Continuing with our exploration of climate change effects on different levels of biological organization, in this chapter we focus on the ecosystem level. An 'ecosystem' can be broadly defined as a collection of interacting organisms plus their abiotic environment. Key ecosystem-level processes include biomass production, organic matter decomposition, carbon sequestration and nutrient cycling (essentially, these processes are manifestations of the interactions among organisms and the abiotic environment). Here, we discuss how these processes will respond to climatic change and elevated atmospheric CO₂. We also touch on the issue of ecosystem services and how these may be affected by the changing climate.

Climatic change is driven by the concentration of greenhouse gases in the atmosphere. The human contribution to our changing climate is largely driven by our burning of fossil fuels. Fossil fuels are an example of carbon that has been ‘sequestered’ for millions of years. Carbon can basically be in three places at any point in time: in the atmosphere; in living organisms; or in the soil and water. In some forms of soil (see Chapter 9) and in some places in the water (e.g., deep in the oceans) carbon enters these forms and places much faster than it leaves them, leading to an accumulation of carbon. This accumulated carbon is ‘sequestered’ for various lengths of time, from a few years to many centuries. In this chapter we examine the ecosystem processes that lead to carbon sequestration. This first necessitates a brief review of ecosystem processes and then we discuss how climate impacts these processes.

### 7.1 Ecosystems and Carbon

One way to think of an ecosystem is as a collection of pools of organic matter linked by fluxes of energy (with carbon as its ‘currency’, i.e. energy is stored in organic carbon compounds) and nutrients. For example, the vegetation might comprise one pool, while soil organic matter comprises another pool, and litterfall represents a flux from the vegetation to the soil pool (Fig. 7.1). Environmental conditions influence pool sizes and flux rates. As the environment changes with climatic change, we are interested in how the pools and fluxes will be affected, partly because of feedbacks between organic matter in ecosystems and CO₂ in the atmosphere and partly because the size and nature of these pools and fluxes define an ecosystem’s functioning, habitat value and capacity to provide ecosystem services.

Carbon sequestration at the ecosystem level depends on the balance of inputs and outputs to and from the ecosystem as a whole. Inputs come from photosynthetic assimilation of CO₂ into organic carbon compounds and outputs come from respiration, as the organic matter is used for energy and CO₂ is released back to the atmosphere (outputs can also be abiotic in nature, e.g. CO₂ released by fire). Before we discuss the factors regulating the overall carbon balance of an ecosystem, let us briefly review the ‘ins and outs’ of ecosystem carbon cycling in a little more detail: how does carbon enter, move around in and leave an ecosystem? Carbon (CO₂) from the atmosphere is fixed by plants during photosynthesis — in other words, it is converted from an inorganic form to organic compounds in...
plants. At the ecosystem level, the total amount of carbon assimilated by vegetation during photosynthesis (over a given time period) is called ‘gross primary production’ (GPP). Some of that carbon is respired by the plants and thereby returns to the atmosphere as CO₂ (‘autotrophic respiration’, Rₐ). The remainder is available for producing new biomass (some of which will be consumed by herbivores or will be shed as litterfall), supplying rhizosphere organisms with carbohydrates. The amount of carbon left over after autotrophic respiration has been accounted for is called ‘net primary production’ (NPP). Some of the carbon in NPP will be lost to the atmosphere through ‘heterotrophic respiration’ (Rₖ), as living or dead plant and animal material is consumed by organisms at higher trophic levels, including the detrivores (in most terrestrial ecosystems, the majority of heterotrophic respiration comes from the soil organisms consuming dead organic matter). The carbon accumulated annually in an ecosystem after both autotrophic and heterotrophic respiration has been accounted for is called ‘net ecosystem production’ (NEP). It is possible for NEP to equal zero, if the photosynthetic inputs are equal in magnitude to the respiration outputs. These various terms can be assembled into equations that describe their interrelationships:

\[
\text{NPP} = \text{GPP} - R_a \tag{7.1}
\]

\[
\text{NEP} = \text{NPP} - R_h \tag{7.2}
\]

\[
\text{NEP} = \text{GPP} - (R_a + R_h) \tag{7.3}
\]

There are other ways for carbon to leave an ecosystem besides respiration; these additional outputs may be intermittent or regular occurrences. When carbon losses due to disturbance (such as fire) and hydrological fluxes (such as dissolved carbon leaching through the soil profile into streamwater) occur, the amount of carbon accumulating in an ecosystem is also dependent on these outputs, such that:
NEP = GPP – (R_a + R_h + disturbance loss + leaching loss) 

(7.4)

These non-biological carbon outputs are often overlooked in models of climate effects on carbon sequestration (Chapin et al., 2009), but have been receiving more attention lately.

### 7.2 Factors that Regulate Carbon Sequestration

Ecosystem carbon sequestration is controlled by the factors that regulate inputs and outputs of carbon. Here, we examine the controls on NPP, heterotrophic respiration and NEP.

**Net primary productivity**

Net primary productivity (NPP) is controlled by factors that influence its components, namely GPP and autotrophic respiration. GPP is controlled by solar radiation, atmospheric CO₂ concentration, water, nutrients and temperature. These environmental factors can influence the rates of photosynthesis in a given leaf (see Chapter 4), or can dictate the total number of leaves present to capture solar radiation (usually thought of as the total surface area of leaves or leaf area), or both. In other words, productivity can be increased if plants become more efficient at photosynthesis with a given amount of leaf area or if they increase their leaf area by growing more leaves. If environmental changes are drastic enough (or if changes are moderate but some species in a given plant community exist close enough to their environmental limits; see Chapter 6), the vegetation itself may undergo changes in its composition, thereby changing carbon capture by the ecosystem via changing plant characteristics (e.g. a shift to plant species with greater photosynthetic capacity; Chapter 4).

Figure 7.2 shows how the main climatic constraints to NPP vary geographically.

Environmental conditions can also affect the amount of carbon lost from an ecosystem via autotrophic respiration. This process depends, like other physiological processes, on temperature and also on any factor that affects plant growth (more biomass = more respiration). At large spatial scales, plant respiration tends to be roughly a constant proportion of GPP (about half; which in turn means that NPP comprises the other half), but the proportion of GPP lost via plant respiration can be greater under warmer temperatures. Root respiration accounts for the largest proportion of autotrophic respiration in most ecosystems, and often is measured together with respiration of soil heterotrophs. This combination of belowground plant and heterotroph respiration is often called

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**Fig. 7.2.** Climatic constraints to plant growth across the globe. (From Nemani et al., 2003.)
‘soil respiration’. Many field studies of ecosystem carbon dynamics measure soil respiration because it is difficult to separate the two components of CO₂ efflux from soils (autotrophic and heterotrophic respiration).

In general we might expect root respiration (autotrophic) and decomposition (heterotrophic) to respond in the same direction to temperature and moisture changes, and even to changes in atmospheric CO₂ (elevated CO₂ in general stimulates plant growth, see Chapter 4, which in turn stimulates soil microorganisms via increased carbon availability). However, the magnitude of their responses may differ and the balance between them may change. We can also speculate that in some circumstances their responses to a changing environment may differ. For example, imagine a very nitrogen-poor ecosystem where the higher C:N ratios in plant tissues arising from elevated CO₂ cause plants to increase their root biomass – and hence root respiration – in search of more nitrogen. At the same time, the lower quality of plant litter in this already nitrogen-poor system may slow decomposition and hence result in lower rates of heterotrophic respiration. So, while it is difficult to measure these two components of soil CO₂ efflux separately, it is important to at least consider how they may respond differently to climatic change. It has been suggested that warmer temperatures may in general lead to higher allocation of GPP to plant respiration (Ryan, 1991); however, there is little known about how climatic change will affect the balance between GPP and autotrophic respiration and thus NPP. So much less is known about how autotrophic respiration responds to changing temperature and CO₂, that the widely validated notion that plant respiration is equal to about 50% of GPP is often just assumed in estimates of ecosystem NPP response to climatic change.

It is more common to measure NPP than GPP in ecosystem studies, because NPP is easier to measure directly (in terrestrial ecosystems it is usually measured as biomass increment plus tissues shed as litterfall; while this method accounts for most of the NPP in many ecosystems, it represents an underestimate because it neglects other, more difficult to measure pathways for NPP, such as root exudates and tissues consumed by herbivores). Also, NPP is often of more interest than GPP since it represents the organic matter, and the energy it stores, that is available to detritivores and herbivores. All of this gives us good reason to focus on how climate change affects NPP, rather than GPP, in Section 7.3. GPP becomes a more familiar character in Section 7.5 on NPP, where the subject of interest is the balance between gross inputs and outputs of carbon to and from the ecosystem as a whole.

Temperature can affect NPP directly, through effects on rates of physiological processes, and indirectly, through effects on nutrient availability (e.g. warming may increase nitrogen availability by speeding up decomposition and nitrogen mineralization in temperature-limited ecosystems), water availability and species composition (Fig. 7.3; see also Chapter 6). In colder-climate ecosystems, temperature effects may be manifested mainly through the extension of growing season lengths. If a limiting nutrient becomes more available, NPP can increase either because per-leaf rates of photosynthesis are increased or because total leaf area is increased (or both). Temperature also affects water availability due to its influence on evapotranspiration rates. As we have discussed over the past few chapters, in the longer term, shifts in temperature regimes (and precipitation patterns) across the globe will result in shifts in the distribution of organisms, including plants. NPP in a given region will change by virtue of changes in plant functional types and thus ecosystem types, for example from tundra vegetation to boreal forest trees with higher potential NPP rates (Bunn et al., 2005).

CO₂ levels can affect NPP directly through increasing carbon availability for photosynthesis (see Chapter 4), but its main effects will likely be mediated through effects on soil water content. Under elevated CO₂ plants can conserve water by keeping their stomata more closed, thereby reducing transpiration, while still taking in adequate amounts of CO₂ (see Chapter 4). If water is not limiting to plants, they can gain more carbon with the same amount of water use under elevated CO₂. Increases in soil moisture due to conserved water can affect nutrient cycling rates and thus nutrient availability, which is a strong determinant of NPP rates. ‘Trickle-down’ effects of elevated CO₂ on NPP will include those arising from the interplay between carbon and nitrogen cycles in ecosystems. (Nitrogen is a limiting nutrient in many ecosystems; climate change effects on the cycling of nitrogen and other nutrients are discussed in the next section and also in Chapter 13.)

For the most part, elevated CO₂ and changes in water and nutrient availability brought on by
warmer temperatures will likely have the greatest impact on NPP in most ecosystems (compared with direct effects of temperature on physiological processes). In temperate and boreal ecosystems, longer growing seasons will also play an important role.

**Heterotrophic respiration and net ecosystem productivity**

Heterotrophic respiration is largely controlled by those factors that affect soil microorganisms, as these are responsible for most of the \( R_h \) in terrestrial ecosystems. Most of the energy captured by plants in organic matter flows through the detrital food chain as dead plants and animals are decomposed by bacteria and fungi, releasing mineralized nutrients and \( CO_2 \) in the process. The decomposer organisms are directly affected by temperature; their metabolic activity increases with temperature up to very high temperatures as long as sufficient moisture is available. In waterlogged environments, warming-induced soil drying can actually accelerate decomposition, and therefore \( R_h \), by increasing oxygen availability. So, moisture is also an important factor regulating \( R_h \); too much soil water inhibits decomposition due to lack of oxygen, and too little moisture inhibits the diffusion of substances to and from microbial cells (Chapin et al., 2002). The decomposition process is also strongly affected by the quality of the detritus (in most terrestrial ecosystems, mainly dead plant material); that is, the ‘palatability’ of the plant litter to the decomposers. Generally, litter that is high in nutrients and low in recalcitrant compounds, like lignin, is most palatable to soil organisms and decomposes the most rapidly. The C:N ratio in litter, or the ratio between lignin and nitrogen, is often used as an indicator of litter quality, with high C:N or lignin:N ratios indicating poor-quality litter that is likely to decompose slowly.

The relationship between the biochemical nature of plant litter and the decomposers produces some complicated (and really interesting!) feedbacks. For example, a positive feedback may be triggered if some factor in the environment changes such that decomposition rates (and thus \( R_h \)) are increased, causing nutrients to be released more rapidly from the dead organic matter, thereby increasing plant productivity and/or the nutrient concentrations in plant tissues. If more litter is produced, and especially if more high-quality litter is produced as a result, decomposition processes may be further stimulated, thus increasing \( R_h \) even more. In contrast, a negative feedback may be triggered for example if plant litter quality declines due to nutrient deficiency,
causing decomposition rates to be reduced, thereby slowing nutrient release from dead organic matter and exacerbating the lack of nutrient availability. The interactions between multiple stressors (e.g. nutrient deficiency and warming) are discussed further in Chapter 13.

Net ecosystem productivity (NEP) is regulated by the balance between NPP and $R_b$ (or between GPP and the total of $R_b$ plus $R_d$), and so is influenced by the factors that control these processes (Fig. 7.3). Changing environmental conditions may increase NPP, but if those conditions also favour matching increases in $R_b$ there may be no increases in NEP, i.e. the amount of carbon sequestered by the ecosystem as a whole.

In summary, NPP is regulated mainly by the availability of water and nutrients, as mediated by temperature and CO$_2$. With time, changes in these factors (along with growing season length) can result in shifts in species composition and vegetation type, thereby influencing NPP by changing the 'players'. Disturbances such as fire can also affect NPP by disrupting plant life. $R_b$ (mainly from soil organisms – the decomposers) is controlled mainly by temperature, moisture, and plant litter quality and quantity. NEP, which represents an ecosystem's net accumulation of carbon, is regulated by the balance between NPP and $R_b$.

Climate (and atmospheric) change thus has lots of opportunity to affect rates of carbon sequestration, by direct (e.g. rising CO$_2$ levels and temperature) and indirect (e.g. changes in water and nutrient availability) means. Short-term and long-term responses may differ, as plants and decomposer communities acclimatize to the changing conditions, as the balance among limiting factors shifts and changes, and as species replace each other according to geographic shifts in optimal and tolerable environmental conditions.

### 7.3 Impacts on Net Primary Productivity

There is evidence that the warming trend of the past few decades has already produced changes in terrestrial NPP. Globally, a 'greening' trend seems to be occurring, as indicated by increases in terrestrial NPP of about 6% in the final two decades of the 20th century (Nemani et al., 2003). Regionally, changes have been variable, with the largest increases seen in tropical and boreal ecosystems (Fig. 7.4). Increases in tropical NPP have most likely been due primarily to a factor that does not figure prominently in most discussions of climatic change, namely increased solar radiation resulting from reduced cloud cover (Nemani et al., 2003; Fig. 7.2).

![Fig. 7.4. Changes in terrestrial NPP (per cent per year) driven by climate change from 1982 to 1999. (From Nemani et al., 2003.)](image.png)
The >100 ppm post-industrial increase in atmospheric CO$_2$ levels that we have already experienced has likely also contributed to increased plant production in the tropics (Laurance et al., 2004; Wright, 2005) and elsewhere. In northern ecosystems, temperature likely plays a larger role: year-to-year variation in plant production (photosynthetic activity as seen by satellite) in Canadian boreal forest and tundra has been linked to inter-annual temperature patterns, and the current warming trend has resulted in greater productivity in these biomes over the past few decades, as well as a poleward-marching treeline (as discussed in Chapter 5). NPP increases of nearly 20% in China’s ecosystems from 1982 to 1999 have been attributed mainly to longer growing seasons and less so to increased rates of NPP within the growing season (Fang et al., 2003). Increased productivity in tundra ecosystems has been linked to both longer growing seasons and greater rates of NPP during the growing season.

There are already hints that this ‘greening’ trend may not last long; evidence from the past few years shows that while circumpolar tundra vegetation continues to ramp up its productivity, many forested areas in North America are showing declines in productivity, possibly because of late summer drought (Goetz et al., 2007).

Some modelling studies that combine GCMs with global vegetation models predict that the positive trend in global terrestrial NPP will continue well into the 21st century (Cao and Woodward, 1998; Alo and Wang, 2008) due to the combination of warming and elevated CO$_2$. Others predict that climatic changes and elevated CO$_2$ will act on global NPP in opposite ways, with negative effects of warming counteracting the positive effects of elevated CO$_2$ (Cramer et al., 2001; see also Chapter 13).

Zooming in from the global scale to regional and local levels, a tangled web of interactions among environmental variables is revealed. First, let us consider what happens with warming alone (without elevated CO$_2$). Modelling studies and field experiments have shown that the response of NPP to warming depends largely on the availability of water. Warming has a drying effect because it increases evapotranspiration, so water-limited ecosystems would need to see increases in precipitation or increased WUE in order to be able to respond positively to warming. In a modelling study of a variety of ecosystem types, Luo et al. (2008) found that moderate warming alone had little effect on NPP, except in a boreal conifer forest and a wet heath—both temperature-limited ecosystems with moisture to spare (all other ecosystem types in the study were in warmer, drier environments). When increased precipitation was combined with warming—however, all ecosystems included in the analysis responded with greater NPP. Negative interactions occurred when warming was combined with decreased precipitation (Luo et al., 2008). Many other modelling studies predict similar patterns. Chiang et al. (2008) found that the direction and magnitude of NPP response to warming depended on the degree of warming: in US forests, mild warming (about 2°C) and matching increases in precipitation resulted in NPP increases of as much as 25%, while more severe warming (about 5°C) without adequate precipitation increases caused NPP to decline by as much as 60% (Fig. 7.5). Parton et al. (2007) used a physiologically based mechanistic model, parameterized with data from a prairie heating and CO$_2$ enrichment experiment, to show varying responses to warming, again depending on water availability for plant growth. Similarly, a cold, dry spruce forest in China modelled by Su et al. (2007) increased its NPP by 18% in response to warming as long as precipitation also increased.

Predictions about limitations on NPP in a warmer climate are corroborated when experimental warming studies are carried out in field settings. The results from some of these studies echo the modelers’ findings: water deficiencies will prevent NPP from increasing in response to warming. For example, one group of researchers warmed the air by 3°C over plots in a temperate grassland, and found that even though the heated and unheated plots were given the same amount of water, the heated plots dried out faster and had 25% lower NPP (De Boeck et al., 2008). In other cases, nutrient deficiency is the culprit (see also Chapter 13); the tundra warming experiment carried out by Hobbie and Chapin (1998) found no effect of warming on NPP. It turns out that tundra vegetation is not necessarily temperature-limited itself, but its productivity is nitrogen-limited – and nitrogen mineralization is temperature-limited in Arctic ecosystems. The experiment did not heat the soil enough to speed up nitrogen cycling, so the vegetation did not respond to the warming. In a seemingly contrasting example, another tundra ecosystem warming experiment revealed increases in plant biomass production overall (Biasi et al., 2008). In that experiment, soil temperature was raised, stimulating nitrogen cycling and improving the availability of nitrogen.
of this nutrient. The different outcomes of these two studies also point to the importance of species-specific responses (see Chapter 14) and the influence of the dominant species on the overall ecosystem response. In the second study, lichens were the dominant vegetation type and these increased their biomass production significantly, strongly influencing the overall results. In the former study, biomass production of a shrub species increased, while that of other species declined or did not change, leading to no overall change in NPP.

It is possible for NPP to increase without increases in biomass production if the NPP is allocated to rapid turnover pools within the plant, like root exudates. Likewise, it is possible for NPP to increase without increases in long-term carbon storage in plants if the extra NPP is allocated to short-lived tissues (e.g. fine roots instead of woody stems). However, one cannot have increased biomass production without increased NPP. Many studies of the responses of ecosystems to climatic change do not measure NPP completely, but measure plant biomass production instead; reported increases in plant growth or biomass production indicate that NPP is increasing.

Despite a fair amount of variability in the outcomes of individual warming experiments, a meta-analysis of 32 such experiments revealed that, across all of these studies, warming of up to 6°C increased plant productivity by 19% on average (Rustad et al., 2001). This illustrates, however, an issue with much of the research that has been done to date in this field: most of the experiments included in their analysis were performed in temperate, boreal and Arctic ecosystems. So, while there seems to be a general consensus that warming alone can increase NPP, research done in warm, dry climates suggests that NPP will not respond positively to warming (e.g. Peñuelas et al., 2007) and tropical ecosystems have been largely neglected. The jury seems to be out on how these will respond to warming, with some suggestions that, regardless of moisture availability, some tropical ecosystems are close to their upper temperature limits already, beyond which NPP will decline (Doughty and Goulden, 2008). It will be important to sort out climate change impacts on tropical ecosystems, particularly forests, as these contribute more to global NPP than any other ecosystem type.

While there have been numerous field experiments to test the effects of warming, there have also been ecosystem-level experimental manipulations of one of the other major factors involved in climatic change: atmospheric CO₂. There has been much speculation, well-founded in the principles of plant physiology, that CO₂ will have a fertilizing effect on vegetation (see Chapter 4) and that this may help to counteract any negative warming impacts on plant production. Experimenting with the effects of elevated CO₂ has been done on a variety of scales (e.g. individual plants, small plots under chambers), but
we concentrate on the ecosystem-level free-air CO$_2$ enrichment (FACE) experiments (see Chapter 3 for a description of FACE and how this method compares with others).

On balance, across all of the various FACE experiments around the world (although these are mostly in the temperate zone; Fig. 3.8), plant production has increased under elevated CO$_2$ (usually about 550 ppm; Ainsworth and Long, 2005). Not all plants respond equally: trees have shown the greatest responses (on average, biomass production increases of 28%) while, at the other end of the spectrum, C$_4$ plants (mostly grasses) do not seem to respond very much to elevated CO$_2$. C$_3$ grasses on average increased their biomass production by only 10% in FACE experiments, so we might predict that forests and grasslands will respond very differently to elevated CO$_2$. In other words, there will be no one-size-fits-all response; the response of a given ecosystem to elevated CO$_2$ will depend on the type of vegetation that defines it (see Chapter 4). The type of plants present will not be the only factor regulating ecosystem response to elevated CO$_2$, however: limiting resources will also come into play, as will other stressors such as pollutants (see Chapter 13).

Reich et al. (2006) demonstrated experimentally that nitrogen limitation can constrain the positive response of NPP to elevated CO$_2$, however it took 6 years of treatment (in a temperate grassland) to see this response: for the first 3 years, CO$_2$ stimulated growth equally in both ambient and elevated nitrogen treatments. After 3 years, growth was stimulated more in the elevated nitrogen plots, and progressively less over time in the ambient nitrogen plots. Similarly, a young temperate forest exposed to elevated CO$_2$ showed a positive growth response for 3 years and no response for several years thereafter (Oren et al., 2001; Fig. 7.6a). However, when nitrogen fertilizer was added, tree biomass production in the elevated CO$_2$ treatment once again surpassed the controls (Fig. 7.6b). These examples illustrate how nutrient limitation moderates biomass production increases in any nutrient-limited ecosystem.

While the FACE experiments have provided excellent insights into ecosystem responses to elevated CO$_2$, these experiments have been conducted in a limited number of ecosystem types. Tropical and boreal forests, for example, which each represent large carbon reservoirs, have been ignored so far (Hickler et al., 2008). Also, while several FACE experiments have taken place in temperate forests, young stands have been the focus.

Only a small handful of studies have addressed how mature forests may respond to elevated CO$_2$. These ecosystems have accrued large amounts of carbon, but their rates of NPP are low compared with young, rapidly growing forest. Will mature forests respond to elevated CO$_2$ with increasing NPP? Körner et al. (2005) investigated the response of mature deciduous forest in Europe to elevated CO$_2$ and found no evidence of increased biomass production in a 530 ppm CO$_2$ environment. Similarly, neither elevated CO$_2$ nor warming temperatures, nor the two combined, had any effect on tree stem growth over 4 years in a mature forest in Norway (Rasmussen et al., 2002). So, while there is evidence from FACE sites, all in young forests, that elevated CO$_2$ will increase NPP and biomass production, it is not necessarily the case that the same will be true for mature forests.

As we have emphasized elsewhere in this book, rising temperatures and CO$_2$ levels, as well as other climate change factors such as changing precipitation regimes, are happening simultaneously, not separately — what will be the interactive effects of these factors on NPP? As we learned earlier, while the effects of elevated CO$_2$ on NPP are generally positive, warming can have positive or negative effects depending on the initial conditions in a particular ecosystem. Warming can increase nutrient availability in cold-climate, nutrient-limited ecosystems by speeding up temperature-limited nutrient cycling rates. Warming can also exacerbate water limitations by drying out soils in moisture-limited sites. On the other hand, elevated CO$_2$ levels can ameliorate water stress to a degree and, where nitrogen is limiting, can also allow plants to allocate more carbon to fine roots to aid in nitrogen acquisition (Thornley and Cannell, 1996). So, the ultimate outcome of the two factors in combination depends on the water and nutrient dynamics of a given ecosystem (Thornley and Cannell, 1996). These will determine if the warming and elevated CO$_2$ are acting together to increase NPP, or if warming is counteracting the positive effects of CO$_2$.

Modelling studies tend to show that CO$_2$ and warming enhance each other's effects on ecosystems; greater positive effects are often seen when the two are in combination. For example, Su et al. (2007) modelled climate and elevated CO$_2$ effects on spruce forest in north-western China and found
that when just elevated CO$_2$ was modelled, NPP increased only by a small amount due to moisture and nitrogen limitations. When both warming and CO$_2$ changes were taken into account, NPP increased more dramatically, by 25% or more, because available moisture increased and warming stimulated nitrogen cycling and availability. In another study, NPP in most vegetation types in Alaska increased under various climate change scenarios, using various GCMs (Euskirchen et al., 2009; see Chapter 2). Increases were related to extended growing season length, increased nitrogen uptake and greater light capture due to increased leaf area.

On balance, then, we can likely expect (and are already seeing) positive NPP responses to climate and atmospheric change, at least over the next few decades. However, does increased NPP in response to warmer temperatures and elevated CO$_2$ mean that ecosystems will sequester more carbon? To answer that question, we first have to consider that increases in NPP do not necessarily mean that more carbon is being sequestered by plants if that NPP is allocated to pools with fast turnover rates, like root exudates and fine roots, which are quickly lost from the plant and at the mercy of soil organisms. Even if it turns out that increases in NPP do result in increasing biomass in tissues that remain on the
plant for longer periods, we need to consider the other end of the carbon cycle: decomposition and heterotrophic respiration. If heterotrophic respiration keeps pace with NPP, there will be no net carbon sequestration in the ecosystem.

7.4 Impacts on Heterotrophic Respiration

The bulk of heterotrophic respiration in ecosystems comes from the decomposers – mainly soil microorganisms consuming dead plant material. So, most of the interest in the effects of climatic change on heterotrophic respiration is focused on organic matter decomposition and the resultant release of CO₂ from the soil. Globally, soils represent a huge reservoir of carbon – as much as 2400 Pg C to 2 m depth (Jobbagy and Jackson, 2000). In some ecosystems, organic matter can be found many tens of metres below the surface, so this estimate of global soil carbon is actually low. Compare this amount with the carbon in the atmosphere (about 750 Pg, and climbing) and it is obvious why there is great interest in the fate of the carbon currently stored in soil. Even a small increase in the net rate of transfer of carbon from soil to the atmosphere could result in a significant increase to the atmospheric pool.

Within any particular ecosystem, carbon is input to soil mainly via plant litterfall (senesced leaves and other plant tissues, including belowground ‘litterfall’, mainly sloughed fine roots) and exits the soil pool as the litter is decomposed and the carbon is released back to the atmosphere as CO₂ (some carbon may also leave an ecosystem by leaching down through the soil into groundwater). Organic carbon builds up in soil if decomposition processes do not keep pace with litter inputs. With climatic change, the soil carbon pool could increase or decrease depending on how the balance between these inputs and outputs is affected. We have already examined the potential effects of climatic change on NPP and, of course, litter production rates are determined by plant production rates. So, in many ecosystems, climatic change will likely result in increased carbon inputs to soils because of increased NPP. But what about carbon losses from soils via heterotrophic respiration?

We know that the main factors regulating decomposition rates (and thus heterotrophic respiration rates) are temperature, moisture and the composition of the microbial community in the soil. Substrate quantity can also be important – in some ecosystems, the decomposer community is carbon-limited and will respond positively to increased inputs of carbon-rich plant litter. Climatic change has the potential to alter any or all of these regulating factors. For example, warming may increase the activity of the decomposer community or could lead to changes in community composition. Plant litter quality may change due to elevated CO₂ or due to shifts in plant community composition promoted by warming or changes in moisture levels (for a comprehensive review on the effects of temperature increases, in particular, on decomposition processes, see Aerts, 2006).

As we explore the results of studies of climate change impacts on heterotrophic respiration, it is important to keep a couple of points in mind. First, heterotrophic respiration is not usually (for a variety of reasons) measured directly in field studies; and second, the heterotrophs that are usually focused on in ecosystem ecology studies are the decomposers. Consequently, we see that the research results discussed below encompass a variety of approaches for estimating the effects of climatic change on the activity of soil heterotrophs, while ignoring other heterotrophic organisms (remember that in most ecosystems, more carbon and energy flows through the detrital food web than through aboveground food webs). For example, some researchers have measured CO₂ efflux from soil and made assumptions about the relative contributions of heterotrophic versus root respiration (this has been estimated to be about half each; e.g. Bond-Lamberty et al., 2004), while others have measured the real-time decomposition rate of plant litter, and still others have measured the change in soil carbon content after the application of an experimental treatment.

It is no secret that decomposition rates are positively related to temperature, because microbial activity and hence respiration rates are higher in warm environments than cold ones, and respiration rates generally fluctuate seasonally with temperature. Countless laboratory soil incubations have demonstrated positive relationships between microbial respiration and temperature. In the field, however, warming can lead to drying, the effects of which depend on how wet the environment was in the first place. Drying can slow microbial activity if moisture becomes limited, but drying can also stimulate decomposition in formerly waterlogged environments by increasing oxygen availability.
Ecosystem-level warming experiments have shed some light on how heterotrophic respiration may respond to climatic change. A meta-analysis of 32 such experiments (all located in temperate, boreal and Arctic ecosystems) found that total soil respiration rates increased by 20% across all sites (Rustad et al., 2001). Some of this increase was no doubt attributable to root respiration, but increases in nitrogen mineralization rates indicated that decomposition rates (and thus heterotrophic respiration rates) were also increasing. A more recent tundra warming experiment (Biasi et al., 2008) similarly relied on indirect evidence; this study also found increases in soil CO₂ efflux and, since soil organic carbon content was significantly reduced over the warming period, the researchers inferred that increases in heterotrophic respiration must be at least partially responsible for this result.

Other warming experiments have demonstrated that the response to warming will not necessarily be straightforward. In a boreal black spruce (Picea mariana) forest, Bronson et al. (2008) experimentally increased soil temperature and found that soil respiration rose by 25% in the first year but in the second year there was only an 11% increase over the control. Because the warming treatments reduced fine root biomass, the authors attributed the increases in respiration to decomposition and attributed the decline in response to depletion of the labile organic carbon pool in the soil (i.e., decomposition outpaced plant litter inputs and the microbial community ‘ran out’ of easily decomposed fresh litter). Others have also observed a decline in the warming response over time. For example, in temperate forest plots subjected to experimental heating, short-term increases in respiration rates were not maintained over the 15-year study period (Bradford et al., 2008). This was attributed to the depletion of soil carbon pools, a reduction in microbial biomass and a change in microbial community composition (to a community with less respiration per unit mass). In other cases, microbial activity may be reduced by warming, even in northern ecosystems, if temperature increases also lead to soil drying (e.g. Allison and Treseder, 2008).

Although alterations of plant litter quality could also have an important impact on decomposition rates and the release of CO₂ from soil, there is not much experimental evidence that plant litter quality is directly reduced by warming in the short term. Instead, it is likely that warming-induced shifts in plant community composition, even just in the relative abundance of existing species, will have a larger effect on litter quality than will changes within the existing plant species (leaving aside, for the moment, any CO₂-related changes to plant quality). Large differences among plant species in the decomposition rates of litter have been widely observed and, in warming experiments, plant community changes have been seen in as few as 5-10 years (Aerts, 2006). For example, as described in Chapter 6, after 9 years of experimental warming in a tundra ecosystem, Chapin et al. (1995) found that deciduous shrub abundance increased at the expense of mosses, lichens and evergreen shrubs. This shift in the vegetation community was attributed to the increased nitrogen availability that had resulted from a warming-induced rise in decomposition rates, and the increased dominance by the deciduous shrub was in turn causing decomposition rates to speed up further — an example of a positive feedback loop. However, the ultimate effects of plant community changes on decomposition processes will depend on ecosystem-specific conditions. In a montane meadow ecosystem heated experimentally for 7 years, soil moisture levels dropped due to increased temperatures, promoting the increased dominance of shrub vegetation over the original forbs and grasses (Saleska et al., 1999). Initially, soil carbon content dropped, as decomposition outpaced litter inputs from the unproductive shrubs. However, the researchers predicted that in the long run, the low-quality shrub litter would lead to slower decomposition rates and carbon build-up in the soil (a negative feedback loop), in contrast to the findings of Chapin et al. (1995) in the tundra.

When it comes to climatic change-induced carbon losses from soils, all eyes are on northern ecosystems, where the equivalent of a perfect storm may be brewing. First, vast organic carbon stores have built up in cold or frozen soils because of temperature limitations on decomposition. Second, this material is thought to be highly sensitive to warming, so dramatic increases in decomposition rates may be seen with even a small amount of warming. Third, it is at these high latitudes that the greatest magnitude of warming is expected to occur.

Permafrost soils in the northern hemisphere (Fig. 7.7) have been estimated to contain half or more of total global soil carbon stocks, and possibly hold twice as much carbon as is presently in the atmosphere (Schuur et al., 2008). As permafrost thaws due to warmer air temperatures, sequestered
organic matter is made available to soil microorganisms. High-latitude soils that are not frozen year round can also contain vast amounts of carbon, such as in peatlands, where organic matter accumulates due to a combination of cold temperatures and the anoxia that accompanies waterlogging. In northern peatlands, warming-induced water-level reductions can interact with direct impacts of warming and result in faster peat decomposition. For example, an 8-year whole-ecosystem warming experiment in subarctic peatlands showed that a temperature increase of 1°C during the growing season could increase peat decomposition rates by more than 50% (Dorrepaal et al., 2009). However, while the reduction of waterlogging can be favourable for decomposition rates, too much of a decrease in water level can result in the drying-out of surface peat layers, which inhibits decomposition.

If peatlands remain waterlogged, or if thawed permafrost soil becomes waterlogged due to lack of drainage, anaerobic decomposition processes will result in the release of methane instead of CO₂ (for example, thawing permafrost can result in thermokarst — the formation of depressions as the ground subsides; if a depression fills with water the soil underneath is waterlogged, leading to methane production). Anaerobic decomposition is slower than aerobic decomposition, but the resulting methane is a more potent greenhouse gas than CO₂.

While it is generally expected that, given adequate moisture, warmer temperatures will increase rates of organic matter decomposition in many ecosystem types, there are still some uncertainties surrounding the sensitivity of decomposition processes to temperature (e.g. Kirschbaum, 2006). However, in cold-climate ecosystems, decomposition is certainly limited by temperature and will speed up with warming in most cases (possible exceptions: waterlogged systems where lack of oxygen may limit decomposition rates despite increases in temperature and systems where dry conditions are exacerbated by warming).

It is important to keep in mind that soil carbon is not a homogeneous entity. Fresh plant litter represents a pool of carbon on the soil surface that is relatively labile (although not all plant litter is equally labile, for example woody material and even conifer needles can be fairly recalcitrant) and can break down relatively quickly depending on
environmental conditions. It does not break down completely, however. As litter decomposes, some of the partially decomposed organic matter, along with by-products of decomposition, collects as humus—this substance is full of organic compounds that resist being decomposed (i.e., they are "recalcitrant"). Humus can become incorporated into the mineral soil (rather than sitting on top, like fresh litter) through the actions of soil organisms like earthworms, and organic carbon compounds can also be carried deeper into the soil profile by water percolating down through the soil, where they may remain for long periods of time. So, soil carbon varies in age from fresh litter (days to months old) to partially decomposed organic matter that may be years to millennia in age. Often a distinction is made between "fast" and "slow" pools of carbon in the soil (although of course there is a gradient of ages within any soil, as opposed to distinct pools). It is possible that climatic change may affect the fast and slow carbon pools in different ways; for example, it has been postulated that warming may speed up the decomposition of fresh litter without affecting the release of carbon from older, more recalcitrant soil organic matter. There is some evidence, however, that the decomposition of older soil organic matter is actually more sensitive to temperature than that of fresh, labile materials (e.g., Conant et al., 2008). This means that the carbon stored for centuries or millennia in some soils (which can equal large amounts compared with the fresh litter layer) may be vulnerable to release as global temperatures rise. The jury is still out on whether and how the different soil carbon pools will respond differentially to warming.

We have explored how increasing temperatures may affect heterotrophic respiration, but how might elevated CO₂ and interactions among various climate change factors affect this ecosystem process? Elevated CO₂ might conceivably affect heterotrophic respiration through changes in plant productivity and litter production, changes in plant litter quality and changes in soil moisture levels. There has been much less research in this area than in the area of temperature effects, and the available evidence suggests a variety of responses. A review of results from both pot-level and field studies found that elevated CO₂ resulted in lower decomposition rates due to reductions in plant litter quality (in particular, higher C:N and lignin:N ratios; Ball, 1997). On the other hand, in a temperate forest FACE experiment, 9 years of elevated CO₂ had no effect on plant litter quality or on the decomposition rates of fresh plant litter (Lichter et al., 2008). The FACE researchers did, however, find evidence of increased decomposition rates of organic matter below the surface in the mineral soil, suggested by increased nitrogen release rates from this material under the elevated CO₂ treatment compared with ambient. Further evidence that elevated CO₂ may increase decomposition rates comes from a review of 47 studies suggesting that the increased plant production brought on by elevated CO₂ would stimulate microbial activity through increased litter inputs (i.e., the microbes' food source becomes more abundant; Zak et al., 2000b). We examine these belowground changes in more detail in Chapter 9.

Because ecosystem-level field studies rarely address combinations of climate change factors, we must, so far, rely on computer modelling studies to gain insight into how temperature, precipitation and CO₂ changes may interact to influence ecosystem functioning. Luo et al. (2008) modelled the interactive effects of temperature, moisture and atmospheric CO₂ changes in a variety of ecosystem types and climate zones, and found that heterotrophic respiration rates increased under warming alone, increased precipitation alone and elevated CO₂ alone. Greater increases were seen, however, under combinations of warming and elevated CO₂ warming and increased precipitation, elevated CO₂ and increased precipitation, and all three combined. Drier conditions, due either to reduced total precipitation or summer drought, resulted in lower rates of heterotrophic respiration. The wettest (though not waterlogged) sites used in the study showed the smallest responses: microbial activity was already high in these systems.

### 7.5 Impacts on Net Ecosystem Productivity

Now that we have examined the inputs of carbon to ecosystems (NPP) and the outputs from ecosystems (heterotrophic respiration), we have arrived at the centre-stage question regarding ecosystem interactions with the atmosphere in a changing climate: what will be the result of the new balance of inputs and outputs in any given ecosystem? Will climatic change cause ecosystems to sequester more carbon from the atmosphere (inputs > outputs) or will they become net sources of carbon (inputs < outputs)?
The amount of carbon retained, or sequestered, in an ecosystem over a period of time (usually considered on an annual basis) is its NEP. NEP is strictly defined as the net result of all fluxes of carbon in and out of an ecosystem, and thus includes not only NPP and \( R_h \) (or GPP, \( R_s \), and \( R_h \), if you prefer to think of it that way), but also other flux pathways such as those due to leaching, fire and erosion (Randerson et al., 2002). However, it is not uncommon for NEP estimates to be based solely on photosynthetic inputs and respiratory outputs, often estimated indirectly as the changes over time in plant biomass and soil organic matter or soil carbon. A similar concept is net ecosystem exchange (NEE), which refers to CO\(_2\) fluxes in and out of ecosystems, and can be measured directly with a technique called ‘eddy covariance’ (see Box 7.1). NEP, which can also be thought of as the carbon balance of an ecosystem, is thus regulated by those factors that affect inputs and outputs of carbon to an ecosystem and the balance between those inputs and outputs.

We have seen that warmer temperatures can affect both NPP and heterotrophic respiration, often increasing both; if these carbon fluxes both increase, they cancel each other out to some degree. So, warming could conceivably have drastic effects on both productivity and respiration, but little overall effect on NEP. Hobbie and Chapin (1998) found just this in a tundra warming experiment: NEP changed little in the face of warming, even though carbon inputs and outputs both increased significantly with the warming treatment (Fig. 7.9).

Ultimately, climate change effects on carbon balance depend on the relative sensitivity of input and output processes, and on their respective magnitudes. For example, in a given ecosystem, \( R_h \) may be more sensitive to warming than is NPP — let us say that warming causes \( R_h \) to increase by 200% while NPP only increases by 40%. This would seem to suggest that warming will turn the ecosystem in question into a carbon source, with a negative NEP; but if the magnitude of the NPP inputs are several times higher than that of the \( R_h \) outputs in the first place, the \( R_h \) can increase significantly without approaching the magnitude of the inputs and the NEP will remain positive though reduced. This is just a hypothetical example. We shall see in some ecosystems that the magnitudes of inputs and outputs of carbon are similar and small changes to one or the other can result in changes to NEP, in some cases even tipping the balance from carbon sink to source.

Ecosystem warming experiments have been carried out in several different types of ecosystem, but most of these studies did not estimate total carbon balance. Tundra warming experiments seem to be the exception, perhaps because the vegetation is of a manageable stature, and because the question of ecosystem carbon balance is especially critical here due to the large amounts of stored carbon in tundra soils and the large temperature increases expected at high latitudes. In a review of a variety of tundra ecosystems subjected to experimental warming, the carbon balance was found to be driven by the response of respiration (total ecosystem respiration, or \( R_a \); Oberbauer et al., 2007). Although the responses varied at different tundra sites, some generalizations could be made. In very wet sites, the increase in respiration was muted due to excessive moisture and increases in GPP meant that NEP increased with warming. In dry sites, NEP declined with warming because the respiration increases were so large (Biasi et al., 2008). Whether or not the increased NEP seen in wet tundra sites would persist under long-term warming remains to be seen; if warming is accompanied by drying in these ecosystems, the boost to NEP may not last long.

While warming experiments are very useful, providing empirical evidence for ecosystem impacts, modelling has the advantage of being able to gauge ecosystem responses to warming in combination with future CO\(_2\) levels. While some studies have shown increases in NEP due to warming alone (e.g. Yarie and Billings, 2002), more often it seems that rising CO\(_2\) will come to the rescue (at least for as long as the CO\(_2\) fertilization effects last), raising NEP in combination with warming, while warming alone leads to declines in NEP. A modelling study of the separate and interactive effects of changing temperature, precipitation and atmospheric CO\(_2\) on a suite of ecosystem types found that while rising temperature alone would decrease NEP in a range of ecosystems, elevated CO\(_2\) combined with warming increased NEP (Luo et al., 2008; Fig. 7.10). Even in dry environments, NEP can increase with warming if combined with rising CO\(_2\) — a modelling study of a semi-arid grassland found that NEP increased by a small amount because of increases in NPP that outweighed increases in respiration (Li et al., 2004). Any warming-induced drying was counteracted by the decreases in plant water losses (via transpiration) caused by the elevated CO\(_2\) (see Chapter 4).
Box 7.1. Sink or source? Assessing ecosystem carbon balance.

One way to determine an ecosystem's carbon balance is to quantify the various pools of carbon repeatedly over time, to see if they are growing or shrinking (e.g., plant biomass can be measured annually to see if it is increasing thereby accumulating carbon, and soil carbon can be measured periodically to look for increases or decreases in this pool; the net result of changes in all of the pools tells us if the ecosystem is losing or gaining carbon over time). These 'inventory' methods are limited by difficulties in capturing pools in their entirety (e.g., belowground plant biomass is notoriously difficult to measure) and by difficulties in dealing with high spatial variability, especially in soil conditions (Baldocchi, 2003).

The eddy covariance method represents a more direct way of assessing ecosystem carbon balance by measuring the continuous movement of CO₂ between land and atmosphere on an ecosystem scale (i.e., net ecosystem exchange, NEE). Photosynthesis results in CO₂ transfer from atmosphere to vegetation, while respiration (of both autotrophs and heterotrophs) results in CO₂ being released to the atmosphere. The net result of this exchange dictates whether an ecosystem is a net source or sink of carbon (recall from Section 7.1 that NEE = GPP - (Rₐ + R₈), keeping in mind that there are other potential terms in this equation, as carbon can also be lost via disturbance, leaching, etc.). As air flows over a vegetation canopy it becomes turbulent, resulting in the formation of downward and upward eddies. The eddy covariance technique involves measurements taken from 'flux towers'—towers used to position micrometeorological equipment just above the vegetation canopy. In a nutshell, analytical equipment measures the speed of the upward- and downward-moving air plus the concentration of CO₂ in these eddies and, via some fairly complicated calculations, estimates can be made of the absolute amount of CO₂ moving into and out of the ecosystem. These estimates can be integrated over periods from hours to years, to determine the sink-or-source status of an ecosystem on the time scale of interest and to explore how carbon balance responds to environmental variability (e.g., seasonal changes, directional climatic change, etc.). For example, Dunn et al. (2007) used eddy covariance to track CO₂ exchange in a 160-year-old black spruce forest in Manitoba, Canada, over the course of 11 years of flux measurements (Fig. 7.8a). They then investigated the relationships between NEE and climate variables, discovering that the ecosystem was a net carbon sink in warmer, wetter years and a carbon source in cooler, drier years (Fig. 7.8b).

There are several different research networks worldwide using flux towers and eddy covariance to assess carbon balance in a variety of ecosystem types (e.g., Fluxnet, Fluxnet Canada, Ameriflux, CarboEurope, etc.). For further reading on this topic, see Baldocchi (2003).
Lagren et al. (2006) modelled NEP in Swedish forests under a 4°C increase in annual temperature and a doubling of CO₂, and found that NEP increased in forests of all age classes (by up to 100% in the coldest, northern forests). Both GPP and total ecosystem respiration (Rₜ + Rₘ) increased, but GPP increased more (by 43 to 47%, compared with increases in ecosystem respiration of 37 to 41%), leading to the increase in NEP (see also Davi et al., 2006). Otherwise, warming resulted in a decline in NEP in most forest types, with coniferous forest NEP declining by half. These patterns were mainly due to the effects on GPP. With elevated CO₂, GPP increased with warming in all forest types over the whole time period. Without elevated CO₂, GPP declined in most forest types due to water stress brought on by increased summer temperatures. The increase in GPP in both of these studies was attributed mainly to an extension of the growing season and to a CO₂ fertilization effect, which was modelled as affecting only photosynthesis and not respiration, thereby having a purely positive effect on NEP. Similarly, a modelling study by Harrison et al. (2008) found that while changes in climate since the mid-20th century have reduced the ability of terrestrial European ecosystems to sequester carbon, changes in atmospheric CO₂ have done the opposite, with the net result being greater NEP. The positive effects of the combination of elevated CO₂ and warming on NEP have been detected repeatedly in modelling studies of a variety of ecosystems all over the world. The positive effects of elevated CO₂ on NEP have been borne out in a temperate forest FACE experiment, where 4 years of experimentally elevated CO₂ resulted in increased NEP. Interestingly, Rₘ also increased in this experiment, but not enough to offset the increases in tree productivity (Hamilton et al., 2002).
Most global-level models of climate warming predict a net release of CO$_2$ from terrestrial ecosystems due to reductions in NPP and increases in carbon release via decomposition (Luo, 2007). However, when elevated CO$_2$ is incorporated, models predict that most terrestrial ecosystems will likely become stronger carbon sinks because of increased NPP while the CO$_2$ fertilization effect lasts (Cao and Woodward, 1998), but that carbon losses will overpower gains in many ecosystems by the end of the 21st century (Cramer et al., 2001; Schaphoff et al., 2006). After reviewing the available evidence from global-level modelling studies, the IPCC’s Fourth Assessment Report (see Chapter 2; Fischlin et al., 2007) concluded that the world’s terrestrial biosphere will likely become a net source of CO$_2$ by the end of this century, meaning that for all of the world’s terrestrial ecosystems collectively, the loss of carbon from ecosystems via respiration will outweigh the intake of carbon through photosynthesis (Fig. 7.11).

As we have seen, the responses of ecosystem carbon sequestration to climatic change depend on more than just direct effects of temperature on photosynthesis and respiration. Other, indirect, effects such as growing season length, species shifts, nutrient cycling and water availability, also come into play (Luo, 2007). The variability of experimental results stresses the need for more empirical research in this area if we are to understand climate change impacts on ecosystem carbon balance and the resulting feedbacks to the atmosphere. It is important to always keep in mind that climate change-related factors cannot be considered in isolation (even though experiments and modelling studies have often done so due to logistical constraints and/or to gain insight into the relative importance of the main effects of the treatments); it will be the interactions among factors (changes in temperature, CO$_2$, precipitation, etc.) that ultimately dictate how climatic change will impact ecosystems.

Climatic change will also affect ecosystems through changes to natural disturbance regimes; for example, the frequency and intensity of fire in forests, grasslands or tundra ecosystems. Fire, and other disturbance agents such as wind and severe storms, can have strong impacts on ecosystem carbon sequestration, potentially dwarfing any direct impact of increases in temperature and CO$_2$ (e.g., Bond-Lamberty et al., 2007). Thus, to fully understand climate change impacts on regional and global carbon balances, we need to consider how disturbances play out over the landscape (see Chapter 10 for a discussion of climate change-disturbance links in forests and Chapter 13 for a discussion of general interactions with disturbance).

### 7.6 Impacts on Nutrient Cycling

Ecosystem nutrient cycling and carbon cycling are tightly intertwined. Nitrogen is the limiting nutrient in many ecosystems (LeBauer and Treseder, 2008) and as such is often the focus of nutrient cycling studies. Plants take up nutrients from the soil to support various physiological functions and these nutrients become incorporated into organic compounds (nitrogen, for example, is found in proteins, enzymes and photosynthetic pigments). When dead plant tissues are shed from the plant, the decomposers break down this organic material into its mineral components, gaining energy for themselves in the process. CO$_2$ is released alongside nutrients in their inorganic form (e.g. ammonium nitrogen); these inorganic nutrients are once again in a form suitable for plant uptake, although some will be used by the microbes themselves (taken up into the soil’s microbial biomass, or ‘immobilized’). Limiting nutrients such as nitrogen are cycled tightly between plants and soil. In some ecosystems, nutrients such as nitrogen are in such short supply, and the competition between plants and microbes so fierce, that plants (and their mycorrhizae) will take up small, nutrient-rich organic
molecules such as amino acids rather than ‘wait’ for these to be further broken down into inorganic form. Because nutrients can be limiting to plant growth and microbial activity, the effects of climatic change (and atmospheric change) on ecosystem processes such as carbon sequestration will hinge, in part, on how nutrient cycles are affected and on nutrient availability in general.

There is considerably less information available on climate change impacts on nutrient cycling compared with carbon cycling. Most models, even those that couple climate and atmospheric change to vegetation dynamics, do not yet include detailed representations of plant–soil interactions and nutrient cycles even though these factors are key to making accurate predictions about climate change impacts (Hungate et al., 2003).

Interestingly, more ecosystem-level research has been done on the effects of elevated CO₂ on nutrient cycling (specifically nitrogen) than on the effects of climate warming. Based on a meta-analysis of nitrogen dynamics in the FACE experiments, De Graaff et al. (2006) reported that elevated CO₂ did not change soil nitrogen concentrations (total soil nitrogen, i.e. including nitrogen in both dead organic matter and microbial biomass) or rates of nitrogen
Net carbon exchange of all terrestrial ecosystems as simulated by the DGVM LPJ (Sitch et al., 2003; Gerten et al., 2004 – negative values mean a carbon sink, positive values carbon losses to the atmosphere). Past century data are based on observations and climate model data were normalised to be in accord with these observations for the 1961–1990 data (CRU-PIK). Transient future projections are for the SRES A2 and B1 emissions scenarios (Nakićenović et al., 2000), forcing the climate models HadCM3 and ECHAM5, respectively (cf. Lucht et al., 2006; Schaphoff et al., 2006). In contrast to previous global projections (Prentice et al., 2001 – Figure 3.10), the world’s ecosystems sink service saturates earlier (about 2030) and the terrestrial biosphere tends to become a carbon source earlier (about 2070) and more consistently, corroborating other projections of increased forcing from biogenic terrestrial sources (e.g., Cox et al., 2000, 2004; White et al., 2000a; Lucht et al., 2006; Schaphoff et al., 2006; Scholze et al., 2006; see Figure 4.3 for maps on underlying ecosystem changes). Note that these projections assume an effective CO2-fertilisation (see Section 4.4.1). (From: Climate Change 2007: Impacts, Adaptation and Vulnerability. Working Group II Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Figure 4.2, Cambridge University Press.)

Fig. 7.11. Net carbon balance of all terrestrial ecosystems combined, projected to the end of the century by models that incorporate future emissions scenarios, climate forcing, vegetation dynamics and CO2 fertilization. Net uptake is indicated by negative values; net release by positive values.

mineralization, but that rates of nitrogen immobilization (in microbial biomass) increased, indicating that microbial biomass growth was stimulated by elevated CO2. This was likely because of the increase in the decomposers ‘food supply’, as increased plant growth led not only to increased leaf litterfall, but also increased belowground ‘litterfall’ (fine root sloughage) and root exudates. Elevated CO2 also increased the C:N ratio of soils, suggesting an eventual decrease in nitrogen availability, as organic material with high C:N is slow to decompose. This could represent a negative feedback on plant growth under elevated CO2: positive plant growth response increases carbon input to soils, which stimulates microbial growth and nitrogen immobilization, reducing nutrient availability to plants and thus slowing the plant growth response.

A related sort of feedback loop is central to the idea of progressive nitrogen limitation (PNL), proposed by Luo et al. (2004) as a potential result of long-term exposure of ecosystems to elevated CO2. If elevated CO2 promotes increased NPP, then plant demand for nitrogen will go up to support increased growth and nitrogen may become increasingly locked up in living and dead organic matter, especially if decomposition rates do not keep pace with increased growth rates. The situation can become exacerbated if diminishing nitrogen availability causes plants to increase the C:N ratios of their tissues, effectively creating more biomass per unit of nitrogen, but reducing the decomposability of plant tissues, slowing nitrogen mineralization rates in the soil (Fig. 7.12).

Although initial levels of available nitrogen will constrain an ecosystem’s plant growth response to elevated CO2, PNL can occur regardless of initial nitrogen status – it is an issue of nitrogen distribution within the ecosystem, rather than the absolute amount of nitrogen present. Regardless of how nitrogen-rich an ecosystem may be to begin with,
if increased plant growth causes more and more nitrogen to be locked up in plant biomass and soil organic matter, and no new nitrogen inputs occur, over time nitrogen can become progressively limiting to plant growth. So, the processes that allow for enhanced carbon sequestration in the beginning (increased plant growth, increased carbon inputs to soils) can in the end slow themselves down through their effects on nitrogen availability.

But how will elevated CO₂ interact with warming to affect nutrient cycling (nitrogen in particular)? There are no easy answers to this question, due to the complexity of the plant-soil interactions that define ecosystem nutrient cycling.

Based on the discussion of climate change impacts on decomposition in Section 7.2 we already have an idea of how nutrient cycling processes may respond to warming, because heterotrophic respiration and the release of CO₂ from organic matter goes hand in hand with nutrient mineralization. In other words, as long as moisture conditions are favourable, it is likely that rates of nutrient release from organic matter will increase in many ecosystems as the climate warms (particularly in colder-climate ecosystems where decomposition is currently temperature-limited). Indeed, a meta-analysis of warming experiments across a variety of ecosystem types (from forest to grassland to tundra) found that net nitrogen mineralization rates (i.e. what's left over after microbial immobilization has been accounted for, so it represents what's available for plant uptake) increased on average by 46% (Rustad et al., 2001). Increased net nitrogen mineralization could have positive effects on plant growth in nitrogen-limited ecosystems via increased nitrogen uptake. And, because mineral nitrogen availability can also constrain microbial activity in some ecosystems, enhanced gross mineralization may further accelerate decomposition rates (Mack et al., 2004).

Climatic change-driven shifts in species composition can also impact nutrient cycling; for example, the encroachment into some tundra ecosystems of shrubby vegetation with nitrogen-rich litter can contribute to faster decomposition rates (Weintraub and Schimel, 2003). Hobbie and Chapin (1998) found that the shift to greater dominance by shrubby vegetation in Alaskan tussock tundra subjected to experimental warming was mediated by changes in the distribution of nitrogen among species: nitrogen uptake by one shrub species in particular increased at the expense of others.
In addition to nitrogen, climate change might also affect other nutrients. Chronic metabolic stress and biomass decline due to ongoing calcium loss are already evident in Canadian aquatic biota (Cairns and Yan, 2009). In some forest ecosystems, calcium and phosphorus may now be as important as nitrogen in limiting tree growth rates (Bigelow and Canham, 2007) and the interactions between these nutrients and climate change may limit growth in temperate and boreal forests, where nutrients are particularly limited (e.g. St Clair et al., 2008). A recent study in fact has shown widespread decline in growth of several tree species in this region and can attribute these declines to drought in only some of the sites, in many other sites nutrient limitation has been suggested (Silva et al., 2010).

7.7 Conclusions

In this chapter we have seen that there is the potential for ecosystems to respond in a variety of ways to climate and atmospheric change. Ultimately, the effects of these changes on ecosystem processes will be specific to each ecosystem and will depend on initial conditions in the ecosystem. In particular, the existing environmental factors that limit biomass production, decomposition and nutrient cycling will determine how these ecosystem processes respond to changing environmental conditions. For example, we can expect warming to increase decomposition rates in cold-climate ecosystems while these rates may be reduced in warm-climate ecosystems where drier conditions result from increasing temperatures. We have also learned that observed and modelled ecosystem responses to climatic change are often the result of indirect effects and interacting factors, rather than direct effects. Consider that increases in NPP with warming are less likely to be due to direct temperature effects on plant productivity than to effects on growing season length, plant community composition or nutrient availability (via increased decomposition rates). And recall that while plant productivity in many ecosystems will likely respond positively to the combination of rising temperature and elevated CO₂, the same cannot necessarily be said about the response to warming alone. As ecosystem processes are impacted by climatic change, so will be the services that these processes support, such as food production, climate regulation, etc. In some parts of the world these services may be enhanced, while in others they may decline, impacting the well-being of humans and other organisms.