Applied Ecology and Environmental Management

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School of Biological Sciences, University of Bristol, England

SECOND EDITION

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Science

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Preface

The world faces very serious environmental problems. This book is about what science—and especially biological science—can do to help. The book deals with a wide range of topics which are usually covered in separate books by different experts, who may well have been trained in different university departments, including biological science, environmental science, forestry, agriculture, range science, fisheries and wildlife, marine science and others. Here the topics are covered in a single book written by one person. I have written such a book because I believe the world needs people who have studied a wide range of environmental problems, who understand how they relate to each other and how they are based on underlying principles of ecological science.

The human population of the world will continue to increase for at least some decades in the new millennium. This is one of the reasons why there are bound to be pressures on resources. This book assumes that in the future there will be increased demand for energy, water, food, timber, and also for new chemicals for many uses. The ecological challenge is to meet these needs in a sustainable way, yet at the same time reducing as far as possible harmful effects on wild species, communities, landscapes and the quality of the environment on which they depend.

Sometimes science can suggest solutions to ecological problems: for example, ways of controlling diseases or minimizing the effects of pollution. Sometimes it can answer practical questions, such as how many fish we can take from an ocean this year without reducing the catch in future years. Sometimes it can help with resolution of conflicts, for example over alternative uses of land. This book is concerned with each of these aspects of applied ecology.

This second edition is much more than an update of the first edition, it is a major rewrite. In the seven intervening years there has been tremendous research activity in many of the relevant subject areas. There have also been important events, such as the successful re-establishment of wolves in Yellowstone National Park and the collapse of the Newfoundland cod stock. These events and research discoveries have not only increased our knowledge and understanding, but have suggested new priorities and led to changes in attitudes. Hence the need for a major rewrite.

This book is not dedicated to my parents, my wife, my children or to any of the other people who have given me personal support during my life. It is dedicated to everyone who is concerned about the future of our world.

Edward I. Newman

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Many other people have helped by their comments on parts of the first edition or on earlier versions of this second edition, by making suggestions or supplying information. In particular, I want to thank Ian Cowx, John Grace, Ted Gullison, Steve Hopkin, Mike Hutchings, Andrew Illius, Michel Kaiser, Jane Memmott, William Newman, Adrian Newton, Julian Partridge, Clare Robinson, Colin Walker and Richard Wall.

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American Association for the Advancement of Science: Fig. 9.5(b).
American School of Classical Studies at Athens: Fig. 4.2.
American Society of Agronomy: Fig. 4.5(a).
American Society of Limnology and Oceanography: Fig. 5.2.
British Trust for Ornithology: Fig. 10.11(a).
Cambridge University Press: Figs 2.1, 2.3, 4.1.
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Chapter 1: Introduction

This chapter explains what this book is about and how it is organized

The size of our world is fixed, but the number of people in it is increasing (see Table 1.1 and Fig. 1.1). This conflict is a basic driving force underlying many of the problems discussed in this book.

Increasing human population . . .

Figure 1.1 shows how the human population has increased during past decades, in the whole world and in two continents: Africa, which had the fastest percentage increase, and Europe, which had the slowest. The graph does not predict populations in the future. There are many alternative predictions for population change during the 21st century, which differ widely (see Chapter 2), but there can be no serious doubt that the total number of people will rise substantially higher than the figure of about 6 billion at the start of the new millennium. Increasing human population puts further pressure on basic resources, including land and soil, oceans, fresh water and energy sources. It will become more difficult to provide adequate amounts of food and timber, creating pressures for more intensive management of soil and pests, and for changes in land use from the present allocation (Table 1.1). This will result in more risks to wild species and to the areas where they live. More people almost certainly means more production of polluting chemicals. These are the principal topics of this book. So one message, right at the start, is that some things are bound to change.

. . . puts pressures on resources

Table 1.1. Area of water, land and principal land uses on the Earth. Land use data for 1992–94, from World Resources 1998/9.

	Area		
	million km^2	% of whole world	% of land area
Whole world	510		
Oceans	376	74	
Fresh water	3	<1	
Land	131	26	
Crops	14.7		11
Permanent grazing land	34.1		26
Forest and woodland	41.8		32
Other land*	39.9		31

* Includes ice, tundra, desert, towns.

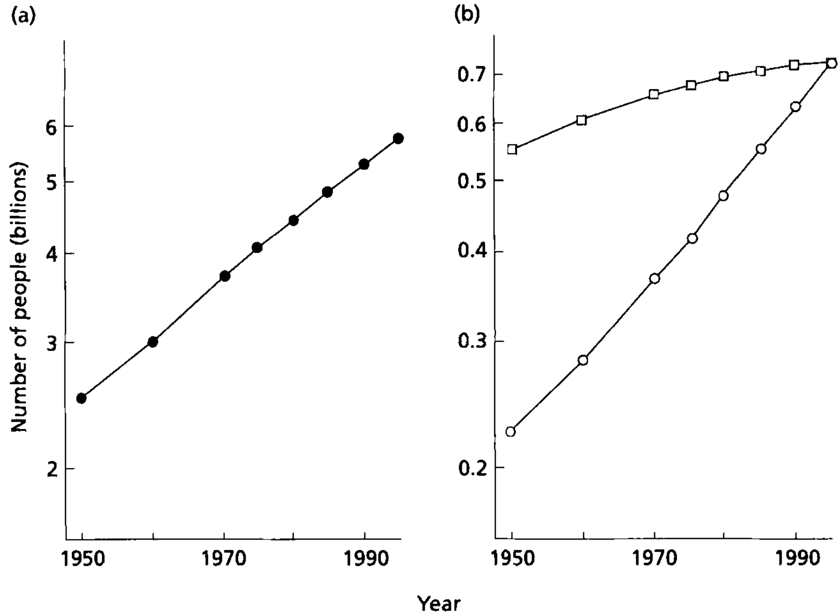

Fig. 1.1 Human population 1950–95. The vertical axes are on log scales. (a) Whole world. (b) □ Europe, ○ Africa. Data from UN Statistics Yearbook 1995.

We should like, if possible, to make things better, for all the people of the world and for the other species in it too. Some topics in this book do aim for that. Can we grow crops in arid areas by using salt water for irrigation? Can we find better ways of breaking down polluting chemicals, using microbes? Can we restore wild species and communities to areas where they formerly occurred? However, much of this book is about how to prevent things getting worse. Can we halt global warming? Can we maintain the fish stocks in the oceans? Can we maintain the productivity of grazing lands and forests long term, but without harming the wildlife? Sometimes we must accept that harmful changes will occur, and the most useful thing ecologists can do may be to give advice on how to minimize the harm. If some of the forests of Amazonia or the US northwest have to be lost, how can we best preserve the species in the remnants?

Difficult choices

Because of these pressures on resources we shall have to make choices, often difficult ones. Should we continue with current or increasing rates of fossil fuel use, in spite of the effect this will have on climate? Should we use a new pesticide to prevent crop loss, even though there is a danger that it may harm other (non-target) species? Should we destroy a community of native species to make more room for food production? Should we extract timber from tropical rainforest, if this will put wild species at risk? These and other choices are discussed in this book. Such choices involve value judgements: how serious is it if a particular species becomes extinct, or if a particular piece of landscape is changed? How do we decide between the needs of people now and in future generations? between food for people and the survival of wild species? This book tries to avoid value judgements. Its aim, instead, is to show how science can help when such decisions have to be made. One of the advantages of a book that covers so many of the major environmental problems of the world is that we can look at these difficult conflicts and choices in a balanced way. Up to now topics such as agriculture, fisheries management, timber production, pollution and conservation have each been dealt with in separate books, and naturally the authors each think their own subject is very important.

Economics and politics applied to environmental problems

Two principal ways of making choices and resolving conflicts are politics and economics. A third is war. All three have been applied to conflicts over natural resources. This book considers economics briefly in a few chapters: for example, how long timescales influence the economics of forestry, and hence decisions about forest management (Chapter 7); and whether we can put a monetary value on wild species (Chapter 10). Politics and regulations also feature occasionally: alternative types of rule for controlling ocean fish catches are explained and discussed in Chapter 5; the US Endangered Species Act is mentioned in Chapter 10. These appearances of economics and regulations are intended as examples, to show how they can interact with science in decisions about management of biological resources. They are deliberately kept few and short. Chapter 2 (on climate change) could, for example, have said much about the negotiations between countries about future carbon dioxide emissions, what they agreed, and how far they have kept their promises; but it does not. The application of politics and economics to management of the environment is very important. This book aims to provide scientific information that will be helpful to politicians and economists, but it does not aim to tell them how to operate politics and economics.

Sustainable systems

One underlying assumption in this book is that we must be prepared to think long term. The word *sustainable* occurs many times in the text. A sustainable system is one that can continue indefinitely, or at least for a long time. A system of growing wheat on a farm is not sustainable unless it can continue to produce as high a yield as it does now. If the farming system results in soil being lost by erosion or the soil structure becoming less favourable for root growth, or an increase in insects harmful to the wheat plant, so there is a long-term decline in yields, then the system is not sustainable. One definition of sustainable grain production requires only that yield be maintained long term. Alternatively, we may also take into account what inputs are needed. If the farming system requires inputs that come from non-renewable sources, for example phosphate fertilizer or fossil fuel, then it can be regarded as not sustainable. A third possible definition requires that the system should not do harm outside its boundaries, for example not put so much nitrate into well waters that they become harmful to people, not use insecticides that kill insects or birds in nearby woods. This book does not confine itself to any one of these definitions of sustainable: we should bear all of them in mind.

Applied science, but based on fundamentals

This book is about *applied* science. The structure of each chapter is designed around a set of environmental problems. So, this book is not pure science with applications tacked on at the end: the applied problems are at the heart of it. Nevertheless, *fundamental* science is crucial to tackling these problems. Why this must be so can be illustrated by Table 10.1 (p. 284), which shows how many thousand species are known in some major groups of animal and plant. We wish to preserve as many as possible of these species, but we do not have the time or resources to do research on every one of them. If we adopt the attitude that we can do nothing about preserving any species until we have performed detailed research on it, almost certainly some species will become extinct before we get round to investigating them. So, their conservation and management must be based substantially on fundamental scientific understanding. That is why Chapter 10, on conservation, considers questions such as: 'How can we decide which species should have higher priority in conservation?'; 'Why can particular species not survive in habitat patches smaller than a certain size?'; 'Can we alter conditions to promote high biodiversity? How?' Or consider biological control of pests and diseases. Some books deal with this case by case, describing in turn each pest species and its successful biological control. Here, Chapter 8 instead considers basic questions such as: 'Can we decide which species are likely to be effective biological control agents, before elaborate testing?'; 'Will a species that initially provides good control evolve to become less effective?'; 'Is biological control safe? How can we be sure it will not harm other, non-target species?'. In these and other chapters, the questions are answered with the aid of examples—particular ecosystems, particular species, particular pollutant chemicals—examples chosen to illuminate the fundamental question, to provide scientific evidence, but never aiming to be a complete list of all those that have been studied.

The fundamental science used in this book covers the whole range of scales in biology, from landscapes and ecosystems, through communities and populations, animal behaviour, physiology and biochemistry, down to single genes; and from the physics of rain formation to the chemistry of pollutant breakdown in soil. Applied ecologists need to be mentally agile. This book has been written primarily for undergraduates studying biological science. It should also be useful to students studying other subjects, such as environmental science, and to many other people who want to find out about the scientific background to current ecological problems, provided they accept the book's strong biological emphasis. For example, in Chapter 2 the section on global climate change passes rapidly over the difficulties of predicting how increases in greenhouse gases will affect future climate, and pays much more attention to how plants and animals will respond to increases in temperature and atmospheric carbon dioxide. Chapter 9 (Pollution) says little about how pollutant chemicals are produced and dispersed, but much about their effects on living things and how to minimize them.

How this book is organized

Following this short introductory chapter there are 10 main chapters. Chapters 2–4 are about basic resources: energy (from the sun and from fossil fuels), water, soil. Then there are three chapters about exploitation and management of biological resources—fish from the oceans, grazing lands, forests; followed by two chapters about things we do not want—weeds, pests, diseases, chemical pollutants—and how to reduce their harmful effects; and finally two chapters on wild species—how to conserve them where they still exist and how to restore them where they have been lost. So, there is a logical progression through the chapters.

Links between chapters

There is also much interaction between chapters: as indicated earlier, this is a key advantage of dealing with so many environmental problems in one book. For example, pest control by chemicals (Chapter 8) produces potential pollutants (Chapter 9). Rainfall (Chapter 3) may be affected by global climate change (Chapter 2), also by overgrazing (Chapter 6) and changes to forests (Chapter 7). The forest chapter considers the effects of different methods of forest management on wildlife as well as on timber production, but there is also further relevant information in Chapter 10 (Conservation), for example on how fragmentation of remaining forests affects wild species. There are also links between chapters at a more fundamental level: there are, for example, fundamental similarities between the population control of fish and pasture foliage (compare Figs 5.4 and 6.3), and between the population biology of disease-causing organisms and of wild animals living in habitat fragments (Chapters 8 and 10). So if you understand one it will help you to understand the other. Thus every chapter contains cross-references to other chapters. If you want to read just one chapter on its own you should be able to understand it well enough, but I hope it will encourage you to read others.

How to find out what is in a chapter

There are no lists of chapter contents, nor does each chapter have a summary in the normal sense. If you want to find out what is in a chapter you can begin by looking at the *Questions* list at the start, which introduces the main problems to be considered. Then follows a list headed *Background science*, but in the text the background science does not come after the problems, nor before them: it is interwoven with them in the chapter. Within the text, headings are sparse: instead, there are many *side headings*, which I hope will guide you through the text without breaking its flow. At the end of each chapter there are *Conclusions*. These are only a selection of the conclusions from the chapter, and they are gross simplifications of what was said earlier in the text. So, if you read the Conclusions and nothing else you will miss a lot.

What I expect you to know already

What do you need to know already in order to understand this book? I have assumed some prior knowledge of biology, such as would occur in an introductory course at university. You also need some knowledge of basic physics and chemistry, such as any biology or environmental science student at university should have. What about mathematics? Ecology is a quantitative subject. Every chapter of this book contains graphs and numbers which are essential to the subject matter. But the mathematics in the book is sparse and simple. A textbook on ocean fisheries by Hilborn & Walters (1992) says near the start: 'Quite frankly, if you are not comfortable writing computer programs and playing with numbers, you should not be interested in fisheries management'. Their book contains more than 300 equations. I have written a chapter on fisheries management for this book which contains three equations, and you certainly do not need to write any computer programs to understand it. Mathematical models are important in ecology: they feature here in many of the chapters, but they are usually presented by words and graphs rather than by equations. The densest mass of equations is in Box 8.3 (p. 218); if you can cope with that, the maths elsewhere in the book should be no problem for you. You also need to know a little about statistics, enough to understand what a correlation coefficient shows and what is meant by 'this difference is statistically significant ($P < 0.001$)'.

There is a glossary near the end of the book, which gives the meanings of technical and specialist words, and of abbreviations. You are expected to know the meanings of more basic scientific terms: if you do not, one of the dictionaries listed below may help you, but they cannot replace the requirement for a groundwork of scientific knowledge. In the text I call a species by its English name, if it has one that is widely used and precise enough. If not, the Latin name is used; this applies to some plants, most invertebrate animals and most microbial species. If the Latin name is used the glossary may give you an English name, or else tell you what major group the species belongs to. If the English name on its own has been used in the text the glossary will give the Latin name.

I have enjoyed writing this book. I hope you will enjoy reading it.

Further reading and reference

Ecology textbooks:
Begon, Harper & Townsend (1996)
Brewer (1994)
Krebs (1994)
Stiling (1996)

Dictionaries:
Allaby (1998)
Lincoln, Boxshall & Clark (1998)
Waites (1998)

Chapter 2: Energy, Carbon Balance and Global Climate Change

Questions

- How many people per hectare can various food production systems support?
- Could low-input systems, on their own, feed the present world population?
- The concentration of carbon dioxide in the world's atmosphere is increasing. What is causing that?
- Could this increase in CO_2 be significantly slowed by using more biomass fuel instead of fossil fuels? or by growing more forest? or by getting the oceans to absorb more?
- What effect will future increases in CO_2 and other gases have on world climate?
- How will future increases in CO_2 and temperature affect (a) crops? (b) wild plants and animals?

Background science

- Energy from the sun reaching the Earth, and what happens to it.
- Primary production of oceans, natural vegetation on land, crops. How crop productivity has been increased.
- The carbon cycle of the Earth: processes, amounts, rates.
- The greenhouse effect. The principal greenhouse gases and their sources.
- How rapidly temperatures changed in the past.
- How fast plants and animals spread in the past, in response to climate change. How fast they can migrate today.

All life depends on energy. Nearly all of that energy comes ultimately from the sun: chlorophyll-containing plants and microorganisms capture solar energy by photosynthesis, and almost all of the remaining living things obtain energy from them, along food chains. This chapter considers how much solar energy is captured by crops and pastureland and is made available to people in their food, and hence how many people different farming systems can support. Many people also use energy obtained by burning fossil fuels—coal, oil and gas—which has increased the concentration of carbon dioxide in the world's atmosphere. Much of this chapter is about the carbon balance of the world, the effects of

Box 2.1 Radiation from the sun and what happens to it.

Radiation emitted by the sun (*solar radiation*) mostly has wavelengths within the range *0.2–3 μm*. This is called *short-wave radiation.*

Fate of the solar radiation reaching the top of the Earth's atmosphere:

reflected by clouds;
absorbed by gases, especially ozone, carbon dioxide and water vapour, which then reradiate it; or
reaches the Earth's surface.

Fate of short-wave radiation hitting plants:

reflected;
passes through to reach soil; or
absorbed by plant. Fate of absorbed energy:
- radiated, as *long-wave radiation* (wavelength > 3 μm);
- used in transpiration;
- used in photosynthesis (primary production); or
- warms plants and surrounding soil and air.

Of the short-wave solar radiation reaching the Earth's surface, about half is *photosynthetically active radiation*, i.e. within the wavelength range 0.4–0.7 μm which can be absorbed by photosynthetic pigments.

Further information: Nobel (1991a); Houghton *et al.* (1996); Robinson & Henderson-Sellers (1999).

increases in CO_2 and other gases, and how living things are likely to be affected in the future.

Solar radiation and primary production

Energy balance of vegetation

Box 2.1 summarizes what happens to the energy in solar radiation that reaches the Earth. Most of the energy in the radiation absorbed by plants is (1) lost as long-wave radiation, (2) used to convert liquid water to vapour, or (3) ends up warming the nearby air. The same is true of radiation absorbed by soil. Plants affect the relative proportion of the incoming energy going into these three 'sinks', which can in turn affect air temperature and rainfall. Chapter 3 (Water) explains how this happens, and considers whether people can alter vegetation sufficiently to have a significant effect on climate.

Primary production

A small but important proportion of the short-wave radiation hitting plants is used in photosynthesis. On the ecological scale this is measured as *net primary production* (or net primary productivity, meaning *rate* of production). *Primary* means production by photosynthetic organisms, as opposed to secondary production by non-photosynthetic (heterotrophic) organisms. *Net* means excluding organic matter used by the green plants for respiration; so the net production is new organic matter that is potentially available to heterotrophs. The net primary production over a year is rarely all still present as extra standing biomass at the end of the year: plants or parts of them are eaten by herbivorous animals, attacked by parasites, or die and are degraded by decomposer organisms. In a true climax ecosystem we should expect that on average the biomass present now is the same as that a year ago: the reproduction and growth of some individuals is on average equalled by the death and decomposition of others.

Table 2.1 shows net primary productivities for some major natural vegetation types. Measuring the productivity of natural vegetation on land poses problems, for example how to measure the amount of primary production eaten by herbivores, and how to measure root growth. Much attention was paid to measuring the productivity of terrestrial vegetation during the 1960s and early 1970s , but not so much since. That is why textbooks, including this one, still quote the summary figures drawn together by Whittaker (1975). These were, inevitably, based on the sites where measurements had been made, which were not evenly distributed across the world and may not be representative. There has been continued research on the primary productivity of the oceans, so more recent data are available. Methods are being developed for estimating primary productivity across large areas of land and ocean by measurements from satellites (see Box 3.2, p. 59; also Chapter 5, Fig. 5.2).

In spite of the uncertainties attached to the figures in Table 2.1, they give us a clear indication of the order of magnitude for primary productivity. It may seem surprising that the figures are so similar for very different ecosystems. It is worth noting the very large variation within the oceans. Much of the area of the world's oceans has productivity less than 3 tonnes ha^{-1} $year^{-1}$ (Behrenfeld & Falkowski 1997); ocean regions with productivities much above that are quite localized, and this has important implications for the management of ocean fish production, as Chapter 5 will explain.

Energy content of plant material

Net primary production is often expressed in terms of the dry weight of the plant biomass produced, as in Table 2.1. However, if we take account of the energy content of the plant material, production can be expressed in energy terms. The energy content of most plant materials, when dry, differs little: it is usually within the range 17–21 kJ/g (FAO 1979; Lawson,

Table 2.1 Range of net primary productivities found among some major terrestrial vegetation types, and in the oceans

Environment	t ha^{-1} $year^{-1}$	Source of data
Tropical rainforest	10–35	1
Savanna	2–20	1
Temperate grassland	2–15	1
Boreal forest (= northern conifer forest)	4–20	1
Oceans	0.2–10	2

1. Whittaker (1975); 2. Barnes & Hughes (1999); Behrenfeld & Falkowski (1997).

Table 2.2 Basic energy data for the world. Values are accurate to only one significant figure, except for fossil fuels

	Total energy per year (Joules × 10^{20})	Source of data
Incoming short-wave radiation reaching surfaces of oceans or land cover	30 000	1
Net primary production	30–50	2
Human food consumption	0.2	3
Human energy use		
fossil fuels	3.1	4
fuelwood	0.2	4
others*	0.4	4
total	4	4

* Includes nuclear and hydroelectricity.
Sources of data. (1) Harte (1985). (2) Values within this range given by Whittaker (1975), Vitousek *et al.* (1986). (3) 5–6 billion people × mean food energy supply per person 1980–92 (FAO Production Yearbook 1994). (4) Data for 1995, from UN Energy Statistics Yearbook 1995, World Resources 1998/9.

Callaghan & Scott 1984), though a few storage tissues such as oil-rich seeds give higher values. The net primary production of the whole Earth, land plus sea, is probably within the range 30–50 × 10^{20} J year^{-1}. This is about 0.1% of the incoming short-wave radiation (Table 2.2). The energy content of the food consumed by the world's human population is only about 0.5% of the world's net primary production. Wood for fuel comprises about another 0.5% of the net primary production. But even taking into account all plant and animal materials used today, their energy content is far less than that of the fossil fuels we use.

Food production per hectare

Table 2.3 shows the energy content of the food produced, per hectare per year, by various contrasting systems. The figures in column (b) range over more than four orders of magnitude. Obtaining fish from the oceans is clearly a very inefficient way of converting solar energy to food energy. However, fish and meat are usually eaten for their protein content rather than primarily as energy sources. Chapter 5 considers in detail the fish stocks of the world's oceans and whether we can exploit them in a sustainable way.

Among the land-based food production systems listed in Table 2.3, the lowest energy capture is by Turkana pastoralists in northern Kenya (line 2). They keep a mixture of animals, migrating with them in relation to the seasonal rainfall. They are almost entirely dependent on their animals for food, milk forming a major component of their diet. Further information on their system of exploiting this unfavourable environment is given in Chapter 6.

Lines 3–5 of Table 2.3 show data from three farming systems which produced crops without inputs such as inorganic fertilizers or synthetic

Table 2.3 Energy content of food produced per hectare by various systems, and number of people that could be supported by that food

Production system	Energy in food (GJ ha^{-1} $year^{-1}$) (a)	(b)	People supported (per ha) (c)
Low-input systems			
1. Fish from oceans, 1986–95		0.004	
2. Migratory pastoralists, Kenya, 1981–82.		0.025	0.005
3. Shifting cultivation, Papua New Guinea, 1962–63	19	1.4	0.3
4. European open-field system, England, 1320–40	12	5	1
5. Southern India, 1955	18	8	2
Modern high-input systems			
6. Beef cattle, lowland England		5	1
7. Wheat, Canada		31	6
8. Wheat, UK		106	21

Notes on columns: (a) Calculated by (energy in food from arable crops)/(land area under arable crops that year). (b) Calculated by (total food energy produced)/(total land area of farm or village). (c) Assumes: energy production as in column (b); population limited by food energy supply; mean food energy use per person 14 MJ day^{-1} (typical for developed countries; FAO Production Yearbook 1994).

Notes on rows: **1.** (Total annual fish catch)/(total area of ocean). See Chapter 5. **2.** Most of the food came from herded cattle, sheep, goats, donkeys and camels, plus a little from growing sorghum and from wild plants and animals. From Coughenour *et al.* (1985); see Chapter 6. **3.** About one-tenth of the area usable by the village was cultivated at any one time, the remainder was regenerating forest fallow. Meat was obtained by feeding some of the crop produce to pigs, plus a small amount of hunting in the forest. From Bayliss-Smith (1982). **4.** One farm in Oxfordshire. Arable mostly cereals; three-field rotation, one field uncultivated each year. Also some pasture and haymeadow, giving some animal produce. Production data from farm records (Newman & Harvey 1997), energy per g from Altman & Dittmer (1968). **5.** Irrigated rice + unirrigated millet. No fertilizers or other inputs apart from irrigation. Cattle grazed on rough pasture, provided milk. From Bayliss-Smith (1982). **6.** Fertilized pasture, producing herbage equal to 50 kg dry matter ha^{-1} day^{-1} (see Fig. 6.3) for 6 months of the year; plus an equal area to provide winter feed. Cattle growth per feed intake based on Snaydon (1987, Chapter 9). **7,8.** Mean production for 1995–97; data from FAO Production Yearbook 1997. Energy per g from Altman & Dittmer (1968).

pesticides. Column (a) shows the energy content of the plant food (mostly cereal grain) per hectare of the arable fields on which it was grown. On that basis their production is lower than modern high-input wheat farming (lines 7 and 8), but compared with countries such as Canada by a factor of only 2 or 3. However, that is not the most useful comparison: the low-input systems of lines 3–5 could only continue by having some land each year that was not producing crops. *Shifting cultivation* involves abandoning the cropland after a few years to allow forest to regenerate, and clearing another patch of forest to cultivate. The European open-field system also involved a rotation, though the fallow was usually only for 1 year. Grazing land was also an essential component of the system, and this was also the case in the traditional system of southern India. The grazing animals provided some food but also their manure, which was crucial in maintaining crop production. In all three of these systems the extra land was essential for maintaining the fertility of the soil and for control of weeds, pests and diseases. For further information on this, see Chapters 4 and 8. Column (b) shows the energy in all the food (including animal produce) per total area needed to keep the system operating. This is the true food energy capture per hectare of these systems, and it greatly increases the gap between them and modern wheat farming.

Lines 6–8 show energy capture by modern animal and arable farming systems using modern crop and animal varieties, inorganic fertilizers and synthetic pesticides, thereby not requiring land to be left fallow. Meat production is about an order of magnitude lower than that of cereals in its food energy per hectare. This is commonly the case, and results from the extra trophic level in the system. Modern beef production is, as might be expected, vastly higher in food production than that of migratory pastoralists in a semiarid climate; and modern wheat produces far more than the three low-input farming systems.

How many people per hectare?

Column (c) shows how many people could be supported per hectare, for their energy requirements, by each system. These figures may be compared with the number of people that the world needs to feed. At the start of the new millennium there are about 6 billion people in the world (Fig. 1.1). Various projections of future human population have been made (Fischer & Heilig 1997): it is extremely likely that the population will exceed 7 billion during the 21st century, and it could well reach 11 billion or more. However, if we just consider the present population of 6 billion, the world's total arable area of about 1.5 billion hectares (Table 1.1) requires four people to be supported by each hectare. It is clear from column (c) of Table 2.3 that none of the traditional systems could support the world's population on that arable area: only modern crop production systems can produce the required yield. The world also has 3.4 billion hectares of grazing land which, if evenly shared, means about two people to each hectare. Much of that land has low productivity, e.g. because of low rainfall, but even the high-input cattle system of Table 2.3 line 6 cannot support two people per hectare. So, meat production could not on its own feed the world's future population, though it can make a contribution by supplementing food from arable crops. This book does not dismiss low-input farming systems as worthless: they feature substantially in several later chapters and there is much we can learn from them. But Table 2.3 makes clear that systems that were adequate in the past can no longer support the total world population of the present or the future.

Energy captured in food can be compared with the productivity of natural ecosystems. Taking 10 tonnes ha^{-1} $year^{-1}$ as an example (a productivity figure within the ranges given in Table 2.1): as the energy content of most plant materials is not far from 20 kJ/g, productivity of 10 tonnes ha^{-1} $year^{-1}$ is equivalent to about 200 GJ ha^{-1} $year^{-1}$. All the productivity values in Table 2.3 are below that, even modern wheat. However, Table 2.3 refers only to the energy in edible parts, Table 2.1 to the whole plant. Nevertheless, it is a fact that on farms in developed countries using modern methods, productivities are lower than in some natural ecosystems. Primary productivity is limited by the efficiency of photosynthesis, which is able to convert only a small proportion of the solar energy falling on the plant into chemical energy. Total incoming short-wave radiation in temperate regions is mostly within the range $3–7 \times 10^4$ GJ ha^{-1} $year^{-1}$ (Sims *et al.* 1978; Monteith & Unsworth 1990), so a productivity of 100 GJ ha^{-1} $year^{-1}$ by wheat represents an efficiency of energy conversion of about 0.2%.

How crop yields have been increased

Since the middle of the 20th century there has been much research activity devoted to photosynthesis, which has transformed our understanding of how it operates—the mechanisms of capture of light and CO_2, the biochemical reactions and their control. One might hope that this knowledge would allow us to increase the efficiency of photosynthesis in crop species, but so far it has not. Plant breeding has increased the yields of crop plants, but by changes other than the efficiency of the photosynthetic process (Lawlor 1995; Evans 1997). Breeding has produced varieties where a larger proportion of the total plant weight goes into the edible parts, where the foliage expands more rapidly at the start of the season and stays green longer at the end. Alternatively, in some tropical crops the growing season has been shortened, allowing two, three or even four crops to be grown per year. Modern varieties can benefit from larger amounts of fertilizer: older varieties of cereals tend to 'lodge' if heavily fertilized, i.e. they are easily blown over, whereas modern, short-strawed varieties lodge less readily. Ample supplies of nitrogen lead to a higher rate of photosynthesis per unit weight of leaf, mainly because there is more chlorophyll and more of key enzymes. Apart from the breeding of new varieties, increased crop yields since the mid-19th century have been mainly due to increased use of irrigation and inorganic fertilizers, and to improved control of weeds, pests and diseases (see Chapters 3, 4 and 8).

Lawlor (1995) discussed why selection for high-yielding varieties has not led to higher efficiency of photosynthesis, and whether this is something we may achieve in the future. Genetic engineering techniques provide potential new methods of manipulating steps in the photosynthetic process. One possibility is to improve the efficiency of *Rubisco*, the enzyme of the initial CO_2 capture step in plants with C3 photosynthesis. It is not 100% specific for CO_2: it also reacts with O_2, and the resulting *photorespiration* is a wasteful process which reduces C capture. It may be possible to improve the specificity of Rubisco for CO_2. More rapid removal of products of photosynthesis, from the cells where they are formed to other parts of the plant, could also speed up the process.

Fossil fuels and the carbon balance of the world

The lifestyle of the world's richer countries is much dependent on fossil fuels. Table 2.2 shows that our worldwide use of energy for heating, cooking, transport, operating factories and so on, is about 20 times that of the food we eat. Most of it comes from fossil fuels. The world's resources of fossil fuels are finite, but predicting how long they will last is notoriously difficult. If the present rate of use of coal and oil is compared with known reserves that are likely to be extractable, this suggests that coal will last 1–2 centuries and oil about half a century (UN Energy Statistics Yearbook 1995). However, the world's total coal is estimated to be at least 10 times as much as the 'known recoverable'. The size of known stocks of oil tends to depend on how much money and effort the oil companies spend on exploration, so there are likely to be reserves not yet discovered. In any case, it may never be possible to use all these reserves, because of the effect the released CO_2 would have on the world's climate. This chapter considers that topic in detail, first the changing carbon balance of the world and the increase in atmospheric CO_2, then the predicted effects of increases in CO_2 and other gases on climate. That section makes substantial use of a fat book called *Climate Change 1995*, written by numerous experts belonging to the Intergovernmental Panel on Climate Change (Houghton *et al.* 1996). A slimmer book by Houghton (1997) summarizes many of the key facts. The final main section of this chapter will then draw on many sources of information to consider how living things (crops and wild species) may respond to these changes in CO_2 and climate.

During the 19th and early 20th centuries it was obvious that burning coal released soot and other pollutants, which affected the atmosphere of cities. It was known that CO_2 was released as well, but there was no obvious reason to worry about it. The world's atmosphere is so large, surely any extra CO_2 would be so much diluted it could not possibly have any effect? This assumption has proved to be incorrect. To measure whether the CO_2 concentration in the atmosphere is changing requires very accurate equipment, carefully used. Reliable continuous measurements started in 1958, on Mount Mauna Loa in Hawaii and subsequently at other sites. We also now know CO_2 concentrations before 1958, back over more than 200 000 years, by measurements on small bubbles of air extracted from ice cores several kilometres deep from Greenland and Antarctica (Moore *et al.* 1996, Fig. 3.21). In these cores there are annual layers visible, caused by the different falls of snow in winter and summer, so the bubbles can be dated accurately. Figure 2.1 shows how the CO_2 concentration has changed since 1750. In 1750–1800, in the early years of the industrial revolution, the concentration was about 280 $\mu l\ l^{-1}$ and rising slowly. During the 1990s it was rising at about 1.5 $\mu l\ l^{-1}$ per year, and by 2000 it has passed 360 $\mu l\ l^{-1}$.

Measuring CO_2 in the atmosphere

Because this increase will affect living things (as will be explained

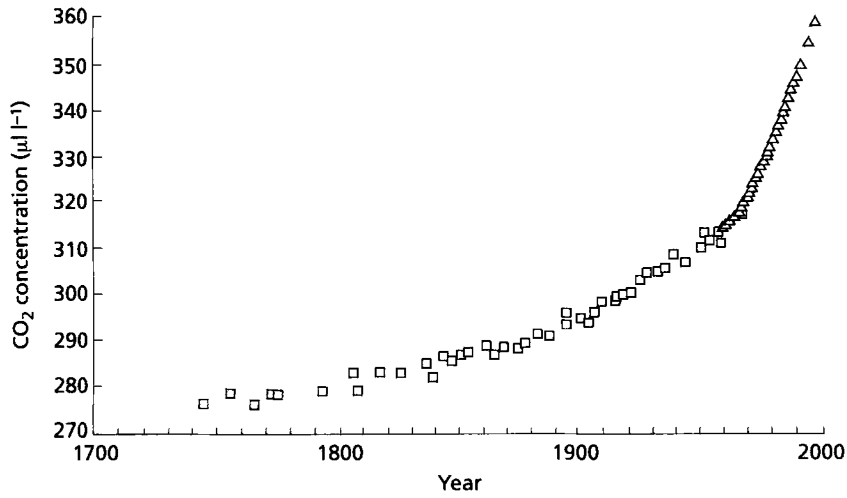

Fig. 2.1 Concentration of carbon dioxide in the Earth's atmosphere since 1750. □ Bubbles in Antarctic ice cores; Δ air at Mauna Loa, Hawaii. From Houghton (1997).

later), it is important to know what is causing it. This will give us a basis for predicting how fast CO_2 concentrations will rise in the future, and how various possible actions by people might affect that. Figure 2.2 gives estimates of the amount of carbon in major global pools, and the rates of transfer between them. To estimate such figures for the whole world is difficult, and they are expected to be accurate only to one significant figure. Nevertheless, it is informative to compare the size of each pool with the amount in the atmosphere. The amount of carbon in the world's fossil fuel reserves is probably more than 10 times as great as the amount in the atmosphere's CO_2: therefore, if we keep on burning it we have the potential to increase atmospheric CO_2 greatly. Terrestrial plants, organic matter on land and in the oceans each have a C pool of the same order of magnitude as the atmosphere, so a change in any one of those three could influence how much is in the atmosphere. Compared with these, the amount of C dissolved in the oceans as inorganics (mainly HCO_3^-) is enormous, so even a small percentage change in that could have a large effect on the atmospheric CO_2 pool. The world's rocks contain enormous amounts of C, in the $CaCO_3$ of limestone and as organic matter in sedimentary rocks. The recycling of that C, by natural weathering, operates on a much longer timescale than concerns us here, though a small amount of CO_2 is released from limestone during the manufacture of cement (Table 2.4). Another small release from the deep Earth is by volcanic eruptions.

Carbon storage: pools

C transfers between pools

Figure 2.2 also shows rates of transfer between pools, and Table 2.4 shows more precise figures for the 1980s for transfers to and from the atmosphere. The rate of increase of CO_2 in the atmosphere (3.3 Gt year^{-1}) was less than the input from fossil fuels plus cement (5.5 Gt year^{-1}).

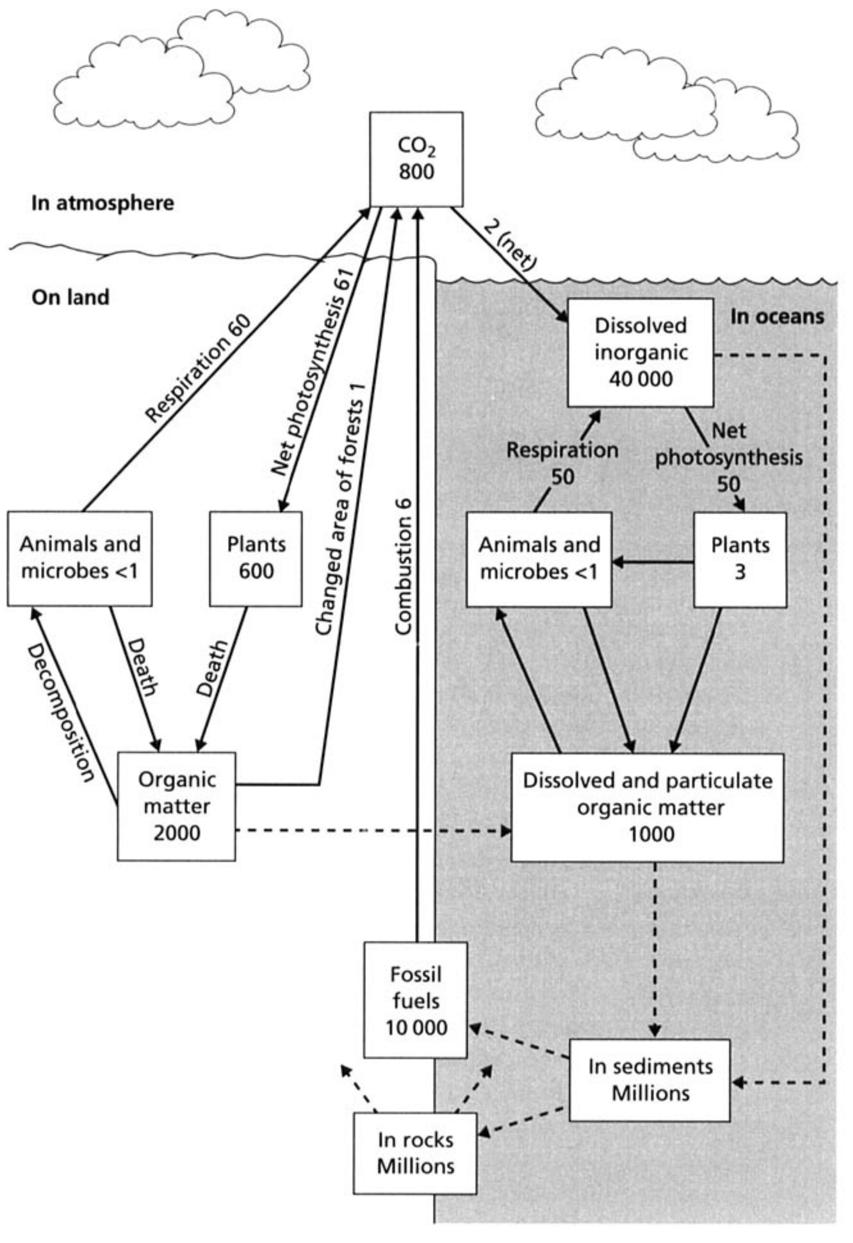

Fig. 2.2 Carbon cycle of the Earth, showing amounts of C in pools and rates of transfer between pools. Dashed lines: rates uncertain. Units: pools, Gt; rates, Gt year^{-1}. (1 Gt = 10^9 tonnes = 10^{15} g.) Most rates are for the 1980s, but fossil fuel combustion rate and amount of C in the atmosphere are for the 1990s. Based on Houghton *et al.* (1996, Chapters 2 and 10); Houghton (1997); Berner (1998).

Both these figures are fairly accurately known. The difference is approximately accounted for by CO_2 transferred into the oceans: as the atmospheric concentration increases, some of the CO_2 dissolves in the

Table 2.4 Rates of transfer of CO_2 to and from the world's atmosphere during the 1980s, expressed as Gt C $year^{-1}$

Inputs to atmosphere	
Burning fossil fuels	5.3
Released during manufacture of cement	0.2
Tropical forest converted to other land use	1.6
Total	**7.1**
Removed from atmosphere	
Into oceans	2.0
Temperate zone forest regrowth after felling	0.5
Increased biomass of existing vegetation	1.3
Total	**3.8**
Increased concentration in atmosphere	**3.3**

Based on Houghton *et al.* (1996), Houghton (1997); see also Dixon *et al.* (1994), Phillips *et al.* (1998).

oceans and adds to the HCO_3^- pool there. The rate of this transfer is known with fair confidence, thanks to a ^{14}C pulse-labelling experiment in the 1950s and early 1960s. Tests of nuclear bombs during that period increased the concentration of radioactive $^{14}CO_2$ in the atmosphere, and following the subsequent fate of that pulse allows us to estimate the rate at which CO_2 is entering the oceans (Houghton *et al.* 1996). Changes in concentrations of the natural stable isotope ^{13}C have also provided independent estimates which agree (Quay *et al.* 1992).

Are living things a source or sink for C?

We need also to consider how living things make a net contribution to changing the CO_2 concentration. Figure 2.2 shows the photosynthetic capture of C each year exactly equalled in the oceans by C loss through respiration, and on land almost equalled. If you have been trained as a physiologist this may surprise you: plants take up CO_2 when they photosynthesize. However, we must think of the whole ecosystem, not just the plants. We should expect that in an ecosystem at steady state, C uptake and loss will balance. In a forest, trees and other plants are growing and so are storing C in new tissue; but animals are eating parts of them; other parts (and sometimes whole trees) are dying and being decomposed. So, heterotrophs are returning C to the atmosphere. Wheat plants on a farm absorb CO_2 while they are growing; but when they are harvested the stubble and roots are left to rot; the grain is made into bread, which is eaten and respired by people. So, again, the C gets back into the atmosphere. Living things can only act as net sources or sinks for C if their mass changes significantly. This will have to be mass of plants or of dead organic matter: the total biomass of animals and microbes is too small to have any significant effect.

If forest is cut down and replaced by vegetation with a smaller biomass per hectare, there is a release of CO_2 by burning or decomposition of the forest plants. There may also be net release of C from soil over some years, if the amount of organic matter declines (see Chapter 4 for information on soil organic matter turnover). In recent decades there has been loss of forest in the tropics, as the land is converted to other uses. On the other hand, in temperate regions there has been a net increase of forested land, as forests regrow after previous felling (see Chapter 7). The amounts of C involved in these changes are difficult to estimate; Table 2.4 gives figures near the centre of likely ranges. Tropical deforestation is a substantial contributor to total CO_2 production by human activity. It is only partly offset by net uptake by regrowth forests in the northern temperate zone.

To balance, Table 2.4 must have a further sink for 1.3 Gt year^{-1}, not accounted for by changed area of forest. One possibility is that in ecosystems which we have assumed to be in steady state the vegetation is in fact increasing in biomass. Some evidence does support this. Phillips *et al.* (1998) analysed data from 120 long-term plots in forests in the humid tropics of South and Central America. The standing biomass has evidently increased, and if these plots are representative of the whole of humid tropical America this would provide a C sink of 0.6 Gt year^{-1}. However, data from Africa, Asia and Australia (from fewer plots) showed no consistent biomass increase. There are several possible reasons why standing plant biomass could be increasing at the moment:

1 A response to increasing atmospheric CO_2 (see later);

2 A response to increased N deposition, as gases, aerosols and dissolved in rain (see Chapter 4);

3 Regrowth after past disturbance, e.g. abandoned shifting cultivation in the tropics.

There may be a major C sink in the vegetation of North America (Fan *et al.* 1998), but so far it has not been identified. Another possibility is that organic matter is increasing in soil and as peat, or is being washed into the oceans and joining the deep sediment (Woodward *et al.* 1998).

Thus there are various sources and sinks, known or possible, that are large enough to have a significant effect on the rate of C increase in the atmosphere. One message is that the way we manage forests in future could be important.

The greenhouse effect and climate change

In spite of its increase since 1800, carbon dioxide is still a rare gas—less than 0.04% of all the gas in each litre of air. Could it possibly have any effect on the world's climate? The answer is yes.

As explained in Box 2.1, radiation from the sun is short-wave (wavelength less than 3 μm), whereas radiation from plants and any other object at a temperature that occurs on Earth is long-wave (>3 μm). Short-wave radiation mostly passes through the glass of a greenhouse. Inside, much of it is absorbed by the plants, benches, floor and other objects, which reradiate some of it as long-wave. The glass is less transparent to

Box 2.2. The principal greenhouse gases.

	Main sources of origin
Water vapour	Evaporation from water surfaces. Transpiration by plants.
Carbon dioxide	See Fig. 2.2
Methane (CH_4)	Produced by microorganisms in natural wetlands, rice paddy fields, guts of ruminant mammals (including sheep and cattle). Fossil natural gas, leaking from gas wells, oil wells and coal mines.
Nitrous oxide (N_2O)	Produced by microorganisms in soil (denitrifiers). N fertilizers. Burning fossil fuels and plant materials.
Ozone (O_3)	Photochemical reactions between other gases.
Halocarbons	No natural sources. Manufactured for use in refrigerators, as aerosol propellants, and for other purposes.

Further information: Houghton *et al.* (1996); Moore *et al.* (1996); Houghton (1997).

Increase in the greenhouse effect

long-wave than to short-wave, so it absorbs some of the outgoing long-wave and reradiates some of it back inwards. This *greenhouse effect* keeps the greenhouse warmer than the outside air during daylight hours. There are gases in the atmosphere whose molecules act in a similar way to the glass of a greenhouse, letting much short-wave radiation pass through but absorbing more outgoing long-wave and radiating it back again. These are known as *greenhouse gases* (see Box 2.2). The principal natural greenhouse gases are water vapour, carbon dioxide, methane, nitrous oxide and ozone. If all these were removed from the atmosphere the temperature near the ground would quickly become about 21°C colder than it is at present (Houghton 1997). So, the greenhouse effect is undoubtedly a Good Thing for human beings and for life on Earth. What we are concerned about here is a potential *change* in the greenhouse effect: if the concentration of greenhouse gases increases we should expect the world to get warmer. In addition to the known increase in CO_2 (Fig. 2.1), methane and nitrous oxide are increasing. Ozone is decreasing in some parts of the upper atmosphere but increasing in the lower atmosphere. In addition to the natural greenhouse gases there are synthetic gases, manufactured by people and then released, which can have a significant greenhouse effect. Of these, CFCs (chlorofluorocarbons, e.g. $CFCl_3$) were found to be destroying ozone in the upper atmosphere and their manufacture has been stopped in most countries. By the mid-1990s their concentration in the atmosphere had stabilized or begun to decrease (Houghton *et al.* 1996, Fig. 2.10). However, other halocarbons are being manufactured to replace them as refrigerants and aerosols, and the manufacture of halocarbons for other uses has continued. These are increasing in the atmosphere, and may in time become abundant enough to have a significant greenhouse effect.

The effect of each of these gases on global temperature depends on their abundance and also on their greenhouse warming effect per molecule. Water vapour is by far the most abundant of the greenhouse gases, but its effect is often ignored in calculations because it varies so much from place to place and from day to day. However, it should not be ignored, because future climate change may increase the average water vapour content of the atmosphere, thereby causing a feedback effect on warming. Among the other greenhouse gases, CO_2 is estimated to have caused about two-thirds of the increase in greenhouse effect since 1800, the remainder being due mainly to methane, nitrous oxide and CFCs.

Aerosols can cause cooling

In order to predict how climate will change in the future we need to consider not only greenhouse gases but also *aerosols*, solid particles and droplets so fine that they remain suspended in the air almost indefinitely. These increase the reflection of short-wave radiation and so have a cooling effect on climate. One source of aerosols has increased substantially during the last 200 years: SO_2 from burning of fossil fuels (especially coal) forms sulphate aerosols (see Box 9.4, p. 258), so the increased cooling effect from them may have partially offset increased warming from greenhouse gases. Since about 1980 the production of SO_2 has decreased in North America and much of Europe, but it is probably still increasing elsewhere (OECD 1997; Houghton 1997), so it is difficult to predict how world SO_2 production will change in the future.

Predicting future climate change

Predicting how the world's temperature will change in future involves predicting how the concentrations of greenhouse gases and aerosols will change, and then how temperature will respond. Because most of the increase in greenhouse gases is caused by people, how much these gases increase in future is (at least in theory) up to us. Even for an agreed projection of future greenhouse gas and aerosol abundance, predicting climate is very difficult. This is partly because there are lots of potential feedbacks: climate change may alter cloud cover, ice cover, ocean currents, plant biomass and various other things that can themselves influence climate. Since this book is primarily about biological aspects of environmental problems, I do not dwell here on the difficulties of long-term climate prediction but instead present a 'central' prediction for temperature rise up to 2100, and then move on to considering how living things would respond to it.

Figure 2.3(a) shows the predicted CO_2 concentration up to 2100 under the 'business-as-usual' scenario, more formally known as IS92a. This assumes no major changes in people's attitudes and priorities towards energy consumption, with continuing increases in the world's population and energy consumption per person up to 2100. IS92a also predicted, on this basis, increases in other greenhouse gases (Houghton *et al.* 1996). Figure 2.3(b) shows estimates of how much the temperature near the