

50. D. Tilman, D. Wedin, J. Knops, *ibid.* **379**, 718 (1996).
51. S. Naeem, L. F. Thompson, S. P. Lawler, J. H. Lawton, R. M. Woodfin, *Philos. Trans. R. Soc. London Ser. B* **347**, 249 (1995).
52. ———, *Nature* **368**, 734 (1994).
53. J. H. Vandermeer, in *Agroecology*, C. R. Carroll, J. H. Vandermeer, P. M. Rosset, Eds. (McGraw-Hill, New York, 1990), pp. 481–516; B. R. Trenbath, *Adv. Agron.* **26**, 177 (1974).
54. D. U. Hooper, *Ecology*, in press; D. U. Hooper and P. M. Vitousek, *Ecol. Monogr.*, in press.
55. R. H. MacArthur, *Ecology* **36**, 533 (1955).
56. C. S. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958); D. Tilman, *Ecology* **78**, 81 (1997).
57. R. J. Hobbs and L. Atkins, *Aust. J. Ecol.* **13**, 171 (1988).
58. R. T. Wills, *ibid.* **18**, 145 (1993).
59. D. M. Richardson and R. M. Cowling, in *Fire in South African Mountain Fynbos: Ecosystem, Community and Species Response at Swartboskloof*, B. W. van

- Wilgen, D. M. Richardson, F. J. Kruger, H. J. van Hensbergen, Eds. (Springer-Verlag, Berlin, 1992), pp. 161–181.
60. R. J. Hobbs, D. M. Richardson, G. W. Davis, in *Mediterranean-Type Ecosystems: The Function of Biodiversity*, G. W. Davis and D. M. Richardson, Eds. (Springer-Verlag, New York, 1995), pp. 1–42.
61. J. F. Richards, in *The Earth as Transformed by Human Actions*, B. L. Turner II, Ed. (Cambridge Univ. Press, Cambridge, 1993), pp. 163–178.
62. F. Berendse and R. Aerts, *Funct. Ecol.* **1**, 293 (1987).
63. A. Kattenberg *et al.*, in *Climate Change 1995. The Science of Climate Change*, J. T. Houghton *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 285–357.
64. J. Alcamo, Ed., *IMAGE 2.0: Integrated Modeling of Global Climate Change* (Kluwer Academic, Dordrecht, Netherlands, 1994).
65. P. R. Ehrlich and A. H. Ehrlich, *Extinction. The Causes and Consequences of the Disappearance of Species* (Random House, New York, 1981).

cline associated with loss of soil quality and increased plant health problems (4); the growth in yields from intensive paddy rice in Asia is also in question (5).

At the same time that environmental concerns are increasing, so are concerns about feeding a rapidly growing human population and reducing hunger. Demographers predict that the population will grow to between 8 billion and 10 billion in the 21st century. Meanwhile, some 800 million people are malnourished today. Although malnutrition and hunger are currently more related to poverty and inequitable food access than to inadequate food production per se, many regions of the world, particularly parts of Africa, are not self-sufficient in food production (6). Thus, agricultural intensification remains a major target of research and development. Reconciliation of these two needs—increased world food production with greater protection of the environment for the future—is subsumed under the umbrella of “sustainable development” and presents a major challenge for science in the 21st century. Understanding how ecosystems are altered by intensive agriculture, and developing new strategies that take advantage of ecological interactions within agricultural systems (7), are crucial to the continuance of high-productivity agriculture in the future.

Agricultural Intensification and Ecosystem Properties

P. A. Matson,* W. J. Parton, A. G. Power, M. J. Swift

Expansion and intensification of cultivation are among the predominant global changes of this century. Intensification of agriculture by use of high-yielding crop varieties, fertilization, irrigation, and pesticides has contributed substantially to the tremendous increases in food production over the past 50 years. Land conversion and intensification, however, also alter the biotic interactions and patterns of resource availability in ecosystems and can have serious local, regional, and global environmental consequences. The use of ecologically based management strategies can increase the sustainability of agricultural production while reducing off-site consequences.

Biological Consequences of Agricultural Intensification

Expansion of agricultural land is widely recognized as one of the most significant human alterations to the global environment. The total area of cultivated land worldwide increased 466% from 1700 to 1980 (1). Whereas the rate of expansion has slowed in the last three decades, yields (food produced per area of land) have increased dramatically (2, 3) and have outpaced global human population growth. This remarkable scientific and technological achievement is based largely on intensification of management on land already under agriculture, accomplished through the use of high-yielding crop varieties, chemical fertilizers and pesticides, irrigation, and mechanization. In the developing countries, this intensification fell under the

general heading of “the Green Revolution,” which began in the 1960s with the transfer and dissemination of high-yielding seed (3). Intensification and rise in crop yields have been evident in both developed and less-developed countries, and are demonstrated by the long-term yield pattern for corn and wheat in eastern Colorado (Fig. 1), where irrigated corn yields have increased by 400 to 500% since 1940, and wheat yields have increased up to 100%.

Concerns have developed, however, over the long-term sustainability and environmental consequences of the intensification of agricultural systems. It is now clear that agricultural intensification can have negative local consequences, such as increased erosion, lower soil fertility, and reduced biodiversity; negative regional consequences, such as pollution of ground water and eutrophication of rivers and lakes; and negative global consequences, including impacts on atmospheric constituents and climate. Concerns about the ability to maintain long-term intensive agriculture are also growing. In India, for instance, the intensive rice-wheat systems of the Punjab are beginning to show signs of serious de-

One key feature of agricultural intensification has been increasing specialization in the production process, resulting in reduction in the number of crop or livestock species, or both, that are maintained, often leading to monoculture (Fig. 2). The composition of the plant community, as determined by the farmer, may be described as the “planned diversity” of crop systems; ultimately, this crop diversity is critical not only in terms of production but because it is an important determinant of the total biodiversity. It influences the composition and abundance of the associated biota such as those of the pest complex and the soil invertebrates and microorganisms, which in turn affect plant and soil processes (8). In the following sections, we discuss the role of these biological components of the system and the ways they are altered by cultivation.

The pest complex. In both agricultural and natural ecosystems, herbivorous insects and microbial pathogens can have significant impacts on plant productivity. The reduction in plant species richness that accompanies agricultural intensification leads to changes in the community composition of the pest complex—herbivorous insects, their natural enemies (predators and para-

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sites), and the microbial community attacking crops (9). The low planned diversity of monocultural agricultural systems typically results in greater crop losses from an insect pest complex that is less diverse but more abundant (10, 11). The trend for higher insect pest densities in monocultures is especially strong for specialist herbivores with a narrow host range. Lower insect pest densities in more diversified host systems result partly from changes in host-finding and insect movement, but may also result from the higher predation rates, higher parasitism rates, and higher ratios of natural enemies to herbivores that are characteristic of polycultures (10, 12).

The diversity of crop species in an agroecosystem has a much less predictable effect on microbial pathogens than on insects. Microclimatic conditions play an important role in the development and severity of plant disease, and crop diversification can either encourage or inhibit pathogen growth, depending on the particular requirements of the organism. Whereas fungal pathogens can be lower in polycultures (13), the opposite effect is also seen. Generalizations are difficult because the effects of intercropping depend on a variety of dispersal processes, infection efficiency, and the rate of disease progress (14). For viruses, the situation is somewhat clearer. The majority of viruses that are transmitted by insects tend to be found at lower incidence in polycultures, due to the effects of plant species diversity on their insect vectors (15).

In contrast to the variable effects of crop species diversity on pathogens, the genetic diversity of crops can significantly reduce pathogen impacts on crop productivity. Both multiline cultivars and varietal mixtures have been used effectively to retard the spread and evolution of fungal pathogens in small grains. There is some evidence that they may also be useful for the control of plant viruses (16). Typically, these mixtures include both resistant and susceptible crop genotypes. The reduction in pathogen spread is greater than would be expected on the basis of the proportion of resistant genotypes in the mixtures, and therefore appears to be because of the effects of diversity, per se, on the ability of pathogens to disperse. Although genetically diverse grain crops are now in widespread use in many parts of the world, there is great potential for using multilines and mixtures in other crops.

In the recent era of agricultural intensification, the potential for using crop diversity to manage insect and microbial pests has not been extensively exploited. Currently, pest management is primarily accomplished through the use of pesticides, and 5 million tons of pesticide are applied annually to crops worldwide. As a result,

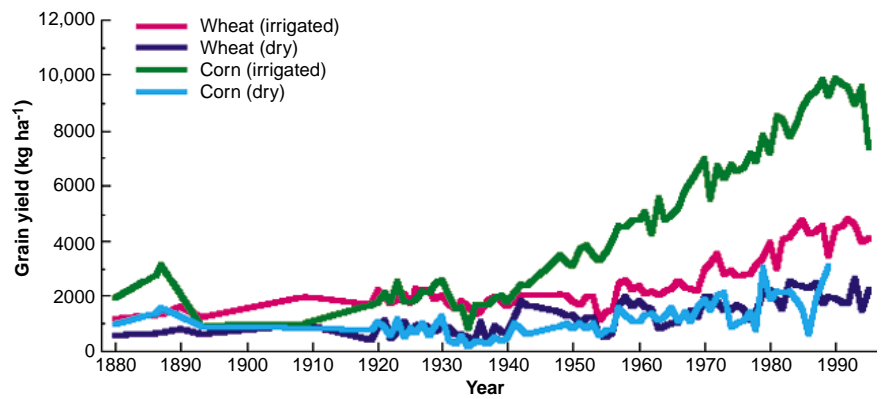


Fig. 1. Changes in grain yield for dryland and irrigated winter wheat and corn for Weld County in northeastern Colorado (annual state agricultural statistics).

pesticide resistance has become a ubiquitous problem, as have the environmental and human health threats associated with pesticide transfers to water and air (see later section). Although integrated pest management (IPM), which advocates the use of host plant resistance, biological control, and cultural controls along with pesticides, has been promoted for decades and has had some notable successes (17), it has been widely adopted in relatively few crops and has yet to significantly affect the amount of pesticides used worldwide. This limited acceptance stems in part from economically attractive pricing and policies that encourage the use of pesticides and the fact that implementation of IPM requires knowledge-intensive management.

Soil biota. In natural ecosystems, soil nutrient cycling, soil structure, and other properties are substantially regulated by the activity of a highly diverse soil community of microbes and invertebrate animals (18). The composition, abundance, and activity levels

of the soil community have been shown to be markedly different in agricultural systems from those in the natural ecosystems from which they are derived (19). In comparisons of tropical forest and agricultural systems, Lavelle and Pashanasi (20) reported that taxonomic diversity and population abundance of the macrofauna in the agricultural systems they studied were typically less than half that in primary forest; similar changes are evident across a wide range of tropical ecosystems (21). However, the trend is not absolute; the abundance and biomass of the fauna in tropical pastures, for example, are often enhanced. These soil fauna communities are usually dominated by a single or small number of species, highly adapted to the changed environment.

The changes in the soil community under agriculture can be attributed to a variety of causes (22). The initial conversion from natural forest, entailing as it does the removal and/or burning of a large plant biomass and subsequent tillage, is a major per-

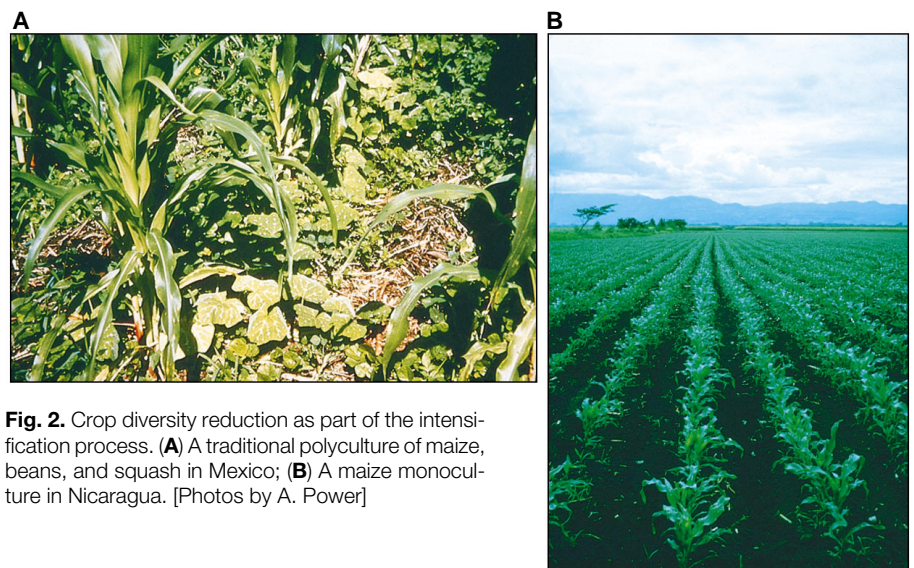


Fig. 2. Crop diversity reduction as part of the intensification process. (A) A traditional polyculture of maize, beans, and squash in Mexico; (B) A maize monoculture in Nicaragua. [Photos by A. Power]

turbation of the soil environment with immediate effects on soil biota. The composition and activity of the soil biota is also strongly influenced by the physical environment at the soil surface, typically reflected in amplified diurnal and seasonal extremes of temperature and moisture (23). The substantial decrease in the quantity and the change in chemical composition of organic inputs to the soil in agricultural systems are also significant factors in changing the competitive balance between different organisms (24).

Although it is clear that cultivation leads to major changes in the soil biotic community, the significance of these changes to agroecosystem functions is less well established (25). Some functions, particularly within the nitrogen (N) cycle, are carried out by very specific organisms. Others, such as decomposition and nutrient mineralization, are mediated by the interactions within a diverse community of organisms. From studies of keystone organisms such as termites, earthworms, N-fixing bacteria, mycorrhizal fungi, and nematodes, it is evident that reduction in diversity of soil biota under agricultural practice may profoundly alter the biological regulation of decomposition and nutrient availability in the soil. These biological functions have been largely substituted in intensive agriculture by the use of fertilizers and mechanized tillage. Management practices can, however, be designed to maximize the presence and function of soil biota. For example, switching from extensive to reduced tillage reduces the severity of physical effects at the soil surface as well as increasing organic inputs through crop residue retention. This practice results in significant changes in the composition and structure of the soil food web (24).

Changes in Natural Resources

Soil organic matter. The loss of soil organic matter with conversion of natural ecosystems to permanent agriculture is one of the most intensively studied and best documented ecosystem consequences of agriculture (26). Soil organic matter is a critical component of both natural and managed ecosystems, providing the organic substrate for nutrient release and playing a critical role in maintenance of soil structure and water-holding capacity, and reduction in erosion. Long-term studies of organic matter loss following agricultural conversion have documented the decreases in soil carbon (C) associated with cultivation (26, 27). In temperate zone agriculture, soil organic matter losses are most rapid during the first 25 years of cultivation, with losses of 50% of the original C typical (Fig. 3). In tropical soils,

such losses may occur within 5 years after conversion. Losses of soil C, however, can be counteracted somewhat by increased crop residue, as is evident in the trend for soil C levels in U.S. agriculture (Fig. 3).

Whereas the trend of organic matter loss is clear, the rate and amount of loss depends on a number of factors, including climate and soil type as well as numerous factors directly influenced by cropping systems, such as the amount of organic inputs, crop coverage of the soil, tillage practice, and length and type of fallow. For example, Metherell *et al.* (28) have demonstrated that soil C losses associated with the winter wheat–fallow rotation were 50% lower for no-till compared to conventional tillage. No-till does not always increase total soil C to a depth of 20 cm, but most studies indicate that soil C in the top 5 cm is increased (29). Because of the interacting nature of these controls, models of soil organic matter change and equilibrium under disturbance and management such as CENTURY (30) and ROTH-AMSTED (31) have been developed and are now being applied worldwide to evaluate the consequences of various types of management. It is evident that many of the management strategies that fall under the “sustainable agriculture” rubric, including low- or no-till cultivation, use of cover crops, green manure, animal manure, and use of more high-yielding varieties, will increase soil organic matter levels over those typical of intensive management of the recent past, with a concomitant increase in soil fertility and water-holding capacity. In addition, these management strategies may also reduce the role of soils as sources and increase their role as sinks for carbon dioxide.

Water and nutrients. In many terrestrial ecosystems, water or nutrients, especially N and phosphorus (P), limit growth of plants. Plants have evolved strategies that allow them to persist under these limitations. Not surprisingly, water and nutrients are also the main constraints to agricultural production. The capacity to overcome these constraints in order to allow optimum conditions for the new higher yielding varieties of crops has been central to the production increases of the Green Revolution. Thus, the use of irrigation and fertilization has increased dramatically, especially since the late 1960s (Fig. 4).

Most prime land for rain-fed cultivation is in use; the development of irrigated land has increased at the rate of 2.2% per year between 1961 and 1973, with lower rates in the decades since then (3). At a global scale, 40% of crop production now comes from the 16% of agricultural land that is irrigated, including much of the critical rice-growing areas (3, 32). Production from these systems accounts for a substantial portion of the increased average yields accom-

plished through Green Revolution technologies. For example, the national food self-sufficiency attained in India in the last several decades arose substantially from the growth of rice and wheat under irrigation in the semi-arid plains of the Punjab. Continued increases in agricultural production will require sustained or increased supply of irrigation water. Even now, however, over-pumping is a serious concern in many regions, old reservoirs are losing capacity due to siltation, and new ones become difficult or impractical to site (33). Moreover, scarcity of water can be expected to increase as competition for withdrawals increases with human population growth and development. In addition to being an important user of a limited water supply, irrigated agricultural lands in arid and semiarid regions are being continuously degraded by salinization and waterlogging. In developing countries, approximately 15 million ha have experienced reduced yields due to salt buildup and waterlogging (3).

Similarly, intensive high-yield agriculture is dependent on addition of fertilizers, especially synthetic N produced through a fossil fuel-consuming industrial process that converts abundant atmospheric N to available forms and, secondarily, P, which is mined from P-rich deposits in rock. As a result of this dependence, vast quantities of fertilizer are produced and applied each year (Fig. 4). By 1990, 80 million metric tons of N were produced in industrial N fixation each year, and another 40 million tons were fixed by crop plants carrying out biological N fixation; together, these human-controlled inputs were equivalent to annual N inputs via natural processes (34).

Whereas the same suite of nutrient cycling processes that operate in unmanaged ecosystems also operate in agricultural systems, the relative importance and magnitudes of individual processes vary. In unmanaged ecosystems, most of the nutrient supply results from the turnover of soil organic matter mediated by soil organisms. Inputs of N occur via atmospheric deposition or biological N fixation, and outputs via gas emissions, solution loss, and erosion; both inputs and outputs are relatively small compared to nutrients moving in the internal cycle. The cycle is altered profoundly in many agricultural systems due to the removal of nutrients at crop harvest, reduced nutrient release from organic matter, large additions of inorganic N that are immediately available for plant uptake, and increased losses. As noted in earlier sections, soil organic matter and the soil organisms that process it and ultimately release nutrients from it are substantially altered. Low nutrient supply is offset by fertilizer N, some of which is consumed by crop plants, leading to increased production

and yield as well as improved grain or product quality. However, added N also can be lost from the system in the form of trace gases emitted to the atmosphere or as nitrate leaching in solution from the soil to surface or groundwater. These losses occur because of the pulsed nature of the additions of relatively mobile forms of N, which are often not synchronized to plant demand, and because the reduced content of soil organic matter and disruption of the soil biological community result in the inability of the soil microbial community to retain and mediate the transfer of the excess nutrients. A reasonable estimate is that from 40 to 60% (30, 35) of the N that is applied is used by the plants; the rest is left in soil or lost. Consequently, as discussed below, N fertilizers have enormous real and potential environmental consequences at local, regional, and global scales, some of which feed back to negatively affect agricultural production.

High nutrient inputs to agricultural systems often have significant, positive effects on pathogen and insect pest populations. Response to N concentration in crops is particularly strong for many insects and fungal pathogens (36, 37). Because N fertilization often has its strongest effects on plant-soluble N (38), sap-feeding insects like aphids, leafhoppers, and planthoppers are likely to show strong population increases in response to N fertilization. The high rates of N fertilization that accompanied the introduction of high-yielding varieties in rice throughout Southeast Asia consistently led to outbreaks of the brown planthopper, *Nilaparvata lugens*. Pest management manuals distributed by the International Rice Research Institute in the Philippines now instruct farmers to apply less N fertilizer and to avoid N pulses that lead to outbreaks (39). The negative impacts of such devastating pests on crop yields can outweigh any positive effect of additional N on crop production.

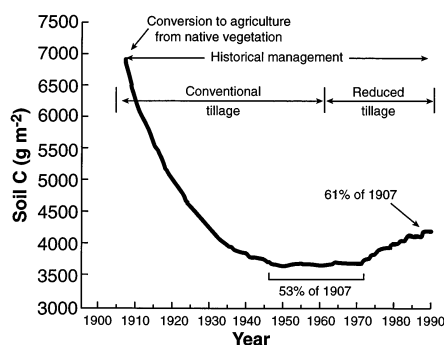


Fig. 3. Simulated total soil C (for soil depth of 0 to 20 cm) changes for the central U.S. corn belt (57). Points at which soil C was 53 and 61% of concentration at conversion to agriculture (in 1907) are indicated.

A range of crop pathogens, including fungi, bacteria, and viruses, also cause more severe damage when N inputs are high (37). Moreover, the particular form of fertilizer N applied to a crop can have significant impacts on pathogen dynamics and disease severity. For example, soil-borne pathogens like *Rhizoctonia* and *Fusarium* appear to cause more damage when N is applied as ammonia than nitrate (40). Soil processes that affect the form of N available to plants may also affect disease severity. In contrast, the response of insect pests to N fertilization does not appear to depend on the form of N applied (36).

Interactions Between Agroecosystems and Surrounding Regions

Although agroecosystems are typically managed in isolation from other ecosystems within a region, the physical, ecological, and biogeochemical changes that take place within them have numerous consequences for adjacent, and even distant, ecosystems. Similarly, the neighboring systems can influence agroecosystems. For example, the position of an agroecosystem within a landscape of diverse land uses can significantly influence pest dynamics. In temperate systems, it is well documented that hedgerows and woodlots, long recognized for their usefulness in preventing erosion, can also harbor natural enemies that provide significant pest control in adjacent agroecosystems (41). Although similar data from tropical systems are rare, anecdotal information suggests that such natural areas can also support natural enemies of crop pests in the tropics (42). The structure and diversity of the agroecosystem can also influence the movement of wildlife between natural and agricultural systems and affect their use of such systems. Perennial, vegetationally diverse agroecosystems with complex structure can provide important habitats for many birds that are typically found in undisturbed ecosystems. For example, many traditional cacao and coffee systems in the

tropics (grown as polycultures with overstory and understory plants) have been demonstrated to be good habitats for migrant and resident forest birds (43), and these birds may be important consumers of pest insects (44).

A well-known effect of agricultural fertilization with N is leaching of nitrate from soils to water systems, leading to increased concentrations of nitrate in drinking water and downstream surface water systems. Nitrate concentrations in the major rivers of the northeastern United States have increased three- to tenfold since the early 1900s, an increase that is related to the use of fertilization as well as other human activities (45). Moreover, contamination of ground water is common in agricultural regions around the world. High nitrate concentrations in drinking water represent a human health concern, causing methemoglobinemia. Nitrate also influences the health of natural systems. Eutrophication of estuaries and other coastal marine environments can cause low- or no-oxygen conditions in stratified waters, leading to loss of fish and shellfish resources and to blooms of nuisance algae and organisms that are toxic to fish (45, 46). Whereas N in runoff or leaching from agricultural systems influences coastal marine productivity, agricultural sources of P dominate the eutrophication process in many freshwater aquatic systems. Most of the P lost from agriculture is transported over the surface via runoff and erosion, but leaching of organically bound P may be an important pathway in some systems.

Fertilizer use also leads to increased emissions of gases that play critical roles in tropospheric and stratospheric chemistry and air pollution (47). For example, nitrogen oxides (commonly known as NO_x) are emitted from worldwide agricultural soils at estimated rates of up to 25% of the global fossil fuel combustion source (48). Once in the atmosphere, NO_x is a critical regulator of tropospheric ozone, an important component of smog; it affects human health as well as the health of agricultural crops and natural ecosystems. Chameides *et al.* (49) suggest that as much as 35% of cereal crops worldwide may be exposed to damaging levels of ozone. Furthermore, NO_x and ammonia, also emitted from agricultural systems, may be transported and deposited in gaseous or solution forms to downwind terrestrial and aquatic ecosystems. This deposition constitutes, in effect, inadvertent fertilization, and can lead to acidification, eutrophication, shifts in species diversity, and effects on predator and parasite systems (50). Finally, fertilized agriculture is also a critical source of several greenhouse gases, including carbon

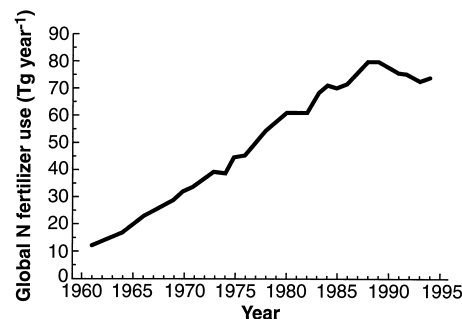


Fig. 4. Annual global N fertilizer consumption is shown for a 35-year period (58) (1 Tg = 10^{12} g).

dioxide, nitrous oxide, and methane (34, 47, 50).

As is the case with fertilizers, a significant fraction of pesticide that is applied to agricultural systems fails to reach the target pests and instead moves into adjacent ecosystems via leaching or aerial drift, where it can have important impacts on the diversity and abundance of nontarget species and can have complex effects on ecosystem processes and trophic interactions (51). Chlorinated hydrocarbons such as dichloro-diphenyl-trichloroethane (DDT) can persist in the environment for decades after their use, while organophosphates and carbamates are short-lived but acutely toxic. Furthermore, many of the residues are hormone mimics or immunosuppressants that may have significant implications for public health.

As noted earlier, irrigated agricultural lands in arid and semiarid regions are being degraded by salinization and waterlogging; irrigation also influences the quality of water systems outside of the agricultural system. Irrigation return-flows typically carry more salt and minerals than the surface or groundwater source that supplied it, due to evaporation and concentration in the agricultural systems, potentially affecting downstream agricultural and natural systems. Irrigation withdrawals also can leave downstream systems so depleted in water that riparian systems and fish and wildlife populations are damaged (52).

The high rates of water and wind erosion associated with cultivated agriculture (53) reduce the soil resources in agricultural land, but also can lead to sedimentation in reservoirs and lakes that reduce the lifetime of water systems. High levels of suspended sediments can also reduce net primary production in freshwater and marine systems, ultimately affecting fish and aquatic invertebrates feeding and reproduction. Finally, wind erosion contributes significantly to the aerosol content of the atmosphere, which plays critical roles in climate as well as air pollution.

Roads to Sustainable Agriculture

The biological and environmental consequences of agricultural intensification are increasingly apparent and have become a focus of detailed study in Europe and North America. In these regions, where food self-sufficiency has been abundantly realized, legislation has been introduced to promote more sustainable means of production. Even in regions such as sub-Saharan Africa, where self-sufficiency in food production is still a distant target, a focus on sustainability is being applied to agricultural development. The dimensions of sustainable agri-

culture are multiple (54), but in this context sustainability may be defined as meeting current production goals without compromising the future in terms of resource degradation or depletion.

The challenge, therefore, is to realize increased production while avoiding the more extreme of the effects detailed above. The development of more ecologically designed agricultural systems that reintegrate features of traditional agricultural knowledge and add new ecological knowledge into the intensification process can contribute to meeting this challenge. The renewed interest in agroforestry, intercropping, and mixed arable-livestock systems is an indication of the interest in ecologically designed systems. Moreover, integrated nutrient-organic matter management and pest management approaches are receiving increasing attention as pathways to sustainable high-production agriculture and reduction of off-site problems. Broad implementation of such strategies will require the contributions and interactions of social as well as natural scientists, national and international agricultural research institutions, industry, policymakers, and farmers.

The use of inorganic, industrially produced fertilizers has been one of the key factors in enabling the enormous increase in food production in the last five decades, yet the biological and environmental consequences of their use are substantial. Requirements for increased food production that the world faces, particularly in the tropical regions, cannot conceivably be met without increased nutrient inputs. However, in order to avoid the accompanying acceleration of environmental degradation, the efficiency of use must be increased greatly. The capacity of the soil system to supply nutrients and retain applied nutrients is undermined by practices that diminish the role of soil organisms and lead to depletion in soil organic matter. One key to nutrient use efficiency lies in the spatial and temporal matching of nutrient resources and plant demand. The adoption of emerging technology that allows inputs to be applied differentially across fields to match crop demands ("precision agriculture") provides a technological step toward increased efficiency that will be immediately useful in some regions. Strategies that help synchronize nutrient release from organic matter and nutrient supply from inputs with plant demand require less-advanced technology but are information intensive. These will require better integration of industrial fertilizers, organic matter inputs (such as crop residues, manure, and organic household and industrial wastes), organic matter stocks and turnover, the biotic community that

regulates soil fertility, and plant demand (9, 55). The scientific basis of that integration, and the economic and social cost of such practices, must be much better understood and incorporated into implementation practices (56).

A second example of opportunity for improved biological management of agricultural systems lies in integrated methods for pest management. The integration of crop diversification, host resistance, nutrient management, and biological control has the potential to substantially reduce our reliance on pesticides, while still maintaining yields. The challenge is to improve our understanding of the interactions between these modifications in the cropping system, so that we can better predict and manage pest problems. It is clear, however, that by manipulating trophic levels above and below the pest, we can influence pest population dynamics and behavior in ways that reduce crop damage without the negative environmental consequences that often accompany pesticide use.

REFERENCES AND NOTES

1. W. B. Meyer and B. L. Turner II, *Annu. Rev. Ecol. Syst.* **23**, 39 (1992).
2. O. B. Grigg, *The World Food Problem* (Blackwell, Oxford, 1993); R. L. Naylor, W. Falcon, E. Savaleta, *Popul. Dev. Rev.* **23**, 41 (1997).
3. R. L. Naylor, *Annu. Rev. Energy Environ.* **21**, 99 (1996).
4. K. K. M. Nambiar, *Soil Fertility and Crop Productivity Under Long-Term Fertilizer Use in India* (Indian Council of Agricultural Research, New Delhi, 1994).
5. K. S. Cassmann et al., in *Soil Management: Experimental Basis for Sustainability and Environmental Quality, Advances in Soil Science*, R. Lal and B. A. Steward, Eds. (Lewis, Boca Raton, FL, 1995), pp. 181-224; K. S. Cassmann, R. Steiner, A. E. Johnston, in *Agricultural Sustainability: Economic, Environmental and Statistical Considerations*, V. Barnett, R. Payne, R. Steiner, Eds. (Wiley, Chichester, UK, 1995), pp. 231-244.
6. United Nations Food and Agriculture Organization, *Agriculture: Towards 2010* (FAO, Rome, 1993).
7. G. P. Robertson, in *Agricultural Ecology*, L. Jackson, Ed. (Academic Press, New York, in press).
8. M. J. Swift and J. S. I. Ingram, Eds., *GCTE Report No. 13*. (Global Change and Terrestrial Ecosystems, Wallingford, UK, 1996).
9. A. G. Power and A. S. Flecker, in *Biodiversity and Ecosystem Processes in Tropical Forests*, G. H. Orans, R. Dirzo, J. H. Cushman, Eds. (Springer-Verlag, New York, 1996), pp. 173-194.
10. D. A. Andow, *Annu. Rev. Entomol.* **36**, 561 (1991).
11. A. Tonhasca Jr. and D. N. Byrne, *Ecol. Entomol.* **19**, 239 (1994).
12. E. P. Russell, *Environ. Entomol.* **18**, 590 (1989).
13. M. A. Boudreau, *Plant Pathol.* **42**, 16 (1993); _____ and C. C. Mundt, *Phytopathology* **82**, 1051 (1992).
14. M. A. Boudreau and C. C. Mundt, *Ecol. Appl.* **4**, 729 (1994).
15. A. G. Power, in *Agroecology: Researching the Ecological Basis for Sustainable Agriculture*, S. R. Gliessman, Ed. (Springer-Verlag, New York, 1990), pp. 47-69.
16. _____, *Ecology* **72**, 232 (1991).
17. R. L. Naylor and P. R. Ehrlich, in *Natures Services*, G. C. Daily, Ed. (Island Press, Washington, DC, 1997), pp. 151-174.
18. P. S. Giller, *Biodiversity Conserv.* **5**, 135 (1996).
19. P. Lavelle, C. Gilot, C. Fragoso, B. Pashanasi, in *Soil Resilience and Sustainable Land Use*, D. J. Green-

- land and I. Szabolcs, Eds. (CAB International, Wallingford, UK, 1994), pp. 291–308.
20. P. Lavelle and B. Pashanasi, *Pedobiologia* **33**, 283 (1989).
 21. Tropical Soil Biology and Fertility Programme, *Biology and Fertility of Tropical Soils*. TSBF Report 1997 (TSBF, Nairobi, Kenya, 1997); P. Lavelle, personal communication.
 22. Special issue on Soil Biodiversity, Agricultural Intensification, and Agroecosystem Function, M. J. Swift, Ed., *Appl. Soil Ecol.* **6** (August 1997); M. H. Beare, G. Tian, V. M. Reddy, S. C. Srivastava, *ibid.*, p. 87; C. E. Pankhurst, B. M. Doube, V. V. S. R. Gupta, P. R. Grace, Eds., *Soil Biota: Management in Sustainable Farming Systems* (CSIRO, Australia, 1994).
 23. B. R. Critchley *et al.*, *Pedobiologia* **19**, 425 (1979); J. A. Ingram and M. J. Swift, in *Research Methods for Cereal/Legume Intercropping*, S. R. Waddington, A. F. E. Palmer, O. T. Odje, Eds. (CIMMYT, Mexico City, 1989), pp. 200–214; G. Tian, L. Brussaard, B. T. Kang, M. J. Swift, in *Driven by Nature—Plant Litter Quality and Decomposition*, G. Cadisch and K. E. Giller, Eds. (CAB International, Wallingford, UK, 1997), pp. 125–134.
 24. M. H. Beare *et al.*, *Ecol. Monogr.* **62**, 569 (1992).
 25. M. J. M. Anderson, in *Biodiversity and Ecosystem Function*, E.-D. Schulze and H. A. Mooney, Eds. (Springer-Verlag, Berlin, 1993), pp. 29–41.
 26. E. A. Paul, K. Paustian, E. T. Elliott, C. V. Cole, *Soil Organic Matter in Temperate Ecosystems* (CRC Press, New York, 1997).
 27. I. C. Burke *et al.*, *Soil Sci. Soc. Am. J.* **53**, 800 (1989).
 28. A. K. Metherell *et al.*, in *Soil Management and the Greenhouse Effect*, R. Lal, J. Kimble, E. Levine, B. A. Stewart, Eds. (Lewis, Boca Raton, FL, 1995), pp. 259–270.
 29. K. Paustian, G. P. Robertson, E. T. Elliott, in (28), pp. 69–88.
 30. W. J. Parton and P. E. Rasmussen, *Soil Sci. Soc. Am. J.* **58**, 530 (1994).
 31. D. S. Jenkinson, *Philos. Trans. R. Soc. London Ser. B* **329**, 361 (1990).
 32. S. Postel, in *State of the World 1996*, L. R. Brown, Ed. (Norton, New York, 1996), pp. 40–59.
 33. S. L. Postel, G. C. Daily, P. R. Ehrlich, *Science* **271**, 785 (1996).
 34. P. M. Vitousek and P. A. Matson, in *Biogeochemistry of Global Change: Radiatively Active Trace Gases*, R. Oremland, Ed. (Chapman & Hall, New York, 1993), pp. 193–208.
 35. K. Paustian, W. J. Parton, J. Persson, *Soil Sci.* **56**, 476 (1992).
 36. J. M. Scriber, in *Nitrogen in Crop Production*, R. D. Hauck, Ed. (American Society of Agronomy, Madison, WI, 1984), pp. 441–460.
 37. D. M. Huber, in *CRC Handbook of Pest Management in Agriculture*, D. Pimentel, Ed. (CRC Press, Boca Raton, FL, 1981), pp. 357–394.
 38. W. J. Mattson Jr., *Annu. Rev. Ecol. Syst.* **11**, 119 (1980).
 39. W. H. Reissig *et al.*, *Illustrated Guide to Integrated Pest Management in Rice in Tropical Asia* (International Rice Research Institute, Los Banos, Philippines, 1986).
 40. D. M. Huber and R. D. Watson, *Annu. Rev. Phytopathol.* **12**, 139 (1974).
 41. M. A. Altieri and L. L. Schmidt, *Agric. Ecosyst. Environ.* **16**, 29 (1986); N. Boatman, *Field Margins: Integrating Agriculture and Conservation* (British Crop Protection Council, Farnham, UK, 1994).
 42. A. G. Power, in *Forest Patches in Tropical Landscapes*, J. Schelhas and R. Greenberg, Eds. (Island Press, Washington, DC, 1996), pp. 91–110.
 43. C. S. Robbins *et al.*, *Comparison of Neotropical Migrant Bird Populations Wintering in Tropical Forest, Isolated Fragments, and Agricultural Habits* (Smithsonian Institution Press, Washington, DC, 1992); J. M. Wunderle Jr. and R. B. Waide, *Condor* **95**, 904 (1993); R. Greenberg, in *Forest Patches in Tropical Landscapes*, J. Schelhas and R. Greenberg, Eds. (Island Press, Washington, DC, 1996), pp. 59–90.
 44. R. Greenberg and J. Salgado Ortiz, *Auk* **111**, 672 (1994).
 45. R. W. Howarth, G. Billen, D. Swaney, A. Townsend, *Biogeochemistry* **35**, 75 (1996).
 46. National Research Council, *Managing Wastewater in Coastal Urban Areas* (National Research Council, Washington, DC, 1993); S. W. Nixon, *Ophelia* **41**, 199 (1995).
 47. F. J. Williams, G. L. Hutchinson, F. C. Fehsenfeld, *Global Biogeochem. Cycles* **6**, 351 (1992); R. J. Cicerone and R. S. Oremland, *ibid.* **2**, 299 (1988); S. J. Hall, P. A. Matson, P. Roth, *Annu. Rev. Energy Environ.* **21**, 311 (1996); P. A. Matson, C. Billow, S. Hall, J. Zachariesson, *J. Geophys. Res.* **101**, 18533 (1996); G. P. Robertson, in *Agricultural Ecosystem Effects on Trace Gases and Global Climate Change*, L. A. Harper, A. R. Mosier, J. M. Duxbury, D. E. Rolston, Eds. (American Society of Agronomy, Madison, WI, 1993), pp. 95–108.
 48. R. Delmas, D. Serca, C. Jambert, *Nutrient Cycling in Agroecosystems*, in press; E. A. Davidson, W. Kinglerlee, *Nutrient Cycling and Agroecosystems*, in press.
 49. W. L. Chameides, P. S. Kasibhatla, J. Yienger, H. Levy II, *Science* **264**, 74 (1994).
 50. P. M. Vitousek *et al.*, *Ecol. Appl.*, in press; J. N. Galloway, W. H. Schlesinger, H. Levy II, A. Michaels, J. L. Schnoor, *Global Biogeochem. Cycles* **9**, 235 (1995).
 51. D. Pimentel and C. A. Edwards, *Bioscience* **32**, 595 (1982); S. J. Rische, D. Pimentel, H. Grover, *Ecology* **67**, 505 (1986).
 52. S. Postel and S. Carpenter, in *Natures Services*, G. C. Daily, Ed. (Island Press, Washington, DC, 1997), pp. 195–214.
 53. P. Crosson, *Science* **269**, 461 (1995); D. Pimentel, Ed., *World Soil Erosion and Conservation* (Cambridge Univ. Press, Cambridge, 1993).
 54. J. K. Lynam and R. W. Herdt, *Agric. Econ.* **3**, 381 (1989); A. M. Izac and M. J. Swift, *Ecol. Econ.* **11**, 105 (1994); B. Becker, *Issues Agric.* **10**, 63 (1997).
 55. P. L. Woerner and M. J. Swift, Eds., *The Biological Management of Tropical Soil Fertility* (Wiley, Chichester, UK, 1994).
 56. M. J. Swift, in *The Role of Soil Biota in Sustainable Agriculture*, L. Brussaard and R. Ferrera-Cerrato, Eds. (Advances in Agroecology, Lewis, MI, 1997).
 57. Figure is modified from A. S. Donigan Jr. *et al.* [EPA Report. EPA/600/R-94-067 (1994)].
 58. FAOSTAT, statistics database. <http://apps.fao.org/>
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The Management of Fisheries and Marine Ecosystems

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The global marine fish catch is approaching its upper limit. The number of overfished populations, as well as the indirect effects of fisheries on marine ecosystems, indicate that management has failed to achieve a principal goal, sustainability. This failure is primarily due to continually increasing harvest rates in response to incessant sociopolitical pressure for greater harvests and the intrinsic uncertainty in predicting the harvest that will cause population collapse. A more holistic approach incorporating interspecific interactions and physical environmental influences would contribute to greater sustainability by reducing the uncertainty in predictions. However, transforming the management process to reduce the influence of pressure for greater harvest holds more immediate promise.

Fishing the oceans is a significant human enterprise. Fisheries provide direct employment to about 200 million people (1) and account for 19% of the total human consumption of animal protein. Globally, first-sale fishery revenues produce about U.S.\$70 billion, and fishes represent important commodities in trade from developing countries, showing net exports of about U.S.\$13 billion in 1993 (2). Recent assessments by the United Nations Food and Agriculture Organization (FAO) of the state of the world's fisheries indicate a leveling off of

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landings in the 1990s, at about 100 million tons (3). Almost half of the individual fish stocks are fully exploited, and another 22% are overexploited (Fig. 1). Because of the complexity of marine ecosystems and the difficulty in sampling them, fishery scientists have only rarely taken an ecosystem approach to management. It has been proposed that this lack of ecosystem approaches to fisheries management contributes to world overfishing and stock depletion (4). Despite multiple definitions of ecosystem management, there is widespread and growing commitment by natural resource management agencies to this approach. The Ecological Society of America advocates a definition that emphasizes the holistic consideration of interactions among components of the ecosystem to achieve sustainability through adaptive management (5).