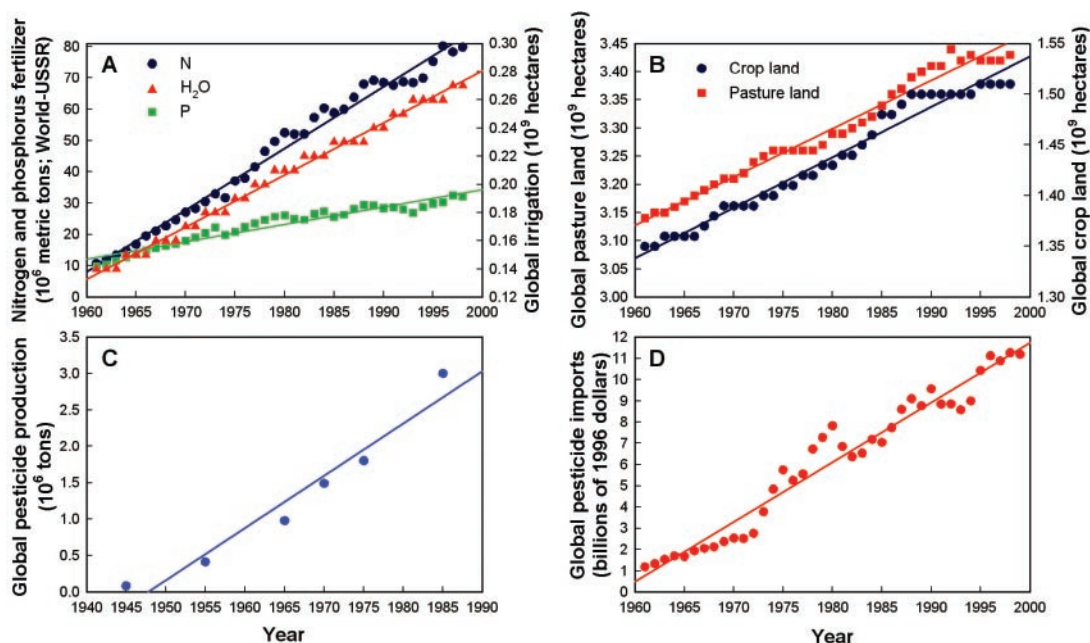

Table 1. Univariate and multivariate forecasts for years 2020 and 2050, based on trends observed in the past 35 to 40 years and their dependence on population and GDP. Parentheses show R^2 values for each regression. Levels of significance:
$**P < 0.0001$; $*P < 0.01$; NS, $P > 0.05$. The value in 2000 is based on temporal extrapolation from the latest available data, generally 1998. Mean projections are means of the three univariate and the one multivariate projection.

	Fertilizer (10^6 MT)		Irrigated land (10^6 ha)	Pesticide		Crop land (10^9 ha)	Pasture land (10^9 ha)
	N	P		Produced (10^6 MT)	Imported (10^9 1996 U.S.$)		
Value in 2000	87.0	34.3	280	3.75	11.8	1.54	3.47
			Mean projections				
Forecast 2020	135	47.6	367	6.55	18.5	1.66	3.67
Forecast 2050	236	83.7	529	10.1	32.2	1.89	4.01
			Individual projections for 2050				
Univariate							
By year	186	62.0	465	7.33	25.8	1.79	3.90
	(0.986**)	(0.927**)	(0.998**)	(0.946*)	(0.957**)	(0.976**)	(0.977**)
By population	166	56.2	417	8.02	22.2	1.73	3.79
	(0.980**)	(0.910**)	(0.996**)	(0.990*)	(0.951**)	(0.974**)	(0.979**)
By GDP	343	98.3	761	18.1	48.8	2.20	4.59
	(0.964**)	(0.904**)	(0.992**)	(0.995*)	(0.955**)	(0.973**)	(0.977**)
Multivariate	249	118	473	7.06	32.0	1.83	3.75
	(0.989**)	(0.979**)	(0.998**)	(0.994 NS)	(0.960**)	(0.977**)	(0.982**)

population, and per capita GDP, combined with projected values for these in 2020 and 2050. We present all four forecasts for 2050 to illustrate similarity and variability, and mean forecasts for 2020 and 2050 (Table 1). The averages for 2020 allow a mid-course evaluation of the 50-year forecasts.

The doubling of global food production during the past 35 years was accompanied by large increases in global nitrogen (N) and phosphorus (P) fertilization and irrigation [Fig. 1A and (5)]. If past trends in N and P fertilization (18, 19) and irrigation (18) and their dependence on population and GDP continue, our mean forecast is for global N fertilization to be 1.6-fold times present amounts by 2020 and 2.7 times present values by 2050 (Table 1). By 2050, N fertilization alone would annually add 236 × 10^6 MT of N to terrestrial ecosystems (20), compared with 140 × 10^6 MT from all natural sources (2). Individual forecasts for N fertilization in 2050 range from a 1.9-fold increase based on its dependence on population to a 3.9-fold increase based on GDP. P fertilization is forecast to be 1.4 times current amounts in 2020 and 2.4 times current amounts in 2050. P estimates for 2050 range from 1.6-fold to 3.4-fold increases (20). Irrigated area (18), a measure of agricultural demand for water, is forecast to be 1.3 times the current area in 2020 and 1.9 times as great in 2050.

Humans annually already release as much N and P to terrestrial ecosystems as all natural sources (2, 3). The large projected increases in N, P, and irrigation water [Table 1 and (20)] would have significant environmental impacts. Irrigation increases salt and nutrient loading to downstream aquatic ecosystems, can cause salinization of soils, and has impacts on streams and rivers because of damming and removal of water (21). In many areas, there is insufficient water for projected demands (21, 22). N and P leakage from agricultural systems causes major environmental problems (2, 3, 8, 23). About half of fertilizer N and P is captured in harvested crops (23–25) and, after consumption, enters human and livestock waste streams. About 70% of harvested crops are fed to livestock in developed countries (23), but few livestock wastes are treated for N and P removal. Thus, much N and P from fertilizer and animal wastes enters surface and groundwater (3, 25), and N also is volatilized to the atmosphere as ammonia and deposited regionally (23–25).

The major environmental consequence of P addition is eutrophication of surface waters, particularly freshwater lakes and streams (3). For N, consequences include eutrophication of estuaries and coastal seas, loss of biodiversity and changes in species compositions in terrestrial and aquatic ecosystems, groundwater pollution with nitrate and nitrite, increases in the greenhouse gas N_2O, increases in NO_x and resulting tropospheric smog and ozone, and acidification of soils and sensitive freshwaters (2, 8, 23, 25,

26). Eutrophication is the biggest pollution problem in most coastal waters (23), and, with overfishing and aquaculture (27), is a major threat to marine biodiversity. Agricultural nutrient pollution has led to increased blooms of toxic algae in many coastal systems and to the large hypoxic ("dead") zone in the Gulf of Mexico (24, 28). In total, projected increases in N and P fertilization and irrigation would cause significant losses of biodiversity, as well as marked changes in the composition and functioning of both terrestrial and aquatic ecosystems (2, 3, 8, 23, 25, 26, 28).

Although society benefits from pesticides, some cause environmental degradation or affect human health (29, 30). Some pesticides, depending on persistence and volatility, disperse globally (29), bioaccumulate in food chains (31) and have impacts on human health and the health of other species far from points of release and many years after release. If past patterns continue, global pesticide production (30), which has increased for 40 years (Fig. 1C), would be 1.7 times that at present by 2020 and 2.7 times the present amount by 2050 (Table 1). Projections for 2050 range from 1.9- to 4.8-fold increases. World trade in pesticides (18), another estimate of trends in pesticide use, would be 1.6 times present levels by 2020 and 2.7 times present levels by 2050 (Fig. 1D and Table 1). Should trends continue, by 2050, humans and other organisms in natural and managed ecosystems would be exposed to markedly elevated levels of pesticides.

Land use and habitat conversion are, in essence, a zero-sum game: land converted to agriculture to meet global food demand comes from forests, grasslands, and other natural habitats. Increases in agricultural land, a major quantified cause of global habitat destruction, are a conservative estimate of losses of native ecosystems. Global trends for pastureland [Fig. 1B and (18)] suggest a net increase of 2.0 × 10^8 hectares of pasture by 2020 and of 5.4 × 10^8 hectares by 2050 (Table 1). If past trends (Fig. 1B) continue, global cropland (18) would increase by a net of 1.2 × 10^8 hectares by 2020 and of 3.5 × 10^8 hectares by 2050 (Table 1). The combined total represents an average global agricultural land base in 2050 that would be 18% larger than at present. These are net global changes. Because analyses like those of Table 1, but for developed countries, project a net withdrawal of 1.4 × 10^8 ha of land from agriculture by 2050, the net loss of natural ecosystems to cropland and pasture in developing countries by 2050 would be 10^9 ha, about half of all potentially suitable remaining land (22, 32).

The conversion of 10^9 hectares of land to agriculture would represent the worldwide loss of natural ecosystems larger than the United States. Because of regional availabilities of suitable land, this expansion of agricultural land is expected to occur predominantly in Latin America and sub-Saharan central Africa (1, 22). It

could lead to the loss of about a third of remaining tropical and temperate forests, savannas, and grasslands and of the services, including carbon storage (33), provided by these ecosystems. Additional natural habitat would be lost worldwide to urban and suburban development, to roadways, and to the rotation of low-quality lands through agriculture. Species extinction is an irreversible impact of habitat destruction. Interactions between climate change, species invasions, and habitat fragmentation could cause further diversity losses, because many species may be unable to migrate through fragmented habitats to reach regions with suitable climates and soils (34).

Just as demand for energy is the major cause of increasing atmospheric greenhouse gases, demand for agricultural products may be the major driver of future nonclimatic global change. Our forecasts have high variance, but even the lowest projections are cause for concern. The projected 50% increase in global population and demand for diets richer in meat by a wealthier world are projected to double global food demand by 2050 (22), creating an environmental challenge that may rival, and significantly interact with, climatic change. The actual impacts of agricultural expansion will depend on how large the expansion actually is and on how it is achieved. Our projections of global environmental impacts assume a continuation of past practices, i.e., mainly of agricultural intensification by means of fertilization, irrigation, pesticide application, and crop breeding. We implicitly assume that the increasing yields of the Green Revolution can continue unabated for 50 more years. If this does not occur, perhaps because of water shortages, evolution of resistant pests and pathogens, emergence of new pests and pathogens, or diminishing returns from fertilization and selection for higher-yielding varieties (1, 18, 35, 36), the projected food demand would be met only if the agricultural land base increased more than we have projected, i.e., by an extensification of agriculture. Alternatively, food demand could be lowered if the trend toward diets richer in meat were reversed or if global population stabilized at a lower than projected level.

The Green Revolution greatly reduced world hunger. Comparable advances in agricultural production are needed during the coming 50 years to assure a sufficient, secure, and equitable global food supply (1), but these advances must follow new trajectories if the problems we have identified are to be minimized. An environmentally sustainable revolution (1), a greener revolution, is needed. It must be based on the total costs and benefits of agriculture, including agriculture-dependent gains and losses in values of such ecosystem goods and services as potable water, biodiversity, carbon storage, pest control, pollination, fisheries, and recreation (37, 38).

Existing knowledge, if widely used, could significantly reduce the environmental impacts

of agriculture and increase productivity. Integrated pest management, application of site- and time-appropriate amounts of agricultural chemicals and water, use of cover crops on fallow lands and buffer strips between cultivated fields and drainage areas, and appropriate deployment of more productive crops can increase yields while reducing water, fertilizer, and pesticide use and movement to nonagricultural habitats (*6, 7, 21, 23, 35, 39–41*). Treatment of animal wastes is necessary, especially in developed countries, where more than a third of fertilizer N passes through livestock (*23*). Currently, animal wastes receive little or no treatment and are a major source of surface water pollution and terrestrial N deposition (*23, 28*). Preservation and restoration of wetlands and riparian zones can remove N by denitrification before it reaches watercourses and can trap P in soils.

Comprehensive land-use planning could mitigate some effects of agricultural expansion. Some agricultural impacts could be ameliorated if the 1.4×10^8 hectares projected for removal from agriculture in developed nations were restored to provide ecosystem services (*37*), such as carbon storage, preservation of biodiversity, and production of potable water. Alternatively, if kept in agriculture, this land could save a comparable area of natural ecosystems in developing nations from destruction if food so produced could meet demands of developing nations. The capability of the remaining natural lands to supply ecosystem services and to preserve biodiversity could be increased by planning the pattern and location of agricultural development so as to save biodiversity hot spots; to minimize fragmentation; to maximize the range of ecosystem types preserved; and to preserve wetlands and riparian zones that protect surface waters from inputs of nutrients, pesticides, eroded soil and pathogens. Such actions would continue a global trend of setting land aside as nature reserves and national parks (*42*). Cumulatively worldwide, an area roughly the size of the Indian subcontinent is designated for conservation of biodiversity. Many preserves, though, are inadequately protected, and some may be sustainably protected only if incorporated into local economies (*43*).

Even the best available technologies, fully deployed, cannot prevent many of the forecasted problems. Major international programs are needed to develop new technologies and policies for ecologically sustainable agriculture. Region-appropriate education, incentives, and legal restrictions will be required to encourage adoption. The research needs are diverse. We must seek, by breeding and biotechnology, gains in the fundamental efficiency of crop N, P, and water use (*21, 35, 36*). Advances in precision agriculture that decrease N and P inputs are needed, as are methods that manage soil organic matter and microbial communities to reduce nutrient leaching and to optimize soil fertility (*6,*

35). Methods are needed to efficiently close the nutrient cycle from soil to crop to livestock and back to agricultural soil, and to prevent the occurrence and the spread to humans of livestock pathogens. Ways to better control crop pathogens and pests are needed, such as by greater use of natural enemies, crop diversity (*40*), and biotechnology, if deployed so as to reduce evolution of pest resistance. Methods to forecast quantitatively the impact on ecosystem functioning of loss of habitat, loss of biodiversity, changes in species composition, and increased nutrient inputs need development. Because most agricultural expansion will occur in developing countries, the discovery and adoption of appropriate practices likely would require aid from developed countries, including International Monetary Fund and World Bank loans, or debt forgiveness. Moreover, regional differences in food demand and in the potential of extensification versus intensification to meet these needs (*21, 22, 32, 35, 44*) means that, although the problems are global, solutions must be local, regional, and global.

If global population stabilizes at 8.5 to 10 billion people, the next 50 years may be the final episode of rapid global agricultural expansion. During this period, agriculture has the potential to have massive, irreversible environmental impacts. The minimization of these impacts, while providing sufficient and equitably distributed food, will be a great challenge. Although there are likely to be mechanisms and policies that can reduce, or perhaps reverse, many of the trends that we have identified, these solutions will not be achieved unless far more resources are dedicated to their discovery and implementation.

References and Notes

1. G. Conway, *The Doubly Green Revolution* (Penguin Books, London, 1997).
2. P. M. Vitousek, H. A. Mooney, J. Lubchenco, J. M. Melillo, *Science* **277**, 494 (1997).
3. S. R. Carpenter *et al.*, *Ecol. Appl.* **8**, 559 (1998).
4. D. W. Schindler, *Ambio* **28**, 350 (1999).
5. D. Tilman, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5995 (1999).
6. P. A. Matson, W. J. Parton, A. G. Power, M. J. Swift, *Science* **277**, 504 (1997).
7. P. A. Matson, W. McDowell, A. Townsend, P. Vitousek, *Biogeochemistry* **46**, 67 (1999).
8. National Research Council, *Global Change Ecosystems Research* (National Academy Press, Washington, DC, 2000).
9. S. L. Postel, G. C. Daily, P. R. Ehrlich, *Science* **271**, 785 (1996).
10. S. L. Pimm, G. J. Russell, J. L. Gittleman, T. M. Brooks, *Science* **269**, 347 (1995).
11. J. E. Cohen, *How Many People Can the Earth Support?* (Norton, New York, 1995).
12. *World Population Prospects: The 1998 Revision*, vol. I, *Comprehensive Tables* (UN Department of Economic and Social Affairs, Population Division, New York, 1999).
13. A. Maddison, *Monitoring the World Economy 1820–1992* (Development Center of the Organization for Economic Cooperation and Development, Paris, 1995). GDP was extended to 1998 using annual percent increases in (*17*).
14. National Research Council, *Our Common Journey: A Transition Toward Sustainability* (National Academy Press, Washington, DC, 1999).
15. Reference (*14*) forecasts constant-dollar global GDP

growth of 2.7% year^{-1} from 1995 to 2050. We used a more conservative 2.5% based on analysis of the 40-year trend (*13*) in the annual rate of growth of constant-dollar global per capita GDP.
16. J. T. Houghton *et al.*, *Climate Change 1995: The Science of Climate Change* (Cambridge Univ. Press, Cambridge, 1996).
17. *World Development Indicators*, CD-ROM (World Bank, Washington, DC, 2000)
18. Food and Agriculture Organization of the United Nations, FAOSTAT homepage [on-line] (2001). Available at: http://apps.fao.org/. Cropland refers to the FAO land-use category of "arable and permanent crops." Pasture is FAO's "permanent pasture."
19. Fertilizer projections are for the entire world except the former USSR, whose economic problems added variance to the relationship.
20. If the former USSR is included, the 2050 global fertilizer projection for N is 270×10^6 MT year^{-1} and for P is 110×10^6 MT year^{-1}. If N fixation by combustion of fossil fuels and by crops doubled by 2050, these plus N fertilization (including the USSR) would add 390×10^6 MT year^{-1}, 2.8 times more N than all natural processes combined.
21. S. L. Postel, *Pillar of Sand: Can the Irrigation Miracle Last?* (Norton, New York, 1999).
22. N. Alexandratos, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5908 (1999).
23. National Research Council, *Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution* (National Academy Press, Washington, DC, 2000).
24. A. F. Bouwman *et al.*, *Global Biogeochem. Cycles* **11**, 561 (1997).
25. R. W. Howarth *et al.*, *Biogeochemistry* **35**, 75 (1996).
26. E. A. Holland, F. Dentener, B. Braswell, J. Sulzman, *Biogeochemistry* **46**, 7 (1999).
27. R. L. Naylor *et al.*, *Nature* **405**, 1017 (2000).
28. J. A. Downing *et al.*, *Gulf of Mexico Hypoxia: Land and Sea Interactions* (Task Force Report No. 134, Council for Agricultural Science and Technology, Ames, IA, 1999).
29. *Assessment Report: Arctic Pollution Issues* (Arctic Monitoring and Assessment Program, Oslo, Norway, 1998).
30. World Health Organization, *Public Health Impacts of Pesticides Used in Agriculture* (WHO & UN Environment Program, Geneva, 1990).
31. K. A. Kidd, D. W. Schindler, D. C. G. Muir, W. L. Lockhart, R. H. Hesslein, *Science* **269**, 240 (1995).
32. N. Alexandratos, *World Agriculture: Toward 2010* (Wiley, Chichester, UK, 1995).
33. W. H. Schlesinger, *Biogeochemistry: An Analysis of Global Change* (Academic Press, San Diego, CA, 1997).
34. O. E. Sala *et al.*, *Science* **287**, 1770 (2000).
35. K. G. Cassman, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5952 (1999).
36. V. W. Ruttan, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5960 (1999).
37. G. C. Daily, *Nature's Services: Societal Dependence on Natural Ecosystems* (Island Press, Washington, DC, 1997).
38. G. C. Daily *et al.*, *Science* **289**, 395 (2000).
39. J. Walsh, *Preserving the Options: Food Production and Sustainability* (CGIAR, Washington, DC, 1991).
40. Y. Zhu *et al.*, *Nature* **406**, 718 (2000).
41. P. L. Woomer, M. J. Swift, Eds., *The Biological Management of Tropical Soil Fertility* (Wiley, Chichester, UK, 1994).
42. M. J. B. Green, J. Paine, *State of the World's Protected Areas at the End of the Twentieth Century*, IUCN (The Conservation Union) Protected Areas Symposium, Albany, Western Australia, 23 to 29 November 1997 (World Council on Protected Areas, Gland, Switzerland, 1998). Available at www.wcmc.org.uk/protected_areas/albany.pdf
43. D. Janzen, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5987 (1999).
44. J. Groot, J. R. Penning, F. W. T. De Vries, P. W. J. Uithol, *Nutr. Cycl. Agroecosys.* **50**, 181 (1998).
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