Ecosystem physiology responses to global change

H.A. Mooney, J. Canadell, F.S. Chapin III, J.R. Ehleringer, Ch. Körner, R.E. McMurtrie, W.J. Parton, L.F. Pitelka and E.-D. Schulze

Box 7.1 Summary

- Most ecosystems exposed to double ambient CO_2 show higher peak season net carbon uptake than those growing at current-ambient CO_2. For grasslands, above-ground biomass increased by an average of 14%, although individual responses for a given system and year range from negative to +85%. The wide range of the biomass response shows the highly interactive nature of the CO_2 response with other environmental factors, including water and nutrient availability, and temperature. For instance, low-temperature dominated systems, such as alpine grassland, Arctic tundra, and cool climate coniferous forest trees, are among the least responsive to elevated CO_2, showing in some instances no growth response and complete acclimation of peak season gas exchange after a few years. Annual Net Ecosystem Productivity (NEP) has not been reliably measured under elevated CO_2. Faster growth in juvenile trees does not indicate whether forests as a whole will sequester more carbon or not.
- The general predictions of the degree of responsiveness of plant growth to elevated CO_2 for some of the most important functional groups (e.g. insensitivity of C_4 species relative to C_3 species; larger biomass response of species with N-fixing symbionts) are not consistently realized in complex species assemblages exposed to elevated CO_2 under natural growth conditions.
- Contrary to early predictions, litter of high CO_2-grown plants does not necessarily decompose more slowly. The basis for this result is the finding that the ratio of carbon to nitrogen in naturally senesced litter grown at elevated CO_2 is normally no higher than in the same tissue grown at ambient CO_2, despite the higher C : N in green tissues. A great deal of variation, however, occurs among species. This finding has major implications for long-term ecosystem responses.
- Herbaceous plants exposed to elevated CO_2 show a reduction in stomatal conductance, which commonly results in increased soil moisture. This increase in water availability is the dominant driver for the increased net carbon uptake in water-limited grassland systems. There is also a reduction in stomatal conductance in some tree seedlings exposed to elevated CO_2, but this does not seem to be the case for mature trees (forests) given our current experimental

datasets. If the latter is confirmed, some of the feedbacks of the terrestrial biosphere to the climate system may not occur at the intensity currently predicted.

- Tropospheric ozone has negative effects on ecosystem Net Primary Production (NPP), but elevated CO_2 will ameliorate plant ozone injury for those species that decrease stomatal conductance at elevated CO_2. There is also the potential for UV-B to negatively impact NPP.
- Direct effects of increased air temperature on plant growth will be smaller than is often expected because of thermal acclimation. However, there will be developmental acceleration and stimulation of litter decomposition. Indirect temperature effects are mainly associated with warming of permafrost in subpolar biomes, which will cause substantial changes in species composition, litter quality, and nutrient availability. These effects have caused, and will cause, changes in energy and carbon balance that are large enough to provide significant positive feedbacks to global warming.
- Nitrogen deposition is associated with increased NPP in some forests, and appears to be further enhanced by the fertilization effect of elevated CO_2. However, continuous N loading will lead, in the long term, to changes in species composition that may not be associated with increased carbon sequestration at the ecosystem level. Continuous N loading, together with other associated pollutants, could lead in many instances to soil acidification with a subsequent decrease in NPP.
- Model predictions show that the combined effect of elevated CO_2 with higher air temperature and N deposition increases N mineralization and NPP, while soil C storage is decreased by increasing soil temperature. However, little is known about the overall carbon balance of terrestrial ecosystems under elevated CO_2.
- In the short term (years to decades), changes in plant physiology within species will dominate the response to altered climate and atmospheric composition. Species show a wide range of responses (sensitivity) to changes in atmospheric CO_2, air temperature, UV-B, tropospheric ozone, and nitrogen deposition. In the long term (decades to centuries), changes in ecosystem physiology will be dominated by changes in the relative abundance of species, and the physiological properties associated with them.

Box 7.2 Future needs

There is a need to:

- understand rhizosphere, mycorrhizal and soil processes under elevated CO_2 and temperature in undisturbed systems, and assess belowground carbon pools (e.g. root biomass, soil carbon fractions);
- understand physiological developmental processes in mature trees under changes in climate and atmospheric chemistry, and develop new conceptual sights to guide the interpretation of short-term experiments (FACE Experiments) to long-term predictions ($>$ 10 years);in

- understand nitrogen dynamics with respect to elevated CO_2, particularly of litter and decomposition processes, and the implications for carbon sequestration in ecosystems;
- resolve the effects of elevated CO_2 on evapotranspiration in general, and for mature forest trees in particular (i.e. on stomatal and canopy conductance and LAI responses);
- undertake more experimental work to determine the interactive effects of increased CO_2, air temperature, UV-B, and atmospheric pollutants, including ozone and N-compounds, under natural conditions;
- continue efforts to establish manipulative experiments (e.g. elevated CO_2) in woody ecosystems, particularly in tropical savannas and forests;
- understand soil carbon dynamics with respect to elevated temperature, particularly the controls of soil respiration;
- understand the influence and impact of land-use changes on rooting patterns and ecosystem water-use dynamics, especially in tropical and savanna ecosystems where forest-to-grassland conversions are common;
- understand the capability to scale leaf- and stand-level isotopic discrimination patterns to global carbon models determining regional and interannual source and sink strengths;
- establish stronger linkages with existing ecosystem eddy covariance analyses of water and CO_2 fluxes to help provide mechanistic explanations of how ecosystem physiology constrains biosphere–atmosphere gas exchange dynamics.

7.1 Introduction

In this chapter the impact of environmental change on the physiology of ecosystems is assessed, taking into consideration long-term hydrological and biogeochemical feedbacks. The chapter principally examines the environmental factors that are predicted to change in the coming decades to a century: atmospheric CO_2, temperature, water availability, N deposition, UV-B and tropospheric ozone. Major emphasis, however, is placed on atmospheric CO_2 since there is no controversy that the concentration of CO_2 in the atmosphere has changed substantially since the onset of the industrial revolution and that it will continue to rise into the near future as nations struggle to control their carbon emissions. Various modelling exercises are also presented to show the complex nature of the interactions among multiple global change drivers, which can lead to feedbacks, both positive and negative, on ecosystem responses.

Ecosystem physiology is a relatively new field that has arisen from the need to understand and predict how ecosystems will respond to the changing global environment. It is concerned with the interacting physiological processes that determine exchanges of carbon, energy, water and nutrients of whole ecosystems, and it recognizes that information derived from physiological measurements on one type of tissue and at one time scale may not be extrapolated to a whole system level nor to longer time scales because of interactions within the system. For example, increased carbon gain at the canopy level due to elevated CO_2 may not necessarily result in a proportional increase in biomass accumulation because of altered processes belowground, such as increased root turnover.

The historical development of the study of physiology has been principally based on experiments on individual organs or organisms, and there have been very few studies on the metabolic responses of whole ecosystems at any timescale. Thus, the database is limited. GCTE has therefore made a deliberate attempt to promote whole ecosystem physiological studies, particularly on the impact of elevated CO_2. This has led to the initiation of a dataset comparable across ecosystems.

The capacity of organisms to adjust to changing environmental conditions by redeploying resources in the short term (days to weeks) is well known. Plants also adjust their metabolism in response to environmental change. For example, they may adjust their temperature optimum upward as their growth temperature increases (Billings *et al.*, 1971). Such adjustments must be taken into account when building models of responses to a changing climate. In the longer term, over generations, whole-ecosystem adjustments occur not through metabolic acclimation but through shifts in population abundance and in species composition. Although these changes are demographic and not physiological, they have metabolic consequences at the whole-ecosystem level and must be considered in ecosystem physiology (see also Chapter 8). Since the life-cycle of organisms may vary from days (in the case of microbes) to centuries (in the case of trees), the dynamics of the adjustment response to environmental change are complex. Because all experiments are confined in space (less than a few m^2) and time (less than 10 years), there is a challenge to provide meaningful metabolic information that can be used in models for a wide range of spatial and temporal scales.

7.2 Effects of elevated atmospheric CO_2 on terrestrial ecosystems

7.2.1 The conceptual model

By the early 1990s considerable information existed on the response of plants to elevated CO_2, but the preponderance of studies had been conducted in laboratories or greenhouses. This was a problem for two reasons. First, it was suspected that some of the responses that were seen at lower levels of integration, such as with leaves or single plants, would be dampened at the stand level.

Second, the plant-level studies could not provide information of direct use in documenting the indirect impacts of elevated CO_2 on, for example, feedbacks to the atmosphere or to the soil. For these reasons GCTE established a consortium of elevated CO_2 studies (see Chapter 3) to facilitate the rapid exchange of information among the projects and to periodically synthesize and evaluate the accumulating data. For syntheses of the consortium's main results, see Schulze & Mooney (1993), Koch & Mooney (1996), Körner & Bazzaz (1996), Tinker *et al.* (1996) and Luo & Mooney (1998).

Most of the paradigms of plant responses to elevated CO_2 have been built on the study of agricultural species. In this chapter we focus on the responses of natural systems, including extensively managed pastures and forests. We must know more about CO_2 responses of natural and seminatural systems to predict impacts on the global carbon cycle and biodiversity, since together these systems occupy over three-quarters of the global land surface.

A summary of knowledge at the beginning of GCTE was given graphically in the GCTE Operational Plan (Steffen *et al.*, 1992; Fig. 7.1). This summary figure indicates not only the direct effects of elevated CO_2 on vegetation, but also feedbacks to biogeochemistry and the hydrological cycle. This figure provided a stimulus for ongoing and proposed studies to include processes that had not generally been considered in CO_2 research at that time. There were a number of areas where there was little, if any, information, for example, fate of nutrients under elevated CO_2 and impacts on the soil water balance. Although many gaps remain, substantial progress has been made in reducing uncertainty on many key issues. It was initially thought that the major feedback effects of elevated CO_2 would be through biogeochemical cycles. However, it is now known that the indirect effects on the hydrological cycle are equally or even more important, especially for water-limited systems.

What follows is a general review, mainly but not exclusively, of the results of the GCTE Elevated CO_2 Consortium projects (see Chapter 3). Data from published papers were the primary source, but responses to a questionnaire sent to all the participants in the Consortium (Tables 7.1 and 7.2) were also used.

7.2.2 Effects of elevated CO_2 on ecosystem carbon processes

For practical reasons most elevated CO_2 research has been conducted on vegetation dominated by short statured and short-lived plants (e.g. grasslands) and on young trees. The projects discussed here encompass a wide variety of unmanaged and managed systems, including salt marsh, annual Mediterranean and temperate grasslands, tallgrass prairie, alpine grassland, Arctic tundra, chaparral, oak-woodland, coniferous forest, deciduous trees, and tropical trees (see Tables 7.1 and 7.2). The experiments used a variety of CO_2 enrichment

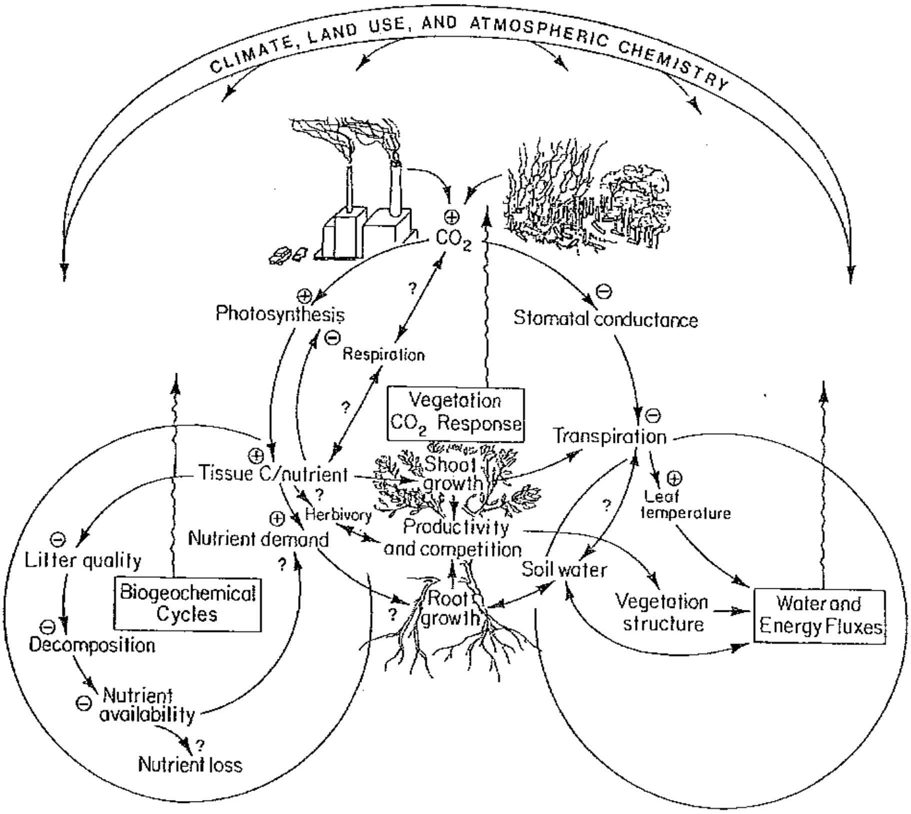


Figure 7.1 Initial research paradigm for the GCTE CO_2 research programme (from Steffen *et al.*, 1992).

technologies, including FACE, OTC, screen aided CO_2 enrichment (SAC), closed chambers (CC), ecocosms and other similar field enclosures, which are discussed in Chapter 2. Studies carried out on vegetation growing around natural CO_2 springs, which provide a valuable understanding of long-term and evolutionary responses to elevated CO_2, were also included.

Net CO_2 exchange

Increased photosynthesis at the leaf-level and net canopy CO_2 uptake (net daily or seasonal CO_2 *uptake per unit ground area) are probably the most consistent responses to elevated atmospheric CO_2* (see Tables 7.1 and 7.2). The current data on peak season CO_2 fluxes in ecosystems exposed to elevated CO_2 suggests that initial responses are always positive (increased net CO_2 uptake), and most often remain positive for some years. Although the degree of stimulation of photosynthesis has been observed in many studies to decline after extended exposure at elevated CO_2, a phenomenon known as 'down-regulation' (see reviews by

Gifford, 1992; Sage, 1994; Gunderson & Wullschleger, 1994; Amthor, 1995; Curtis, 1996), net CO_2 uptake during peak season at the plot level is almost always higher at elevated CO_2 than at ambient CO_2 (Drake & Leadley, 1991). For instance, Drake *et al.* (1996) showed a sustained 36% increase in peak season net canopy CO_2 uptake for a salt marsh over a six-year period, with no indication of a decreasing trend. Similarly Stocker *et al.* (1997) reported increased net canopy CO_2 uptake over two years of CO_2-enrichment in calcareous grassland (+ 34% at peak season and + 22% on a full season basis). Some studies showed net CO_2 uptake responses to have strong interactions with moisture, such as for water-limited Mediterranean annual grassland and tallgrass prairie. They showed little or no stimulation under moist conditions, but a relative enhancement of seasonal net biomass accumulation during dry years or at the end of the rainy season when soils start drying out (C. Lund & C. Field, personal communication; C. Owensby, personal communication). Low-temperature dominated systems, however, have consistently shown complete down-regulation after an initial stimulation of seasonal net CO_2 uptake. This occurred in the Arctic tundra within three years of exposure (Grulke *et al.*, 1990; Oechel & Vourlitis, 1996). Likewise, an alpine grassland, which showed a persistent enhancement of net CO_2 uptake for the first three seasons, exhibited full adjustment by year four (Körner *et al.*, 1997).

Downward adjustments per unit land area may be physiological or morphological. One example of physiological adaptation would be a decrease in rubisco concentration, while a morphological adaptation would be a reduction of leaf area index (LAI).

Another uncertainty as to how elevated CO_2 affects net CO_2 uptake in the long term is the lack of a mechanistic understanding of plant respiration. Mature leaf respiration has been reported to decrease as a consequence of the direct inhibitory effects of elevated CO_2 due to effects on non-respiratory metabolism (see Amthor, 1995 for review). Lambers *et al.* (1996) showed that while elevated CO_2 quite consistently suppresses leaf respiration, results from greenhouse and laboratory experiments showed no clear pattern for root respiration under such conditions. At the ecosystem level respiration either remained unchanged or increased under elevated CO_2.

Table 7.1 *Herbaceous systems responses to elevated* CO_2

Project no.	1	2*	3*	4	5*	6*	7*	8*	9	10	11*	12*	13*	14*
System	Arctic tundra	Alpine turf	Calcareous grassland	Limestone grassland	Tallgrass prairie	Pasture(s)	Pasture	Pasture	Pasture(s)	Pasture(s)	Annual grassland	Mediterran. grassland	Med. herbac. old field	Wetland
Location	Alaska	Switzerland	Switzerland	Lancaster UK	Kansas	Canberra	Zurich	New Zealand	Quebec	Clerm.-Ferr. France	California	Siena Italy	Montpellier France	Maryland
Contact	W. Oechel	C. Körner	C.Körner	J. Wolgenden	C. Owensby	R. Gifford	J. Nösberger	P. Newton	C. Potvin	J. Soussana	C. Field	F. Miglietta	J. Roy	B. Drake
Number of species	15	10	25	34	100	1	12	10	10	2	50	12	12	3
Technology	CC	OTC	SACC	Mesocos. (I)	OTC	Mesocos. (I)	FACE	Mesocos. (I)	OTC	Mesocos. (O)	OTC	CO_2 spring	Mesocosos. (I)	OTC
Yrs CO_2 expos.	3	+	+	3	7	+	+	1.2	4.3	2.2	4	many	3	8
Soils	natural	natural	natural	natural	natural	subsoil	natural	natural	natural	natural	natural	natural	natural	natural
Fertilization/Water	no/no	no/no	no/no	yes/yes	no/no	yes/yes	yes/no	yes/yes	no/no	yes/yes	no/no	no/no	yes/no	no/no
Annual prec. (mm)	n.a.	1600	900	n.a.	835	n.a.	1050	n.a. (874)	—	n.a.	600	700	n.a. (800)	-
Net Ecosyst. Prd.	=	+/=	+	+	+/=	+	+	+	–	+	+	–	+/=	+
Ps downreg.	canopy–total	canopy–some	canopy–some	some	none	.	leaf–some	canopy–some	leaf–none	leaf–some/no	canopy–some	leaf–some	canopy–some	canopy–some
Abovegr. biomass	=	+/=	+	+/=/–	+/=	+/=	+/=	+	+/–	+	+	=	=	.
Sps. biomass rep.	≠	≠	.	≠	≠	n.a.	≠	≠	≠	≠	≠	.	≠	≠
R : S biomass ratio	.	–	–	+	=	–	+	+	.	≠/sps	=	.	+	.
N_2 fixer/non-N_2	.	=	=	=	.	n.a.	+	+	+/–	+	+	.	+/–	.
Total plant N	–	–	–	.	+/=	–	+/=	.	.	=/–	+/=/–	–	+	+
Green tissue C : N	+	+	+	≠/sps	+/sps	+	+(small)	.	.	+/=	+ (small)	+	+/=	+/sps
Abovegr. carbohydr.	+	+	+	≠/sps	.	+	+	.		+/=	+	+	+	+
Litter C : N		=	=		=	+	=	.	.		=	.	.	+/sps
Above-litter prod.	m	=	=	.	+/sps	+	+/=	.	.	.	+		.	.
Litter decomp. delay	m	yes	=	.	=	no	.	.	.	.	yes	.	.	yes

Leaf Area Index	=	=	=	=	+	=/−	+/−	+	=	+	+	=	·	+/=
Evapotranspiration	=	=	=			=/−	·	=		=	·		−/=	
Soil moisture	=	=	+	·	+	+	=	=		+	+	·	+	n.a.
Root turnover	·	+	+	+		·	·	+	·	+	+	·		
Soil respiration	·	=	+/=	=	+/=	·		+	·	+	+	·	+/=	+
Microbial bio/act		=	=		+/=	+/=	=	+		+	+	·	+	=
Microrrhizae infect	·		≠/sps	+	=	=	=	·	·	·	=		+	=
Microflora changes		·	·	·	·	·	yes	+		·	yes	·	yes	yes
N mineralization		=	=	·	·	−/=	·	=		−	+	·		
System N losses		=	=	·	·	=/−	+			=/−	−	·		·
Total soil carbon	·	=	·	·	+	+	+	=		+	=	·		+/=
Leafing date		=	=		=	−			·	=	≠/sps	=	≠/sps	=
Flowering date	·	=	=	≠/yr	=	−	=	·	earlier	=	≠/sps	=	≠/sps	=
Number of flowers	·	+/=	≠/sps	≠/yr	=	−	≠/sps		+		≠/sps	=	≠/sps	+
Seed production		+/=	≠/sps	+/−/sps	=	−	≠/sps	·	·	·	≠/sps	·	≠/sps	·

[a] GCTE Core Research Project; (s), summary of more than one experiment; CC, closed chamber; OTC, open top chamber; FACE, Free air CO$_2$ enrichment; SACC, screen aided CO$_2$ control; (I), indoor; (O), outdoor; Mesocos, Mesocosm (artificial ecosystem); n.a., not applicable; (=), no change; (−), decrease; (+), increase; ≠/sps, different species respond differently.

Table 7.2 *Woody systems responses to elevated co*$_2$

Project no.	1*	2*	3*	4*	5*	6*	7	8*	9*	10*	11*	12*	13
System, species													
Deciduous	Deciduous tress	Conif. tree(s) trees	Conif. forest *Pinus taeda*	Conif. trees *P. taeda*	Conif. trees *P. ponderosa*	Conif. sitka spruce	Conif. trees forest	Conif./decid.	Scrub oak trees	Chaparral(s)	Oak forest	Tropical	trees (s)
Location	Tennessee	Michigan	USA	N. Carolina	California	Scotland	Switzerland	Oregon	Christchurch N. Z.	Florida	California	Italy	Switzerland
Contact	R. Norby	P. Curtis	B. Strain	G. Hendrey	T. Ball	P. Jarvis	S. Hättensch.	D. Tingey	D. Whitehead	B. Drake	W. Oechel	F. Miglietta	J. Amone
Number of species	2	1	1	15	1	1	4	1	2	14	3	5	7–15
Technology	OTC	OTC	OTC	FACE	OTC	OTC	Mesocos. (I)	Mesocos. (O)	OTC	OTC	CC/FACE	CO_2 spring	Mesocos (I)
Yrs. CO_2 expos.	3.5	2	4	2.5	5	3	3	3	4	1	0.9	many	0.3–1.5
Soil	natural	mixed substr.	mixed substr.	natural	natural	natural	.	natural	natural	natural	natural	natural	mixed substr.
Ferilization/Water	no/no	no/no	yes/yes	no/no	yes/no	yes/yes	no/yes	no/yes	yes/yes	no/no	no/no	no/no	yes/yes
Annual prec. (mm)	1360	900	1240	1150	.	1200	1200	n.a. (1000)	600	.	490	–	n.a. (3250)
Net Ecosyst. Prod.	+	+	+	–	+	.	+	+	+	+	+	+	+
Ps downreg.	=	leaf–some	leaf–some	leaf–some	canopy–some	leaf–some	leaf–some	leaf–some	leaf–some	leaf–some	leaf–some	leaf–some	leaf–some
Abovegr. biomass	+	.	+	.	.	+	=	.	.	.	+	.	=
Sps biomass rep.	=	.	n.a.	.	.	n.a.	≠	≠	.	≠	≠	.	≠/=
R : S biomass ratio	=	.	–	.	+	=	+	.	.	+	.	.	+
N_2 fixer/non-N_2	n.a.	.	n.a.	.	n.a.	n.a.	.	.	.	.	yes	.	.
Total plant N	+	.	+	.	+	=	–	.	.	+	.	.	=
Green tissue C : N	=	+	–	=	.	.	+	+	+	+	+	+	+/=
Abovegr. carbohydr.	.	.	+	+	.	+	+	.	.	+	+	+	=
Wood tissue C : N	+	.	–	.	.	.	+				.	+	.
Litter C : N	=	.	–	.	=	.	.	.	.	.	.	.	+/=

Litter carbohydrate	.	.	=	.	.	.	.	.	.	.	.	=	
Above-litter prod.	+	=	+	+	.	.	+	.	.	.	.	.	+/=
Litter decomp. delay	=	.	=	.	.	.	.	.	.	.	.	.	=
Leaf Area Index	+	=	+	+	.	.	−	=	+	+/=	+	+	=
Evapotranspiration	=	.	−	−	+	.	.	−	+	−	−	−	=
Soil moisture	.	.	n.a.	=	.	.	.	+	.	.	=	=	=
Root turnover	.	.	+	.	−	.	.	+/−	=	+	.	.	+
Soil respiration	+	=	+	+	+	.	+	+	+	.	=	.	+/=
Microbial biomass	.	.	+	+	+	.	.	.	.	.	=	.	.
Microrrhizae infecr.	+	.	+	.	=	.	.	.	.	.	=	.	=
Microflora changes	=	.	.	.	yes	.	.	.	.	yes	yes	.	=
N mineralization	.	.	.	.	=	.	.	.	.	.	=	.	+
System N losses	.	.	+	.	=	.	.	=	.	.	.	.	+/=
Total soil carbon	+	.	+	.	+	.	.	=	=	.	.	.	+/=
leafing date	=	=	earlier	=	earlier	=	≠/year	=	.	.	earlier/=	.	.
Seed production	.	.	.	.	.	.	.	.	.	.	+/=	.	.

*GCTE-Core Research Project; (s), summary of more than one experiment; CC, closed chamber; OTC, open top chamber; FACE, Free Air CO_2 Enrichment; (I), Indoor; (O), Outdoor; Mesocos., Mesocosm (artificial ecosystem); n.a., not apply; (=), no change; (−), decrease; (+), increase; ≠/sps, different species respond differently.

Box 7.3 Biomass, NPP, NEP and NBP

When considering responses of ecosystem physiology to global change, direct effects on processes (e.g. growth) and indirect effects via changes in species composition (biodiversity) need to be distinguished. Among the direct responses related to the carbon cycle, three need to be clearly identified: (1) seasonal plant biomass accumulation (often termed 'production'); (2) annual net primary production (NPP, dry matter fixed through photosynthesis minus losses due to respiration and construction costs; losses of newly built biomass to herbivores and litter must also be accounted for. True NPP has rarely been estimated because belowground production and litter recycling usually remain unknown.); and (3) annual net ecosystem productivity (NEP), i.e. the net change in carbon pools per unit land area. It is particularly important to note that seasonal biomass accumulation, the response most commonly investigated, is not a measure of NEP (carbon sequestration). If large areas and long time-frames are considered, both the changes in species composition and in disturbance regimes need to be included in evaluating carbon sequestration. Here the concept of Net Biome Productivity (NBP) is most appropriate. See Sections 10.4 (especially Fig. 10.2) and 12.2.2 for a more detailed discussion of NPP, NEP and NBP in relation to the terrestrial carbon cycle.

Biomass responses

Aboveground biomass accumulation in whole ecosystems exposed to elevated atmospheric CO_2 in the field has been mostly studied in grasslands and crops. These experiments have shown a mean increase of 14% at twice ambient CO_2 when averaged across systems ($n = 9$ studies; 16% when averaged across systems and years, $n = 28$; see Fig. 7.2). This value is much lower than previous values derived from growth chamber and laboratory experiments, which were mostly conducted on single plants; Poorter (1993) reported for 156 species an increased plant growth at a double current CO_2 of 41% for C_3 species and 22% for C_4 species; Idso & Idso (1994) reviewed 342 published papers and found that plant dry weight was 24% higher at double CO_2 compared to ambient CO_2 when water was not limiting and 48% higher when water was limiting. They found that dry weight increased by 53% at double CO_2 in nutrient sufficient conditions and by 48% when nutrients were limiting. Note, however, that a large percentage stimulation by elevated CO_2 does not necessarily mean a large biomass response since often the largest differences between treatments occur during dry years (or treatments) when productivity is low.

It is important to note the highly variable nature of aboveground biomass production response when compared across systems and across years within the same system. Individual values in the CO_2 Consortium results range from negative responses to 85% (see Fig. 7.2) depending on the system and year, which reflects the interactive nature of the elevated CO_2 response with other

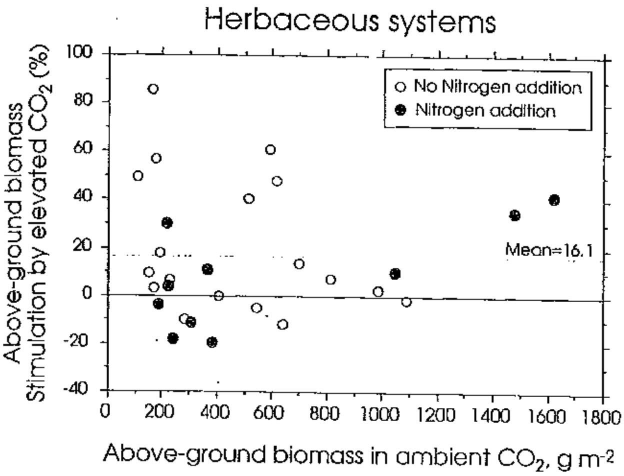


Figure 7.2 Above-ground biomass stimulation by elevated CO_2 of herbaceous ecosystems, with and without N additions.

variables (e.g. water and nutrient availability, species composition, temperature, etc.).

The average aboveground biomass response to double CO_2 of + 14% is of smaller magnitude than some of the measurements of system-plot net CO_2 uptake, which indicates the existence of significant carbon sinks other than aboveground plant growth. In some instances, changes in biomass are too small to be detected, even when net CO_2 uptake is significantly higher at elevated CO_2. This was the case in the Arctic tundra during three growing seasons of elevated CO_2 exposure before the system down-regulated (Tissue & Oechel, 1987), in an alpine grassland (Schäppi & Körner, 1996; Körner *et al.*, 1997), in a tallgrass prairie (Owensby *et al.*, 1996*a*), and in a Mediterranean grassland (Navas *et al.*, 1995) during wetter than average conditions.

No area-based biomass response data exist for mature forest trees exposed to elevated CO_2. When individual trees were investigated, positive biomass responses were found in most cases (Ceulemans & Mousseau, 1994). Seedlings or young saplings of five species in 16 different CO_2 experiments had an average biomass increase of 26% in response to elevated CO_2, with individual values ranging from nonsignificant increases to 58% increase (Jarvis, 1995*b*). However, some of the above studies and others have been conducted under rather fertile conditions and actual responses range from negative (Mousseau & Enoch, 1989) to no change (e.g. Norby *et al.*, 1992) to a several-fold increase under completely unlimited growth conditions (e.g. Idso & Kimball, 1992; Pettersson & McDonald, 1992). The reported responses were strongly dependent on nutrition, competitive environments, experimental duration, and the age of the experimental plant (Eamus & Jarvis, 1989; Loehle, 1995). Tree saplings grown in competitive assemblages in model ecosystems showed no biomass response to elevated CO_2 when nutrient supply was moderate to low (tropical: Arnone & Körner, 1995; boreal: Hättenschwiler & Körner, 1996) but a slightly positive response under more fertile settings (tropical: Körner & Arnone, 1992). Zero biomass responses have also been reported for model communities with young tree seedlings by Williams *et al.* (1986, temperate deciduous), and Reekie & Bazzaz (1989, tropical).

Seedling responses are expected to be quite different from those of adult trees but few experimental data are available for the latter. Cross-continental surveys of tree ring and community dynamics suggest that the most likely response of adult trees to current atmospheric CO_2 enrichment in the boreal zone is close to zero (Schweingruber *et al.*, 1993), while tropical trees may be stimulated (Phillips & Gentry, 1994). Analysis of tree ring data from Mediterranean oaks growing around two separate natural CO_2 springs indicates that initial positive responses are gradually reduced as trees grow in size and disappear after about 30 years (Hättenschwiler *et al.*, 1997). Such a response pattern could resolve the discrepancy between positive seedling responses commonly seen in CO_2-enrichment experiments and actual responses of mature trees. As a consequence, initial tree growth may be accelerated under elevated CO_2, but tree carbon stocks over longer time periods may not necessarily become greater. Whatever the effects on long-term carbon storage, forest dynamics are likely to become enhanced, which is of great significance for forest ecology and is of interest to commercial forest production.

Litter quantity, quality, and decomposition

Changes in litter amount and its chemical composition (quality) can alter the fluxes of carbon and nutrients within the ecosystem, and hence affect plant productivity and carbon sequestration. In young expanding systems litter quantity commonly increases under elevated CO_2 because of increases in leaf biomass and total aboveground biomass (Norby *et al.*, 1996; Jarvis, 1995*a*). Since steady state leaf area index (LAI) achieved at canopy closure in well-watered systems does not seem to increase under elevated CO_2 (Arnone & Körner, 1995; Hättenschwiler & Körner, 1996), enhanced leaf litter production may be a transient effect. Elevated CO_2 typically causes an increase in C : N ratio of green leaves due to starch accumulation (Field *et al.*, 1992). However, this starch disappears at leaf senescense, so the quality of natural senesced litter, with some exceptions (e.g. Cotrufo *et al.*, 1994; Table 7.1) is often indistinguishable from litter produced under ambient CO_2 (Curtis *et al.*, 1989; Kemp *et al.*, 1994; O'Neill, 1994; Franck *et al.*, 1997; Hirschel et al., 1997). Consequently, litter of plants grown under elevated CO_2 in most cases does not differ in decomposition rate from litter grown under ambient CO_2. There is, however, a great deal of variance in decomposition rate among species (Franck *et al.*, 1997) and the long-term consequences of elevated CO_2 on litter pools may be mostly driven by changes in species composition.

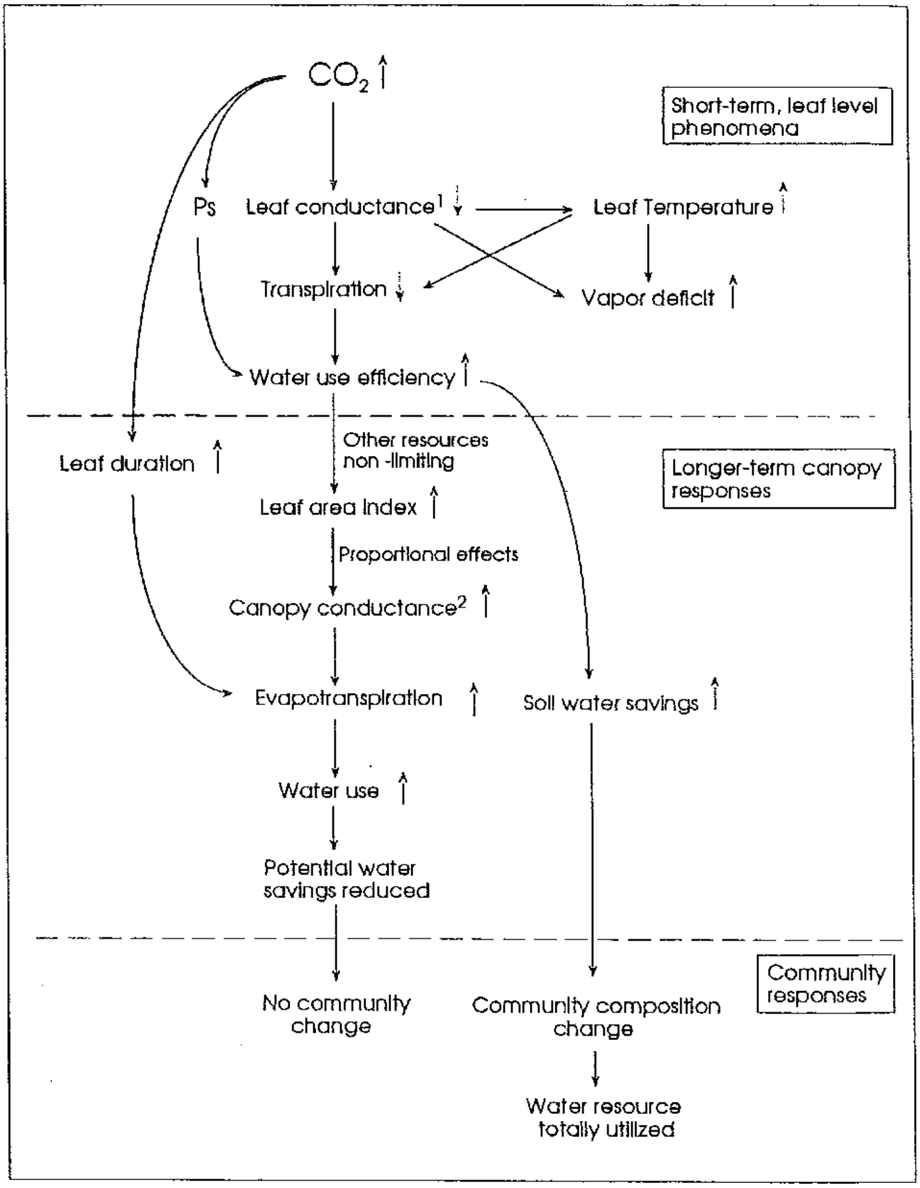
Belowground carbon fluxes and soil carbon sequestration

Although persistently increased peak season net ecosystem CO_2 uptake is a common response to elevated CO_2, changes in overall biomass are usually smaller than expected, and sometimes even nil. A growing body of information indicates that CO_2 enrichment leads to enhanced carbon allocated to below-ground functions (Van Veen *et al.*, 1991; O'Neill, 1994; Körner, 1996; Canadell *et al.*, 1996*b*). Although responses are not consistent across all systems, the increased carbon flow to the belowground compartment is largely driven by accelerated root turnover (Norby, 1994; Pregitzer *et al.*, 1995; Tingey *et al.*, 1995), rhizodeposition (Cardon, 1996), mycorrhizal development (O'Neill *et al.*, 1987; Rygiewitz & Andersen, 1994; Dhillion *et al.*, 1996), and N_2-fixation (Soussana & Hartwig, 1996).

One of the most important goals of research on elevated CO_2 is to investigate whether increased net CO_2 uptake in a high CO_2 world will result in increased long-term carbon storage in ecosystems, in particular in the soil component where carbon residence times are longest. Given that most soils contain 10–20 kg C m^{-2}, it is difficult to detect C sequestration of less than 300 g m^{-2} by direct determination (Hungate *et al.*, 1996). Most often soil C sequestration has to be inferred. However, a few field studies have shown a trend, in some instances nonsignificant, towards increasing soil carbon storage in elevated CO_2 plots (see review by Canadell *et al.*, 1996*b*). Among field studies suggesting soil carbon accumulation are a wetland in Maryland (USA) after six years of CO_2 enrichment (Drake *et al.*, 1996), a Kansas (USA) tallgrass prairie after five years of CO_2 enrichment (Table 7.1), and two experiments with conifer trees (USA) after 4–5 years of high CO_2 (Table 7.2). Isotope-labelling experiments with reconstructed soils have also shown increased carbon deposition under elevated CO_2 (Lekkerkerk *et al.*, 1990), although in deep natural soils such signals are likely to be greatly diluted, and reconstructed soils show effects of disturbance for several years.

7.2.3 Impact of elevated CO_2 on water balance

The effects of elevated CO_2 on ecosystem water balance can be seen at different spatial and temporal scales. The challenge for the GCTE-CO_2 programme has been to interrelate and to model these various spatial scales and temporal dimensions. The spatial and temporal scales are to a certain degree intrinsically interconnected. For example, short-term responses are most often studied at the leaf level, while canopy-level responses are most often studied seasonally.



[1] Short term sensitivity to water stress enhanced under high CO_2

[2] Sensitivity of canopy conductance to evaportranspiration depends on community roughness.

Figure 7.3 Water-mediated responses to elevated CO_2 at the leaf-, canopy-, and community-level.

Interannual responses are often seen at the community level, at least for communities with short-lived organisms. Here we describe the basic CO_2 responses, and their interrelationships and ecosystem consequences (Fig. 7.3).

Leaf level

In the short term and at the leaf level, elevated CO_2 commonly reduces stomatal conductance in herbaceous plants and tree seedlings (Morison & Gifford 1984; Field *et al.*, 1995) and its sensitivity to water stress (Owensby *et al.*, 1996*a*). However, not all species respond equally strongly and some do not respond at all, depending on the degree of environmental stress experienced (Curtis, 1996). With the current experimental data available, adult trees do not seem to exhibit the responses seen in the majority of herbaceous plants or tree seedlings. Several studies in which leaves or branches of tall canopy trees were exposed to elevated CO_2 did not reveal a change in leaf conductance (Barton *et al.*, 1993; Dufrêne *et al.*, 1993; Jarvis, 1995*b*; Teskey, 1995; Körner & Würth, 1996), and first results from FACE studies in *Pinus taeda* are in line with these findings (Ellsworth *et al.*, 1995). Thus, at present, there is no experimental basis for assuming that overall forest transpiration will be reduced under elevated CO_2. Analyses of stomatal densities on leaf surfaces of plants grown under approximately doubled current ambient CO_2 show a mean decrease of 9% (Woodward & Kelly, 1995) but variation is very large and often no response is seen in the field.

Any reduction in leaf conductance would reduce transpiration. In general, this would increase leaf temperature and thus increase the vapour pressure gradient between the leaf and the surrounding air, partially offsetting the effect of the reduced conductance. Substantially higher leaf temperatures may cause the stomata to close further, resulting in a decrease in transpiration. Thus, even at the leaf level, there can be many counterbalancing interactions. However, even if no reduction of vapour loss occurred relative to water lost during the same period, water use efficiency (WUE) would increase. Data for a variety of species indicate that leaf-level WUE is proportional to atmospheric CO_2 concentration (Morison, 1993).

Canopy level

Leaf-level responses commonly do not directly translate into canopy responses (Morison, 1993; Field *et al.*, 1995). Factors that counteract or dampen the effect of leaf responses are (i) canopy conductance, (ii) feedbacks from improved plant water status via enhanced leaf area production (transpiring surface), (iii) prolonged availability of soil moisture and thus less temporal restriction of transpiration, and (iv) contributions of soil evaporation and understory evapotranspiration to canopy scale water balance.

Canopy conductance is perhaps the most important factor and is controlled by canopy height and LAI. Tall and narrow-leafed plants such as conifer trees are well coupled to the atmosphere, and hence stomatal conductance dominates overall conductance. This is less true in broad-leaf forests and particularly in low-stature vegetation such as grasslands, where aerodynamic canopy conductance may be smaller than stomatal conductance. The resistance to water vapour movement through the canopy, rather than the stomatal conductance, may limit the transpiration loss (see also Section 7.4). In such cases evapotranspiration will not change greatly in response to elevated CO_2 (Field *et al.*, 1995). *In situ* measurements of evapotranspiration in vegetation treated with elevated CO_2 have rarely been made, but the few observations available suggest relatively little effect of elevated CO_2 on evapotranspiration (Grant *et al.*, 1995*a*; Stocker *et al.*, 1997; McConnaughay *et al.*, 1996).

Soil level

Reductions of evapotranspiration so small that they cannot easily be detected experimentally may still accumulate to produce measurable increases in soil moisture, particularly during prolonged dry periods. Such effects of elevated CO_2 have been measured in Mediterranean grassland (Field *et al.*, 1996; see also Tables 7.1 and 7.2) and in temperate grassland (Zaller & Arnone, 1997). Such moisture savings appear to be the most influential consequence of CO_2 enrichment in periodically dry vegetation (Jackson *et al.*, 1994). As an example, the tallgrass prairie in Kansas showed no significant increase in aboveground productivity under elevated CO_2 during wet years (1992, 1993), an increase of 40% in an average rainfall year (1990), and about an 80% increase during a dry year (1989) (Owensby *et al.*, 1996*a*). However, the highest elevated CO_2 response occurred during low biomass production years (dry years), and therefore the absolute biomass change (g m^{-2}) may be small.

Increased soil water availability can enhance ecosystem productivity both by extending the growing season and through positive effects on microbial activity and turnover, and hence decomposition and nutrient availability. The extension of the physiological active period is an important mechanism. The gross rate of NH_4^+ mineralization in two California grasslands exposed to elevated CO_2 increased as a consequence of increased soil moisture resulting from decreased stomatal conductance at elevated CO_2 (Hungate *et al.*, 1997). In the Swiss calcareous grassland project, water savings by the majority of species seem to enhance soil activity during dry periods, in particular the activity of earthworms, which exerts a chain reaction on nutrient relations, seed burial, and microgap dynamics in the canopy (Zaller & Arnone, 1997). Hence, even small improvements in water relations associated with CO_2 enrichment appear to exert marked effects on community dynamics and organism interactions. The only data for field-grown forest trees, those for the Mediterranean oak by

Hättenschwiler *et al.* (1997), indicate beneficial effects of CO_2 in dry years as well.

7.2.4 Community responses to elevated CO_2

While fluxes and pools per unit ground area show rather varied responses to CO_2 enrichment, one set of observations is common to all studies in which more than one species were included in the treatment: no two species were found to respond identically. Hence, no matter whether overall biomass responses or carbon accumulation occurred, responses were species- and even genotype-specific, causing continued CO_2-enrichment to become a biodiversity issue (Bazzaz *et al.*, 1989; Bazzaz 1996; Körner & Bazzaz, 1996; Potvin & Vasseur, 1997).

In the long term, these changes may alter species abundance and community composition, which could have an even larger impact on ecosystem functioning than changes on physiological processes of a given species assemblage (Section 8.1 and 12.2.2). One important lesson from the study of species-specific responses to elevated CO_2 in mixed communities is that the grouping of plants into functional types has had little predictive value for CO_2 responsiveness. C_4 species are not consistently nonresponsive, nor are legumes often more responsive than non-legumes, or fast-growing species more responsive than slow-growing species (Poorter, 1993) when investigated in a competitive setting in their natural environment (Owensby *et al.*, 1993; Table 7.1). For instance, the species that exhibited by far the most pronounced biomass response in a highly diverse calcareous grassland exposed to elevated CO_2 was a slow-growing sedge, whereas the five nitrogen-fixing *Trifolium* spp. in that community did not respond (Leadley & Körner, 1996). In the prairie, C_4 species have been shown to be quite responsive to CO_2-enrichment because of their capacity to take advantage of soil moisture as a result of reduced stomatal conductance (Owensby *et al.*, 1993). Likewise, in the California Mediterranean-climate grasslands, more water remains at the end of the growing season under elevated CO_2. The late-season growth of annuals, especially in dry years, may result in altered community composition in a given and subsequent years and cause seasonal biomass production to increase (Field *et al.*, 1996).

Several studies have also shown strong genotype responses to CO_2, with biomass responses not correlating with photosynthetic responses (Curtis *et al.*, 1996). Selection for responsive genotypes, in particular directions, is one of the most likely responses to elevated CO_2. Since species-specific responses to elevated CO_2 include responses of tissue composition, and thus nutritional quality of tissues, herbivores will be co-affected (Lindroth, 1996; Owensby *et al.*, 1996*b*), and even more subtle responses may be seen with species or genotype-specific mycorrhizal relationships (Sanders, 1996).

In the long term, many effects of elevated CO_2 on ecosystem functioning will be driven by the biogeochemical properties of new species assemblages that will be competitively superior in a high CO_2 world. For instance, grass and dicotyledon communities differ in their rate of root production, which may also affect soil structure and humus production (P.B Tinker, personal communication). Thus, any change in grass/dicotyledon species composition may indirectly affect carbon immobilization. Conversely, any shift from evergreen to deciduous forest or shrubland would accelerate turnover and carbon release from the system.

7.2.5 Modelling ecosystem responses to elevated CO_2

A wide variety of models have been used to investigate and project responses of ecosystems to elevated CO_2. While all of these models share a common objective of simulating responses to CO_2, they differ considerably in the specific mechanisms incorporated. When models are calibrated for specific sites or regions under current climate and CO_2, they often agree, but they may diverge when predicting ecosystem responses under scenarios of future climate change and increasing CO_2. It is essential, therefore, to understand how differences in the formulation of specific mechanisms influence their predictions. Given that results are becoming available from ecosystem experiments on the effects of elevated CO_2, it is appropriate to ask whether patterns of change predicted by models are similar to those observed in experiments. This type of analysis will help identify deficiencies in existing models and needs for further experimental data to improve the models.

How ecosystem/biogeochemistry models implement the elevated CO_2 response

A review of several recent ecosystem model comparison activities (Ryan *et al.*, 1996*a*,*b*; VEMAP Members, 1995) suggests that there are at least five major ways that direct effects of atmospheric CO_2 have been included in ecosystem models. These include the effects on: (i) stomatal conductance and water use efficiency, (ii) photosynthesis, including acclimation processes and plant respiration, (iii) carbon allocation and growth, (iv) plant structure and phenology, and (v) plant nutrient concentration.

Table 7.3 summarizes the ways in which the direct CO_2 effect is incorporated into eight ecosystem models (Ryan *et al.*, 1996a; VEMAP Members, 1995). Recent versions of many of these models have been improved to include more of the direct effects of CO_2 on ecosystem processes. Table 7.3 shows that most of the models include the direct effects of atmospheric CO_2 on photosynthesis and respiration. Most incorporate the Farquhar photosynthesis model (Farquhar *et*

Table 7.3 *Comparison of the way that direct CO_2 is incorporated into different ecosystem models.*

	Models							
CO_2 impact	BIOME-BGC*	TEM*	CENTURY^R	GRASS^R	GEM^R	HYBRID^R	PNET-CN^R	BIOMASS^R
Stomatal conductance	−20%	–	−20% Tran	Ball *et al.* (1987)	–	Friend (1991)	–?	McMurtrie (1993)
Photosynthesis	F (C_3)	P	–	F ($C_3 + C_4$)	P	F(C_3)	P	F(C_3)
Carbon allocation	–	–	–	I_N	I_N	I_N	–	N_l
Structure & phenology	–	–	–	I_N	–	–	–	–
Leaf C/N	+20%	I_N	+20%	+20%	I_N	–	V	–

F, Farquhar photosynthesis equation (Farquhar *et al.*, (1980); P, Phenological; I_N, indirect effect of model structure; N_l, Function of leaf N content.
*Version of models used by VEMAP (1995).
^{R}Version of models used by Ryan *et al.* (1998).

al., 1980), either explicitly or using simplified phenomenological models derived from that model.

In several models canopy photosynthesis is linearly related to absorbed light; this relationship has been derived from simulations of detailed canopy models (e.g. McMurtrie *et al.*, 1992*a*; Kirschbaum *et al.*, 1994), and from assumptions of optimal N distribution within canopies (Haxeltine & Prentice, 1996*a*; Dewar, 1996). Respiration is expressed either using a separation into growth and maintenance components incorporating a Q_{10}-temperature dependence, or by assuming that stand respiration is proportional to canopy photosynthesis (Gifford, 1994*b*; Dewar, 1997).

The impact of CO_2 on stomatal conductance is represented either by published equations relating stomatal conductance to environmental variables or by reducing transpiration water loss by a specified amount. The models that do not explicitly incorporate stomatal conductance all have relatively simple water budget submodels. The increase in the live leaf C : N ratio under elevated CO_2 levels is incorporated into almost all models, with some increasing the C : N ratio by a fixed percentage and others stimulating changes in C : N ratio as a result of internal dynamics.

Table 7.3 shows that few of the models include a direct effect of atmospheric CO_2 on carbon allocation or on plant structure and phenology, reflecting uncertainty as to how CO_2 affects these plant processes. Several models incorporate direct effects of water and nutrient stress on plant carbon allocation. However, the ability of these models to simulate observed changes in carbon allocation from field experiments is uncertain since formal model comparisons with data from elevated CO_2 experiments are limited (Coughenour & Chen, 1997). GRASS is the only model that included the impact of CO_2 on plant structure, associated with the indirect effect of water stress on leaf death rates.

Impacts on Forests and Grasslands

GRASSLANDS Parton *et al.* (1995) analysed the impact of climate change and increasing CO_2 on seven major grassland ecosystems around the world. The model predicted that doubling current CO_2 would result in increased plant production, soil C levels, and soil decomposition rates. The greatest predicted increases in plant production were in cold desert steppe systems (owing to warming and CO_2 effects), while the greatest increases in soil C were in humid savanna systems. Net N mineralization rates were reduced by increasing CO_2 as a result of the increase in the C : N ratio of leaves. Soil decomposition rates increased because elevated CO_2 reduced transpiration rates and increased the soil water content.

Coughenour & Parton (1996) evaluated the impact of doubled CO_2 levels on a shortgrass steppe and tallgrass prairie using a detailed plant physiology model (GRASS). The results showed that elevated CO_2 increased plant production, root : shoot ratio, live leaf area and N mineralization, while transpiration per unit leaf area was reduced. The total transpirational water loss per unit ground area per year remained constant because of increases in duration and amount of live leaf area that compensated for a reduction in the transpiration per unit leaf area. The results also showed that the average soil water content was increased during the early part (June) of the growing season at the tallgrass site and during the late growing season (July and August) for the shortgrass steppe. Increased soil water content resulted in elevated decomposition and nutrient mineralization rates.

FORESTS Model comparison exercises are an especially useful mechanism for evaluating models (see Chapter 6). Ryan *et al.* (1996b) evaluated the effect of increasing atmospheric CO_2 and climate change on two coniferous forests by comparing results from eight different forest ecosystem models. All of the models predicted that increasing CO_2 would increase aboveground net production and tree biomass, with a smaller effect on soil carbon. Models that had strong links between nutrient cycling and plant production generally predicted smaller increases in plant production because of nutrient constraints. The models disagreed on the response to increased temperature with the differences resulting from the question of whether increased nutrient availability (resulting from increased decomposition rates) would compensate for increased drought stress. In general, this study shows that there are considerable differences in the way forest models respond to changes in climate and atmospheric CO_2.

Multiple ecosystem comparisons and consequences of different formulations

Recently three biogeochemical ecosystem models were compared in their simulations of the CO_2 response of potential natural vegetation for the entire continental United States (VEMAP Members, 1995*a*). They were BIOME-BGC (Running & Coughlan, 1988; Running & Gower, 1991), CENTURY (Parton *et al.*, 1987, 1993), and TEM (McGuire *et al.*, 1995). The comparison focused on changes in NPP and carbon storage over the entire USA.

Under doubled CO_2, all the models predicted increases in NPP for potential natural vegetation ranging from 5% for CENTURY, to 9% for TEM, and 11% for BIOME-BGC. Changes in carbon storage (vegetation and soils) for the same models were + 2%, + 9%, and + 7% respectively. It is not surprising that there should be differences in the projections since the models differ in how they implement the CO_2 response.

Pan *et al.* (1997) have undertaken a more detailed comparison by evaluating the NPP responses simulated by the three models at specific sites (representing

17 biomes) along temperature and moisture gradients. CENTURY simulated little variation in relative NPP response, with a significant negative relation between precipitation and relative NPP response and no correlation with temperature. For BIOME-BGC and TEM, the ranges in stimulation of NPP were similar, and were far greater than for CENTURY, but the distribution of values differed among biomes. For BIOME-BGC there was a marginally significant negative correlation with precipitation, and a significant negative correlation with temperature. For TEM, there was a negative correlation with precipitation but a positive, highly significant correlation with temperature.

These differences in responses were caused by the way the CO_2 response was implemented (Pan *et al.*, 1997). In BIOME-BGC the effects of elevated CO_2 on NPP resulted from changes in transpiration, soil water and leaf area, with nitrogen feedbacks playing no role. In both CENTURY and TEM, the nitrogen cycle plays a key role in regulating the carbon fluxes. For CENTURY, the decomposition process provides most of the control and the effect of moisture on decomposition is dominant. TEM, however, alters the C : N ratio, which in turn can influence the decomposition rate and the supply of nitrogen; this then feeds back to influence NPP.

An ongoing research effort based on an evaluation of the CO_2 responses of a larger array of ecosystem models (CMEAL Participants, unpublished) aims to improve the representation of the response to CO_2. The models are being run for several sites for which considerable data are available on growth and physiology at ambient and elevated CO_2. In a preliminary model intercomparison four models were run for current and doubled CO_2. Important conclusions from this early experiment include: (i) while the patterns observed among models were often qualitatively similar for particular variables, no two models responded in either a qualitatively or quantitatively similar fashion for the full suite of ecosystem variables; (ii) all of the models predicted a short-term increase in NPP after doubling of CO_2 based principally on increased photosynthesis per unit nitrogen; (iii) models predicted different long-term NPP responses, depending primarily upon assumptions of fixed versus floating C : N ratios for wood or soil and the resultant effect on availability of N for plant uptake; (iv) there were also important differences among models in terms of where N and the increased pool of C are stored in ecosystems at elevated CO_2; (v) all models predicted increased use efficiency of N, water, and light at elevated CO_2, but nitrogen is the only resource for which increased uptake was predicted.

An important lesson from all of the model comparison exercises is the need for good standardisation in protocols to eliminate differences in results that could be due to arbitrary differences in procedures or choices of model parameters. An example of these is seen in patterns of ecosystem nitrogen content and use. Some models have a closed nitrogen cycle, which obviously constrains the ecosystem nitrogen pool and also limits long-term NPP increases; other models have an open nitrogen cycle and predict sustained increases in ecosystem nitrogen and C pools. As noted above, assumptions on wood or soil C : N changes can lead to major differences in predictions (McMurtrie & Comins, 1996). These results highlight the need for better data from experiments on ecosystem pools of N and patterns of distribution within the ecosystem.

Model analyses using new experimental results

Models can be used to evaluate the long-term implications for ecosystems using data derived from shorter term experiments. This section presents results from model simulations undertaken to evaluate the potential consequences of two unanticipated and tentative observations from recent experiments: (i) the reduction in stomatal conductance found in herbaceous systems at elevated CO_2 may not occur for forests, and (ii) the increase in C : N observed in CO_2-fertilized live plant tissue is often not seen in litter. Both observations are contrary to early results and expectations; however, they are the basis for formulations for all current models.

The effects of these two changes were simulated by modifying two existing ecosystem models, CENTURY (Parton *et al.*, 1993 and users manual reference) and G'DAY (Comins & McMurtrie, 1993; McMurtrie & Comins, 1996), applied to a wet Norway spruce boreal forest at Flakaliden, Sweden (Linder, 1995) and a dry *Pinus radiata* forest (Biology of Forest Growth – BFG) near Canberra, Australia (Benson *et al.*, 1992). CENTURY was also applied to the Jasper Ridge annual grassland system in California (Field *et al.*, 1996). These sites were chosen to demonstrate the impact of elevated CO_2 in contrasting ecosystem types. The two models were run to equilibrium conditions using the same observed weather data and then changes in atmospheric CO_2 were imposed (350 to 700 ppm CO_2).

The new understanding was simulated by comparing computer runs where the standard assumptions were used (reduced stomatal conductance and decreased N content of leaf litter) against runs with the new assumptions (no reduction in stomatal conductance for mature trees and no reduction in N concentration in leaf litter). It was assumed that stomatal conductance would be reduced at high CO_2 for grassland, and that the N concentration in leaf litter would be kept approximately constant by reducing internal recycling of N prior to leaf senescence (the fraction of N retranslocated at senescence was reduced from 50% to 40%). In the text these simulations are referred to as STANDARD (old assumptions) and NEW (new assumptions) runs.

Figure 7.4 demonstrates the simulated impact of doubling atmospheric CO_2 on annual net primary production (NPP) at the three sites using the CENTURY

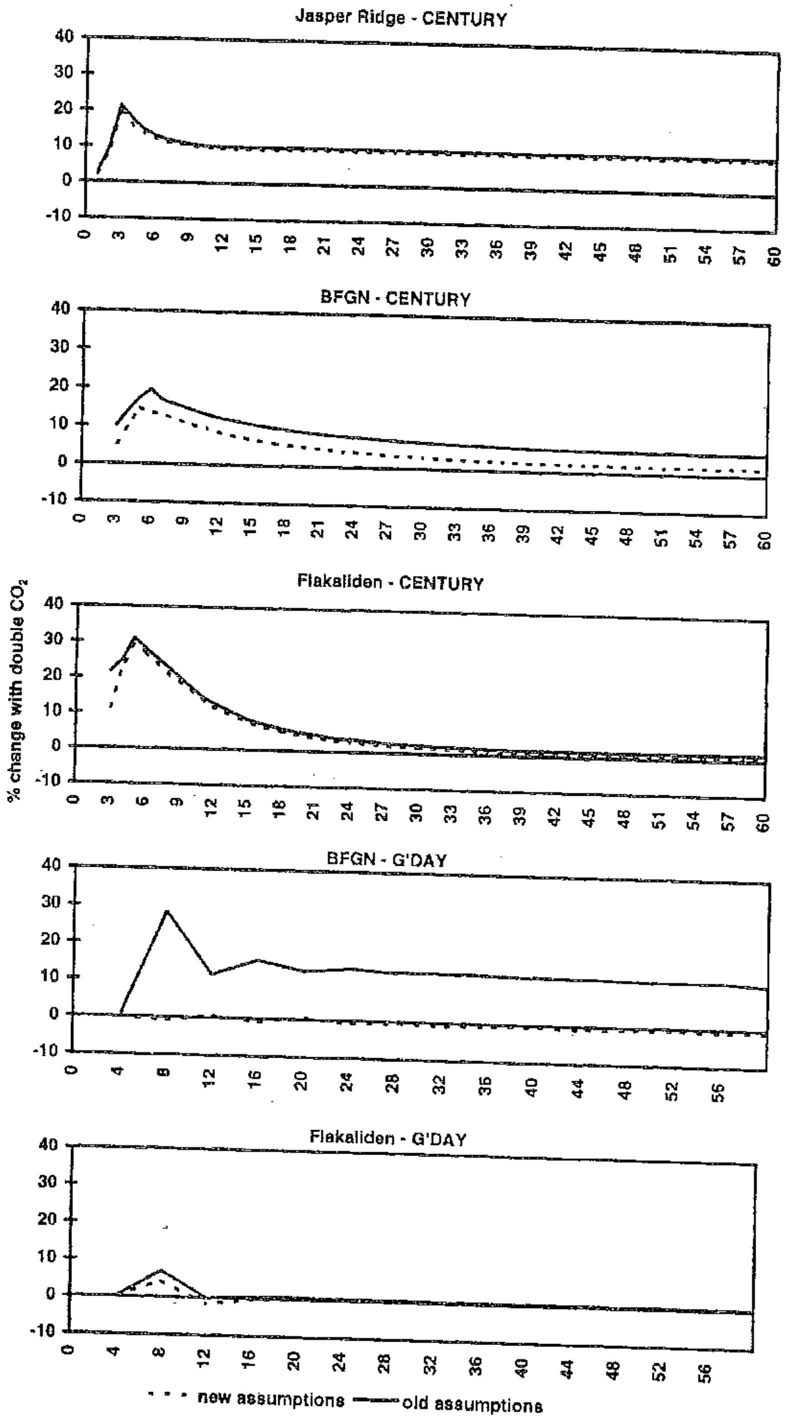


Figure 7.4 The simulated impact of doubling atmospheric CO_2 on annual net primary production (NPP) at Jasper Ridge (USA), Flakaliden (Sweden), and Biology of Forest Growth (BFG – Australia) sites using the CENTURY and G'DAY models (G'DAY was not run for the Jasper Ridge site).

and G'DAY models (G'DAY was not run for the Jasper Ridge site). The results show that following a doubling of CO_2, there is a rapid initial increase in NPP at all sites (+ 5 to 30%) and that this increase is reduced by half or more after 10 years at high CO_2. Comparison of the results for the STANDARD and the NEW CO_2 assumptions shows that the positive response to increased CO_2 is reduced under the NEW CO_2 assumptions and that both models show that this reduction is largest at the BFG site. At the wet Flakaliden site and at the Jasper Ridge site, growth under the NEW assumptions is entirely due to reduced internal N cycling. For both sites there is little difference between simulated NPP under the STANDARD and NEW assumptions, suggesting that altering the N content of dead leaves has little effect on NPP. The difference between the STANDARD and NEW runs would have been more pronounced, however, if we had made the further assumption that changes in litter C : N ratio lead to correlated changes in soil C : N ratio (McMurtrie & Comins, 1996). The need for models to correctly represent C–water interactions is highlighted by the sensitivity of modelled NPP to assumptions about the dependence of stomatal conductance on CO_2.

Figure 7.5 shows the effect of changing the CO_2 assumptions on the average change in annual net N mineralization and soil C levels for the 10 to 20 year period following the doubling of CO_2 levels. The results show that under the STANDARD assumptions there is generally (the only exception is CENTURY result for BFG) a decrease in net N mineralization at high CO_2, because the N content of high CO_2 litter is reduced, leading to enhanced N immobilization during litter decomposition. Under the NEW assumptions litter N concentrations are higher than under the STANDARD assumptions, so that N immobilization is reduced and N mineralization is enhanced relative to the STANDARD assumptions. Under high CO_2 levels there is generally an increase in soil C levels. Using the NEW assumptions results in slightly lower increases in soil C levels, because litter quality is higher, leading to faster turnover of soil C. Thus, both models show that using the NEW direct CO_2 assumptions results in reduced plant responses to doubling atmospheric CO_2 levels with a decrease in the positive effect of CO_2 on plant production and soil C storage.

7.2.6 Progress in predicting elevated CO_2 responses – a lesson from ecosystem physiology

Simple extrapolation from physiological information to ecosystem and global responses would lead to inaccurate predictions about the biotic world under elevated CO_2. This is because such extrapolations do not account for process interactions and feedbacks.

GCTE started with the basic information that there are two primary plant

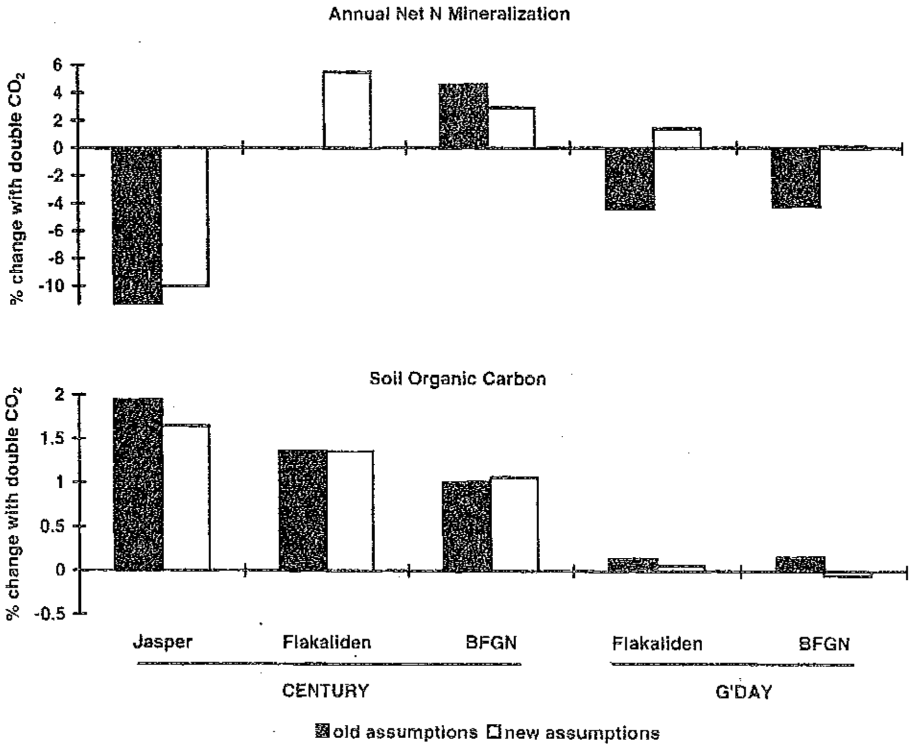


Figure 7.5 Effect of changing the CO_2 assumptions on average change in annual net N mineralization and soil C levels for the 10–20 year period following the doubling of CO_2 levels using the CENTURY and G'DAY models.

responses to elevated CO_2. One type of plant, C_3 plants, would respond positively, and rather strongly, to CO_2, and the other type, C_4 plants, would show little or no stimulation. It was also known that both types of plants would save water under elevated CO_2 and that the tissue produced would be lower in nitrogen and richer in carbon. This information was used to make the following predictions:

- C_4 plants would show limited enhancement under elevated CO_2.
- The enhancement effect would be fairly constant within a photosynthetic type.
- Systems from water-limited environments would show a relatively larger response than systems in other environments.
- Herbivores eating plant tissue from high CO_2 grown plants would have to compensate for the poor quality tissue by eating more (see Chapter 9).
- Decomposition of plant tissue would be slower under high CO_2, resulting in immobilization of nutrients in the litter pool.

What we learned is that:

(i) The projected enhancement of growth by CO_2 predicted from physiological measurements was often not realized. Although increased leaf-level photosynthesis was on average 40% higher under elevated CO_2, aboveground biomass accumulation was only 14% higher (average for nine herbaceous systems). This important finding indicates that whole-plant and ecosystem-level feedbacks were constraining production.

(ii) In systems under high CO_2, C_4 plants actually did comparatively well. This is due in part to the fact that water limitations, which were alleviated under high CO_2, were more important than the direct CO_2 effects in determining competitive outcomes.

(iii) Within C_3 plants there are very different growth responses among species, not necessarily related to conventional functional types, again indicating potential feedbacks on ecosystem processes by changes in community structure. Thus, elevated CO_2 is also a biodiversity issue.

(iv) The predicted increased water savings are observed. In some systems the changing water balance was manifested in a shift in species composition and in others by an increase in canopy development. For water limited systems, the hydrological consequences of elevated CO_2 were often more profound than the direct CO_2-fertilisation effect. Significant increases in soil activity were a consequence of the improved water status.

(v) Most insects appear to show compensatory increased tissue consumption under elevated CO_2. But when given a food choice, net consumption may not change (Arnone *et al.*, 1995). Grazing mammals showed no such compensation, and consequently weight loss occurred (Owensby *et al.*, 1996*b*) (see Chapter 9).

(vi) High CO_2-grown leaf tissues, when naturally senesced, do not often decompose more slowly as hypothesized. The basis for this finding is in part because litter C : N ratio does not always change, as predicted.

7.3 Effects of temperature increase on terrestrial ecosystems

An increased mean global surface air temperature of 1.5 – 4.5 °C is expected to occur within the next century as a consequence of increased atmospheric CO_2 and other greenhouse gases (Houghton *et al.*, 1996). Global warming will affect ecosystem structure and function in many ways, but of special concern are those changes that may result in feedback on the climate system. For example, increased temperature could increase CO_2 efflux from terrestrial ecosystems to the atmosphere, if increased soil organic matter (SOM) decomposition and respiration (efflux that increases exponentially with temperature) is higher than the increased photosynthesis and NPP (a linear to saturating response with temperature; Townsend & Vitousek, 1995; see also Chapter 10). Such an imbalance could further increase atmospheric CO_2 and so act as a positive feedback to global warming.

Much attention has been placed on high latitude ecosystems since General Circulation Models (GCMs) predict the greatest warming in the boreal and tundra regions of the world. Montane systems have also received attention because of their sensitivity to snow cover and soil temperature. Temperature effects in tropical systems could also be important because high rates of respiration result in large quantitative changes in CO_2 efflux in response to small temperatures changes. Therefore, even the small predicted temperature warming in the equatorial regions could release carbon to the atmosphere (Townsend *et al.*, 1992).

7.3.1 Response of high latitude ecosystems to global warming

Although warming will be most pronounced at the poles, Arctic organisms are so well adapted to low temperature and intra-seasonal temperature variations that temperature *per se* does not strongly affect most Arctic processes (Chapin, 1983). For example, photosynthesis, nutrient uptake, and plant growth have broad temperature optima with little difference in rate between 10 and 20 °C (Oberbauer & Oechel, 1989). In laboratory incubations, nitrogen mineralization is unaffected by temperature below a threshold of about 8 °C; above this, mineralization rate increases dramatically (Kielland,1990; Nadelhoffer *et al.*, 1991). Similarly, a 3 °C increase in air temperature in field greenhouses had little effect on plant growth, soil nutrient availability, or species composition over a two- to four year-period in the low and mid Arctic (Chapin & Shaver, 1985, 1996; Havström *et al.*, 1993; Wookey *et al.*, 1993). However, in a high latitude polar desert site, plant growth and reproduction were highly sensitive to small temperature increases above ambient. Of 19 alpine and lowland plant species studied in Switzerland, acclimation to warmer temperatures ranged from full to no acclimation, with complete acclimation occurring in three species (Larigauderie & Körner, 1995).

These adjustments have to be taken into account when building models of responses to climate change. Plants adjust their respiration rates to the prevailing growth temperatures. Thus, information on Q_{10}s derived from short-term measurements of respiration of plants grown at a single temperature may be very misleading when extrapolated to longer time intervals. For example, Gifford (1995) has shown for wheat that a Q_{10} of 1.3 would be more appropriate for longer term extrapolations in models than the commonly used Q_{10} of 2.0. For wild grassland plants Larigauderie & Körner (1995) found a mean 'acclimated' Q_{10} of 1.7 with some species fully acclimated ($Q_{10} = 1$).

Indirect temperature effects associated with changes in thaw depth, nutrient availability, and vegetation will cause substantial changes at high latitudes. Because each Arctic species has a different pattern of response to environment, a 3 °C increase in summer air temperature causes a change in species composition, litter quality, and nutrient availability at a decadal timescale (Chapin & Shaver, 1985; Chapin *et al.*, 1995*b*). Increased nutrient availability increases shrub abundance and decreases the abundance of mosses (an important soil insulator) (Chapin *et al.*, 1995*b*). Some of the vegetation changes observed during the past 15 years are consistent with these experimental manipulations and suggest that regional warming of permafrost, which is more pronounced than can be explained by increases in air temperature (Lachenbruch & Marshall, 1986), could reflect indirect temperature effects on vegetative insulation.

The effects of experimental warming on plant biomass and species composition in subalpine meadows were also primarily indirect (Harte & Shaw, 1995; Harte *et al.*, 1995), with changes reflecting increases in soil temperature and decreases in soil moisture. These changes in soil environment modified the competitive balance between shrubs and forbs, causing a shift toward shrub dominance of the type that normally dominates drier sites. These vegetation changes, in turn, altered shading by the plant canopy and therefore the linkage between energy inputs and soil environment.

Simulation models suggest that a 2 °C temperature increase would cause a 20% increase in thaw depth after 50 years and that warming of 6 °C or 8 °C would cause disappearance of permafrost after 38 or 27 years, respectively (Kane *et al.*, 1992). Permafrost is a critical factor causing a high water table, slow decomposition, and peat accumulation, so temperature increases of these magnitudes, which are within the 10 °C increase predicted at high latitudes with a CO_2 doubling, would cause a qualitative change in the tundra environment.

Decomposition in the Arctic is more sensitive to changes in moisture than temperature (Flanagan & Veum, 1974). Perhaps because of soil drying associated with warmer drier summers during the past decade (Maxwell, 1992), tundra appears to have changed from a net carbon sink to a system that is either a net CO_2 source to the atmosphere (Oechel *et al.*, 1993, Zimov et al., 1996) or is in approximate balance, at least during the growing season (W.C. Oechel & S.A. Zimov, personal communication). Methane flux from tundra also appears much more sensitive to water table depth than to temperature (Whalen & Reeburgh, 1992).

A warming-related increase in depth of the active layer or a change in regional water balance which causes the water table to drop below the soil surface will create a threshold decrease in methane flux to the atmosphere by increasing surface oxidation, leading to a negative feedback to climatic warming. Thus, the net effect of high latitude ecosystems on trace gas feedbacks to climate could depend on the relative magnitude of changes in CO_2 versus CH_4 flux.

Presence of trees at high latitude may be determined more by soil than by air temperature (Murray, 1980), so that expected warming of soils and increase in thaw depth could have a strong effect on treeline advance. A northward advance of treeline could allow greater long-term carbon storage in vegetation. However, the transient response of carbon storage depends on temperature–moisture stimulation of decomposition and carbon loss, which occurs instantaneously, versus a 50–150 year time lag in forest advance and carbon storage (Smith & Shugart, 1993; Starfield & Chapin, 1996; Schulze *et al.*, 1995). Thus, the short-term effects of temperature on whole-system carbon storage may differ from the long-term effects.

Warming is also expected to increase fire frequency in the boreal zone (Flannigan & Van Wagner, 1991), which directly releases CO_2 stored in peat and wood to the atmosphere and increases rates of decomposition (Kasischke *et al.*, 1995). These fire effects on boreal forests could equal or exceed the capacity of individual forest stands to store carbon, further raising questions about the net role of boreal forests as a candidate for the 'missing sink' in the global carbon budget (Ciais *et al.*, 1995).

Northward advance of the treeline in response to climatic warming could act as a positive feedback through reduction in albedo, as snow-covered tundra is replaced by darker forests (Bonan *et al.*, 1992; Thomas & Rowntree, 1992). This albedo feedback by northward-moving forests could have accounted for half of the regional temperature increase observed at high latitudes 6000 yr BP (Foley *et al.*, 1994).

The amplitude of the seasonal change of atmospheric CO_2 concentration has been increasing, with largest increases observed at high latitudes. This could reflect either a longer growing season for plant growth (Keeling *et al.*, 1996*a*), although a 10% change in length of growing season through experimental manipulation of snow cover had no detectable effect on vegetation cover or species composition (Chapin & Shaver, 1996). Alternatively, warming-induced increases in winter respiration could contribute to the increased amplitude of CO_2 at high latitudes (Zimov *et al.*, 1996).

The changes in biotic interactions that will occur with climatic warming are poorly known. A 3 °C experimental warming causes an increase in shrub abundance and a decline in species richness, particularly of insect pollinated forbs, within a decade (Chapin *et al.*, 1995*b*), as in the Colorado subalpine zone (Harte & Shaw, 1995; Harte *et al.*, 1995). These results suggest that migrating caribou, which utilize these forbs during lactation (White & Trudell, 1980), and insect pollinators (Williams & Batzli, 1982) could be adversely affected. Warmer summers also increase insect harassment of caribou with associated declines in feeding and summer energy reserves. By contrast, browsing mammals such as snowshoe hare and moose may benefit from climatic warming because of the proportional increase in shrubs in undisturbed tundra and increased fire frequency with associated increase in the proportion of early successional vegetation.

In summary, direct temperature effects on Arctic processes are subtle, except in polar desert, but indirect temperature effects mediated by changes in nutrient availability, soil moisture, seasonal length, and vegetation have caused, and will cause, changes in energy and carbon balance that are large enough to provide significant positive feedbacks to global warming. Effects of elevated CO_2 are generally small because of prevailing limitation of low temperature, short growing seasons, and nutrients. Two patterns emerge from warming experiments: (i) ecosystem response to warming is greatest in the coldest environments, and (ii) ecosystem responses to warming are less pronounced and have longer time lags than do physiological and growth responses by individual species. Winter warming is likely to be more influencial than summer warming.

7.3.2 Response of mid-latitude and tropical ecosystems to global warming

Less is known about the responses of mid-latitude ecosystems to warming. A network of soil-heating experiments has been established in several ecosystems (Peterjohn *et al.*, 1993). A hardwood forest showed a 1.6-fold increase in CO_2 emissions with soil heating and a 36% decrease in the carbon concentration of the O soil horizon (Melillo *et al.*, 1996*a*). Warming caused soil respiration to increase 40% in the first year and about 20% the following years; methane oxidation increased 20%.

No warming experiments have been conducted on natural ecosystems in the tropics (see Chapter 9 for a discussion of the effects of increasing temperature on rice productivity). Direct species-level effects in natural ecosystems are likely to be pronounced, but ecosystem-level effects are again most likely to be indirect.

7.4 Effects of changes in water availability on terrestrial ecosystems

Water loss from vegetation is an inevitable consequence of plants exchanging gases with the surrounding atmosphere. It cannot be avoided during carbon assimilation because stomatal opening allows both the inward diffusion of carbon dioxide for photosynthesis as well as the outward diffusion and loss of water from plant cells. Yet maintaining a favourable water balance within the plant is essential for metabolism and survival. The amount of water available to plants is determined by a combination of precipitation, the capacity of soils to store water, and atmospheric evaporative demand. While water is generally a limiting resource in most environments (Kramer & Boyer, 1995), too much standing water may also be damaging to plants because of the soil anoxia that typically results during flooding.

This section discusses recent advancements in ecosystem physiology that have improved understanding of water fluxes, especially in relation to other plant processes. This includes a discussion of how the partitioning of water within ecosystems is regulated by plant cover, and the resulting effects of water availability on plant performance at ecosystem levels. Much of the recent research in water and ecosystems has not dealt directly with the question of elevated CO_2, but rather has focused on (i) understanding dynamics and constraints on fluxes between the vegetation and the atmosphere, and (ii) on establishing those principal aspects of ecosystem physiology that constrain fluxes between the ecosystem and the atmosphere. Recent books and reviews on general aspects of water relations in plants that provide a broad introduction to this field include Jones, 1992; Smith & Griffiths, 1993; Schulze, 1994*a*; Kramer & Boyer, 1995; and Kozlowski & Pallardy, 1997.

7.4.1 Ecosystem water loss to the atmosphere

Plant transpiration and evaporation from the soil and vegetation surfaces constitute the transfer of water from ecosystems to the atmosphere. Both the structure and physiology of ecosystems combine to regulate this water loss (Jarvis, 1987; Sperry, 1997). Stomatal conductance describes the physiological regulation of water loss at the leaf level, determined by a variety of biological and physical processes, most of which are now well understood (Jones, 1992; Smith & Griffiths, 1993). Unfortunately, leaf-level transpiration does not directly scale up to the whole plant and ecosystem levels because of canopy-level constraints on gas exchange (Jarvis & McNaughton, 1986; Schulze *et al.*, 1996*b*). These constraints, due largely to ecosystem structure (canopy architecture), are quantified as the aerodynamic conductance, which describes the regulation of water vapour transfer from the leaf surface through the vegetation canopy to the open atmosphere above. If the aerodynamic conductance is large in relation to the potential stomatal conductance, as in meadows, the latter is limiting and transpiration is proportional to the available energy. In contrast, if aerodynamic conductance is small in relation to the potential stomatal conductance, as in forests, the former is limiting and transpiration is proportional to the leaf-to-air evaporative gradient. The magnitude of both stomatal and aerodynamic conductances is not constant, but may change seasonally, or even during the course of a day, with phenology and soil water deficit (Köstner *et al.*, 1992). The Penman–Monteith equation (Penman, 1948; Monteith & Unsworth, 1990) ties together the effects of both the ecosystem structural and leaf physiological components on ecosystem loss of water to the atmosphere, that is, aerodynamic and stomatal conductance, respectively.

While it has been possible to describe the relative effects on stomatal conductance of environmental parameters (Jarvis, 1987), there is no mechanistic model to describe the maximum transpiration performance of different plant functional types with climate. Yet such an understanding is needed to link the impacts of functional types and LAI (Leaf Area Index) with water fluxes to the atmosphere on a regional and global basis. Kelliher *et al.* (1993, 1995) made progress through analysis of a model which explored relationships between maximum surface conductance (soil surface and stomatal conductance together) and aerodynamic conductance in relation to LAI. Canopy conductance is expected to increase with LAI under conditions of both high and low stomatal conductances, but only at low to moderate LAI values. The relationship is predicted to become less sensitive at LAI values above four and maximum canopy conductance is expected to be achieved by an LAI of six. In contrast, the surface conductance shows a compensatory behaviour associated with soil evaporation (assuming the soil is wet), which is high with sparse vegetation and decreases with increasing LAI values. The Kellier *et al.* model leads to some interesting predictions that have ramifications for global models. For instance, in ecosystems whose plants have low stomatal conductances, a wet soil without plant cover will have a higher conductance than a vegetated surface. The measured values of maximum canopy conductance from very different ecosystems fall well within the limits of the predictions of this model, indicating that these results provide a framework for integrating ecosystem physiology with global model predictions.

From the Kelliher *et al.* (1995) analysis, it is clear that there is expected to be a linear relationship between maximum leaf conductance and surface conductance, which would not have been predicted by the Penman–Monteith equation. There is a feedback between stomatal response and plant structure in such a way that if the aerodynamic conductance is high (equilibrium transpiration driven by radiation), plants have high leaf conductance values (e.g. herbaceous species, crop plants). In contrast, if the aerodynamic conductance is low (imposed transpiration driven by the vapour pressure deficit), then the existing plant functional types have low leaf conductances. Both plant functional types may exhibit the same LAI.

Other factors, such as as the nitrogen content of the vegetation, can also affect evapotranspiration. For example, while leaf conductance values are related to leaf structure (Schulze *et al.*, 1994*b*), there appears to be no functional way of relating leaf structure or leaf conductance to plant nutrition other than via classification of plant functional types. CO_2 assimilation is the common link between stomatal conductance and nutritional aspects of leaf physiology (Marschner, 1995). Schulze *et al.* (1994*b*) showed that for different life forms there are linear relationships between maximum leaf conductance and leaf nitrogen content as well as between leaf surface conductance and the maximum capacity for CO_2 assimilation. A global analysis of these patterns indicates that the greatest potential for CO_2 assimilation is located in industrial regions, where fertilizer loads in combination with elevated dry deposition rates overlap with highly productive agricultural plants.

7.4.2 The regulation of water loss by plants within ecosystems

Actual rates of gas exchange and of leaf conductance are typically lower than the maximal values shown by Schulze *et al.* (1994*b*) because of constraints imposed by light, temperature, humidity, and soil water deficit. Several model approaches have allowed for quantifying the extent to which different parameters limit actual gas exchange rates (Running & Hunt, 1993; Sellers *et al.*, 1997). On average, the ratio of actual to maximum photosynthetic rate is between 40 and 60%.

Recent observations suggest that mechanisms for both feedforward and feedback response exist to limit leaf conductance and that both biophysical and hormonal signals may be involved in this regulation (Schulze, 1994*a*). An important constraint on stomatal regulation of water loss from plants appears to be the avoidance of xylem cavitation, which may irreversibly affect the capacity of roots to supply water to the shoots (Tyree & Sperry, 1989; Meinzer, 1993; Sperry, 1997). Recent analyses indicate that plant species differ in their xylem cavitation characteristics and that variations in this physiological characteristic are closely tied to plant distribution (Langan *et al.*, 1997; Pockman & Sperry, 1997; Sperry, 1997).

7.4.3 The capacity of plants within an ecosystem to exploit soil water

A better appreciation of rooting distributions is critical to an understanding of the carbon and water flux aspects of ecosystem function. Variations in rooting patterns within and among ecosystems determine not only the extent of the exploitable soil profile, but also the extent to which deep soil reserves buffer metabolic activities on both interseasonal and interannual bases. Canadell *et al.* (1996*a*) and Jackson *et al.* (1996*a*,*b*) have recently synthesized some of the critical global patterns. Jackson *et al.* (1996*a*) found that there is a shift in rooting distribution patterns towards deeper layers in arid systems. At the same time, Canadell *et al.* (1996*a*) demonstrated a remarkable relation between vegetation type and maximum rooting depth which closely paralleled rooting density behaviour. Both of these studies indicate that global models have historically underestimated the exploitation of soils by roots, especially the capacity of roots to exploit deeper soil layers. The incorporation of appropriate rooting-pattern information into the latest generation of Soil–Vegetation–Atmosphere Transfer Models (SVAT) and other biosphere–atmosphere models is now leading to more realistic simulation of the feedbacks from the land surface back to the atmosphere (Kleidon & Heimann, 1998).

Complementing the ecosystem-level studies showing variations in rooting behaviour is the observation of soil-depth partitioning by different functional types within an ecosystem (Sala *et al.*, 1989; Ehleringer *et al.*, 1991; Dawson, 1993*a*). However, it is important to note that seasonal partitioning of root activities in arid land ecosystems can result in functional differences that are not consistent with simple observations of rooting depth patterns. Variations in the amounts and predictability of precipitation inputs as well as in the frequency of extended drought periods during the growing season have led to differences in the extent to which functional types use and rely on surface versus deep roots (Dawson 1993*a*,*b*; Lin *et al.*, 1996). At this point, it is unclear whether classification of functional types with respect to water use overlaps fully with classification of functional types with respect to nutrient extraction from the soil.

7.5 Effects of altered nitrogen deposition on terrestrial ecosystems

No other elemental cycle has been changed by man as much as the global nitrogen cycle (Mohr & Muentz, 1994; Jordan & Weller, 1996: see also Chapter 1) (Fig. 7.6). It has been altered by (i) land-use changes and the introduction of N-demanding species, (ii) fertilizer addition, (iii) cultivation of N_2-fixing species, and (iv) air pollution leading to nitrogen deposition. The total amount of nitrogen being added by man annually already exceeds the amount assimilated naturally. Current values of N deposition are between 0.5 to 2.5 g N m^{-2} $year^{-1}$ in eastern North America and 0.5 to 6.0 g N m^{-2} $year^{-1}$ in northern Europe (Vitousek, 1994).

Nitrogen has a leaky cycle with feedbacks to the soil through nitrate losses to ground water, and to the atmosphere through denitrification. This latter may not only produce N_2 as the ultimate product, but also greenhouse gases such as NO and N_2O depending on soil chemistry. The greatest anthropogenic effect on the N-cycle was originally via harvest, although more recently N deposition has had a greater impact.

The following section focuses on three aspects of the nitrogen cycle: (i) the effect of N deposition on growth, (ii) its interaction with the carbon and other element fluxes, and (iii) its effects on soil properties, especially soil acidification.

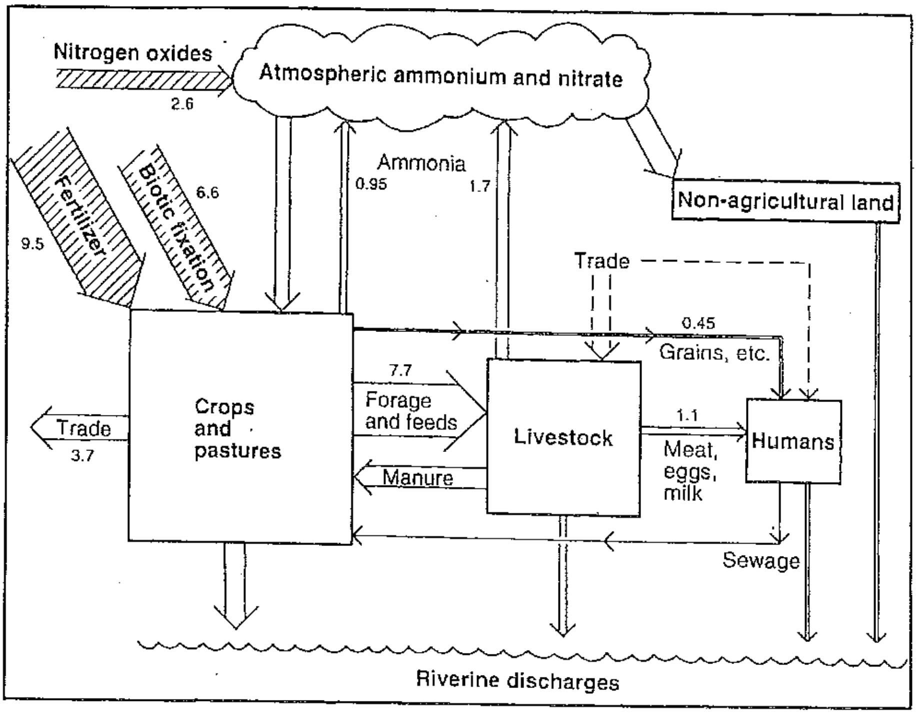


Figure 7.6 Major anthropogenic flows of nitrogen. Shaded arrows show inputs of newly fixed nitrogen through fertilizer application, biotic nitrogen fixation in agricultural lands, and production of nitrogen oxides that are converted to nitrate and deposited from the atmosphere. Unshaded arrows show other anthropogenic fluxes of nitrogen, including atmospheric deposition of ammonium and nitrate, emission of ammonia into the atmosphere, flows through the agricultural food chain, return of nitrogen to crops and pastures in animal wastes, and discharges of nitrogen in rivers. The widths of the arrows are proportional to the sizes of the flows for the entire coterminous United States. The numbers near arrows are our calculated estimates of flows (Tg N y^{-1}). Dashed arrows show potential imports of nitrogen via trade in agricultural products, which are major sources of nitrogen in many regions, although the coterminous United States is a net exporter of nitrogen in agricultural products (from Jordan & Weller, 1996)

The effects of land-use change and of cultivation of legumes on the global N-cycle are discussed further in Chapter 10.

7.5.1 N availability and N deposition on growth

While effects of fertilizers on crop productivity are well documented (Marschner, 1995), it is less clear whether anthropogenic atmospheric N deposition enhances growth under otherwise undisturbed conditions. The effect of N deposition on growth can be demonstrated in forest stands and their tree

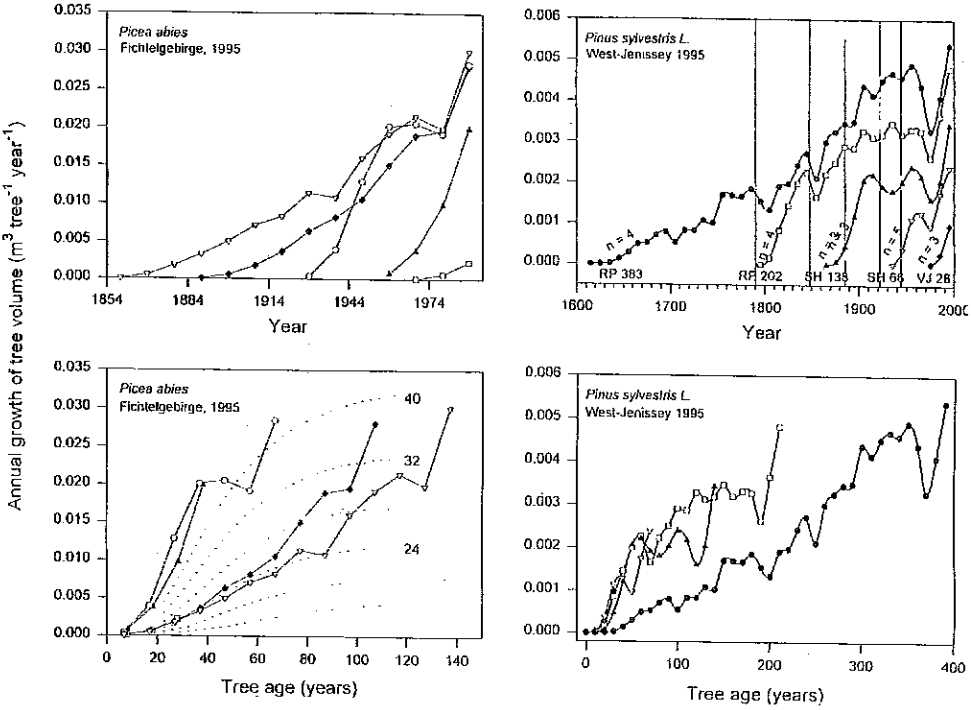


Figure 7.7 Growth of a chronosequence of *Picea abies* stands in Germany and of *Pinus sylvestris* in Siberia. The growth curves are either scaled along real time, or they are compared with respect to age.

ring chronology in Europe (Fig. 7.7; Mund, 1996). The growth rate of young stands was much slower one hundred years ago than in 1996. In addition, the growth rate of old stands has increased at a time when one would expect an age-related decrease in whole stand production; with N deposition the old stand reaches growth rates that are equivalent to those of young stands. A comparison of growth rates with forest inventory yield tables (Assmann & Franz, 1963) indicates that the young stands grow presently at a higher yield class than the old stands did at the time of their establishment, and that the old stands have changed yield classes and presently approach the same yield class as young stands. Similar observations were made with deciduous species (Franz *et al.*, 1993).

This growth response of trees under conditions of N deposition may include some component of response to elevated atmospheric CO_2. Comparable information was therefore collected for a chronosequence of *Pinus sylvestris* stands in Siberia (west Yennesei region), growing far from any source of air pollution (Fig. 7.7). No accelerated growth can be observed in young stands of *Pinus* as compared to old stands at the time of their establishment, and the growth response of old trees reaches a plateau which is interrupted only by N mobilization due to periodic fires. This suggests that elevated CO_2 had no effect in the absence of N deposition. In contrast, the European stands showed a distinct response to N availability. The possibility cannot be excluded that elevated CO_2 has enhanced this effect, but the change in growth rate is consistent with the history of N deposition rather than with the history of CO_2 rise. It is important to note that the increased NPP in forests under conditions of N deposition does not always result in elevated NEP because of the interaction with disturbance regimes (Schulze & Heimann, 1997).

Melillo *et al.* (1996*b*) argued that the effect of soil warming would result in increased wood growth because the C:N ratio in humus is lower than in wood by a factor of three to five. Therefore each mole of nitrogen from decomposed humus could result in three to five moles of carbon immobilization during wood growth. Bauer *et al.* (1997) demonstrated for European forest trees that wood growth is the dominant sink for N and C in trees. Needle N-concentrations were constant along a European transect although wood growth changed with N-deposition.

7.5.2 N deposition on other element cycles and forest decline

Ingestad & Ågren (1988) demonstrated in laboratory experiments that the growth response to N addition reached a distinct maximum if other elements became limiting. There are numerous cations which can be close to deficiency levels. For instance, magnesium concentrations are often low in silicate soils; iron and potassium are low in calcareous soils; and manganese is low in dolomitic soils. With increasing N deposition, these elements reach a level which results in visible colour changes in foliage, as is shown in European maps of forest decline in which needle yellowing is a predominant feature. The symptom is enhanced by canopy uptake of nitrogenous gases (NH_3 and NO_x), which is not balanced by cation uptake by roots (Schulze, 1995*b*).

Young needles are the dominant sink for magnesium in conifers. During the period of needle growth the old needles of the same branch supply the required magnesium (Lange *et al.*, 1989). Uptake from roots under these conditions is still low due to low soil temperatures. If growth of young needles is inhibited (by pruning of buds on alternative twigs of the same branch), then those old needles that supply new growth turn yellow, while those that do not supply new needles remain green. It has been shown that this response is related to N availability (Oren *et al.*, 1988), because it directly affects the amount of new needle growth (Bauer *et al.*, 1997).

Needle discolouration is only one symptom of forest decline; the symptoms of needle loss and interactions with pests and parasites are geographically more extensive. There is presently no general theory for needle loss, which may be caused by drought on acid soils where root growth is restricted to the topsoil. It may also depend on ozone episodes (Sandermann *et al.*, 1997), or be related to acid mist. It is also possible that old needles in conifers serve as a resource store that is no longer needed under conditions of increased N deposition. The interactions are certainly more complicated than in the case of needle yellowing.

Less clear is the interaction of N deposition with pests and diseases. The forest inventories show an increased abundance of insect outbreaks, mildews and other fungal diseases. It remains unclear if these pests are directly stimulated by N deposition or an indirect consequence of a weakened system.

7.5.3 Nitrogen deposition on soils

Even with maximum growth rates, spruce forests immobilize only about 10% of the total amount of deposited N in wood (Schulze & Ulrich, 1991). The rest is denitrified although N_2 is not always the end product. Sometimes N is incorporated into humus (depending on conditions), or leached to ground water. The latter results in soil acidification, a nonreversible change where the transport of strong acids is balanced by an equimolar transport of cations. Critical loads of acid rain deposition (nitrogen and sulfur compounds) are defined by the capacity of soils to regenerate cations.

The processes of soil acidification are much faster than previously thought, and large areas of forest, agriculture, and natural vegetation are affected (Hildebrandt, 1994). The overall effect of N deposition and soil acidification is an accelerated release of nitrate to ground waters (Durka *et al.*, 1994). About 30% of the atmospheric N deposition may reach ground water in acid soils without interfering with soil biology. Since nitrification seems to be inhibited in acid soils, nitrate is formed from dissolved organic C and dissolved organic N by microbial activity in deep soil layers where base cations are again available but are beyond the reach of roots.

Although soil acidification has been associated primarily with acid rain, this is not the only pathway by which soils may acidify. On poorly buffered soils tree harvesting may have a similar effect as acid rain. Similarly, soil acidification has become a major problem in agriculture. Rice cultivation acidifies soil, while the growth of legumes (e.g. *Lupins* sp.) increases the availability of organic nitrogen in soils but at the same time induces soil acidification due to H^+ excretion. Under natural conditions, nitrogen-fixing species occupy a niche in succession on mineral soils where they increase weathering and soil formation (Marschner, 1995).

The effects of soil acidification on whole watershed function have been reported to last many years after acid inputs stop, and have been suggested to be the cause of decreased biomass accumulation in the Hubbard Brook Experimental Forest in the USA (Likens *et al.*, 1996).

7.5.4 N deposition on species composition

In addition to changes in the physiological performance of ecosystems, N loading may eventually lead to changes in plant species composition (Jefferies & Maron, 1997). Ellenberg (1986) scaled the mid-European flora along an indicator value of nitrogen availability. He showed that a large fraction of endangered species grow in habitats which are N-deficient, suggesting that increasing eutrophication from atmospheric deposition may endanger species biodiversity in the long term. Results from 12 years of experimental N addition in grasslands of Minnesota (USA) showed changes in plant species composition, decreased species diversity, and increased aboveground productivity (Tilman, 1987; Inouye & Tilman, 1988). The major change in species composition was the shift from C_4 to C_3 grasses, which brought a decrease in the plant tissue C : N.

7.6 Effects of UV-B increase on terrestrial ecosystems

The depletion of stratospheric ozone as a consequence of increased anthropogenically produced chlorine species has long been recognized (Molina & Rowland, 1974). Because stratospheric ozone is the main attenuator of solar UV-B radiation (280–320 nm), UV-B levels are expected to increase at the Earth's surface. This is of concern because irradiation with sufficiently large UV-B doses can inhibit the Photosystem II function, damage DNA, produce free radicals and lead to photomorphogenetic changes (see Caldwell & Flint, 1994 for a review).

In contrast to mid and low latitude regions, plants at high latitudes have historically been exposed to relatively low UV-B levels. They are therefore expected to be especially sensitive to increasing UV-B and are subject to the greatest relative increases. In the past few years ozone reduction at temperate latitudes has been much higher than previously predicted (Gleason *et al.*, 1993).

Caldwell *et al.* (1989) proposed several mechanisms by which ecosystems might respond to increasing UV-B (Fig. 7.8). It was considered that many of the impacts of UV-B would be indirect although there would also be direct effects on photosynthesis, which would decrease. Some of the indirect effects were proposed to operate through alteration of biosynthetic pathways that would alter tissue quality, making it more resistant to herbivores and decomposers.

There are few experimental data to support Caldwell's hypotheses on the UV-B effects on whole ecosystem processes, and even less data from studies conducted under realistic field conditions. Nevertheless, some field studies have shown decreased leaf-level photosynthesis and plant growth at elevated UV-B (Sullivan & Teramura, 1992; but see Teramura, 1983). For instance, *Pinus taeda* seedlings exposed to elevated UV-B radiation showed a significant growth

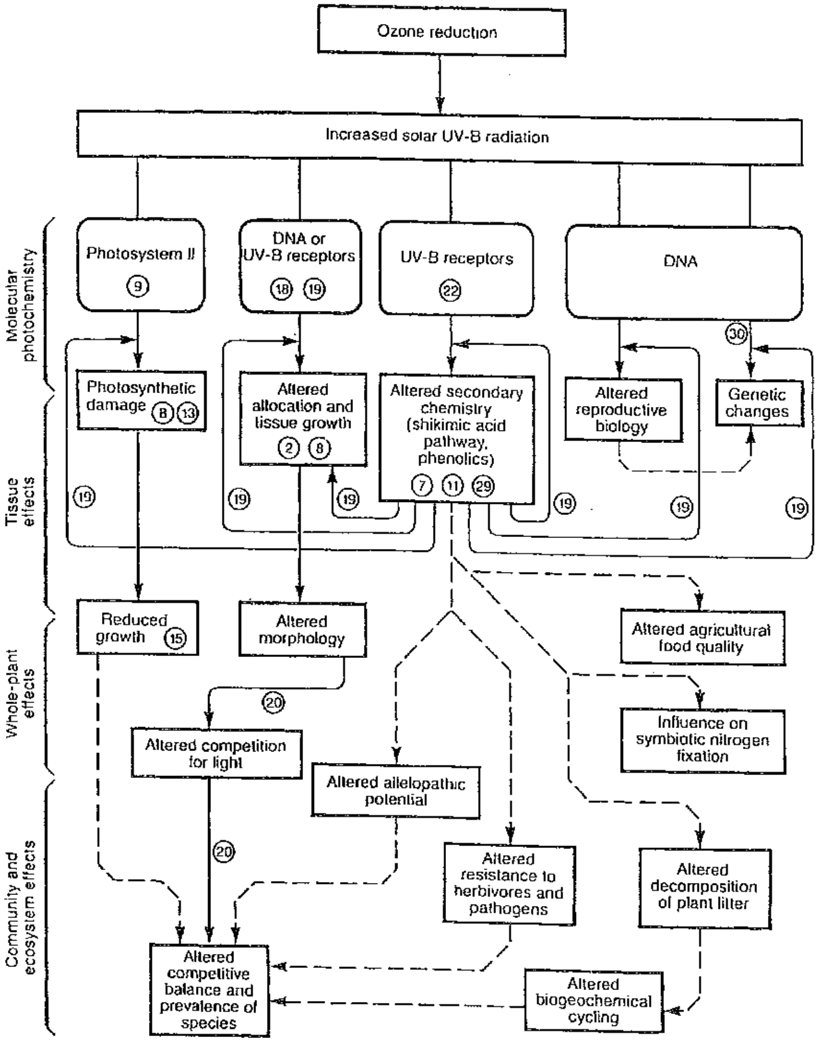


Figure 7.8 Potential consequences of ozone column decrease and corresponding increase in solar UV-B radiation for higher plants at different levels of integration from molecular photochemistry to ecosystems. Putative photoreceptors of solar UV-B that are sufficiently specific to this part of the solar spectrum and that have the appropriate absorption characteristics to result in an appreciable RAF are shown in the round-cornered boxes. These mediate physiological and genetic changes as indicated. The potential implications of these physiological changes for whole-plant function and interactions with other organisms and ecosystem components are also indicated. Solid lines indicate interactions for which there is experimental evidence and the numbers indicate specific references for this information. The dashed lines indicate interactions for which there is as yet no direct experimental evidence. Feedback loops indicate that the flavonoids and phenolics that may be induced by increased UV-B can serve as filtering agents, reducing the flux received by the photoreceptors and, thus, sometimes reducing the response to increased UV-B (from Caldwell *et al.*, 1989).

decrease for only two of seven seed provenances after one year of exposure; however, all groups showed a growth reduction between 12% and 20% after three years of increased UV-B radiation (Sullivan & Teramura, 1992). These results suggest that the effects of increased UV-B are of a cumulative nature and may become very large over the life span of perennial plants such as trees. In addition, the effects of UV-B have been shown to be nonlinear for subarctic grasses; while the equivalent of 15% ozone reduction had a negative effect on growth, 25% ozone reduction had no effect on total plant growth (Gwynn-Jones *et al.*, 1996). It was suggested that UV-B did have a negative effect but increased tillering compensated for the damage within tillering.

Another key process at the ecosystem level is the decomposition of organic matter, which controls nutrient return to soil for microbial and plant growth. Gehrke *et al.* (1995) showed that enhanced UV-B during growth caused a decrease in alpha-cellulose and an increase in tannins in *Vaccinium* sp. leaves after one growing season of exposure. UV-B during litter decomposition decreased the proportion of lignin in the plant residues, decreased colonization by fungal decomposers and decreased total microbial respiration. Since both the *Vaccinium* shrubs under study were deciduous, the effects of UV-B on litter quality and decomposition were obvious within the life span of a leaf.

Species have different responses to elevated UV-B which are not necessarily related to different sensitivity to UV-B radiation but to the growth and allocation response. Some changes in herbivores and detritivores have also been observed as a consequence of changes in the chemical and physical properties of plants (Orth *et al.*, 1990). Caldwell & Flint (1994) therefore suggested that in the long term, elevated UV-B would be most important in altering ecosystem function through changes in species composition.

As the effects of the Montreal Protocol begin to be seen, however, the maximum stratospheric ozone depletion is expected to occur in the next several years, with stratospheric ozone concentrations projected to recover over the next half century (Madronich *et al.*, 1995).

7.7 Effects of tropospheric ozone increase on terrestrial ecosystems

Tropospheric ozone concentrations are currently increasing at a rate of 0.25 ppb yr^{-1} and increasing temperatures, due to climate warming, may exacerbate this trend (Taylor *et al.*, 1994) (Fig. 7.9). Ozone concentrations have tripled in this century and are expected to increase by another 30–40% in the next three decades. Ozone has a direct negative effect on photosynthetic capacity, even at current ambient concentrations (Reich & Amundson, 1985),

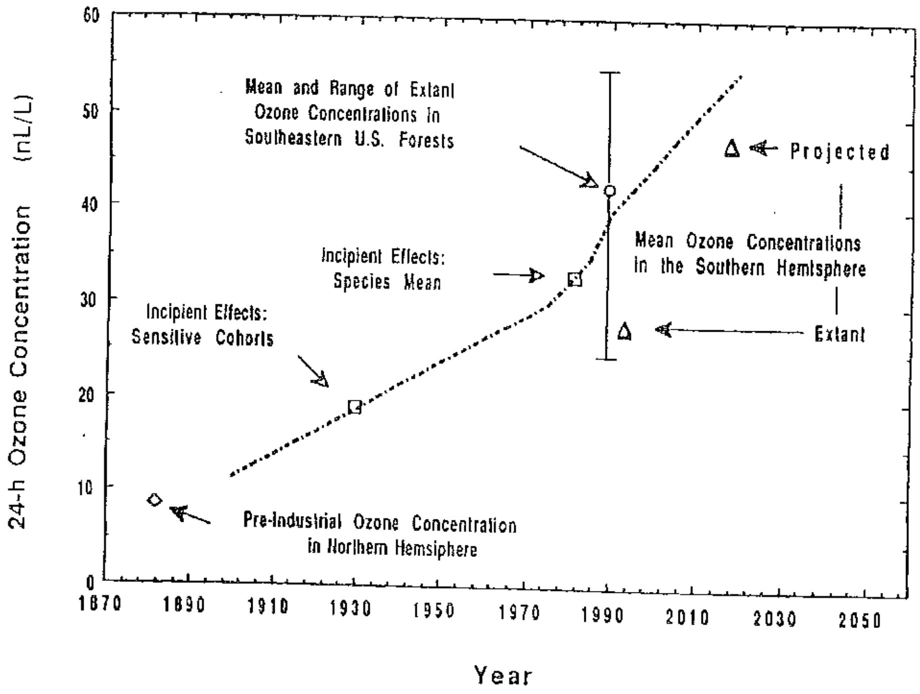


Figure 7.9 Estimate of the long-term changes in tropospheric O_3 in North America, based on extant data for forested landscapes and estimates of the rates of change in tropospheric O_3 in the last century of 0.25 nL L^{-1} yr^{-1} and over the next several decades of 0.5 nL L^{-1} y^{-1} (NAS, 1992). The error bar for the latter part of the 1980 decade indicates the mean and range of 24-h mean concentrations observed in 10 forest landscapes in North America (Taylor *et al.*, 1992) and the corresponding mean (extant and projected in the year 2020) for the Southern Hemisphere (△). The inferred preindustrial O_3 concentration (◇) in the Northern Hemisphere is from Alfonssi *et al.* (1991). The two boxes (□) indicate the O_3 exposure that results in incipient growth effects on seedlings of *Pinus taeda* (loblolly pine); the upper box represents the species' mean, whereas the lower box represents solely the mean of the sensitive cohorts (Taylor, 1994).

the amount of damage being related to the quantity of pollutant that enters a leaf which, in turn, is determined by leaf stomatal conductance. Reduced crop yields due to ozone have been noted throughout the US (Heck *et al.*, 1988). In the longer term, photosynthetic capacity may recover to original levels due to reallocation patterns within the plant.

As is common with other pollutants, ozone has many secondary metabolic effects. Stomatal conductance is reduced in the short term upon exposure to ozone, while leaf duration is reduced in the longer term. This is in contrast to the effects of elevated CO_2, which increases leaf amount (Section 7.2.2). With both CO_2 and ozone, leaf conductance will decrease (Taylor *et al.*, 1994). It has therefore been postulated that increasing CO_2 may, in part, protect plants from ozone damage because of reduced conductance and hence pollutant uptake. Correlations between ozone injury and stomatal conductance have been reported. Volin & Reich (1996) showed that O_3 reduced whole-plant biomass and relative growth rates for a C_3 tree and a C_4 grass, but such effects did not occur when elevated ozone treatments were combined with elevated CO_2. Equally important is the reduction of carbohydrate content induced by ozone exposure, which can be offset by photosynthesis stimulation at elevated CO_2. Thus, ozone and CO_2 responses have the potential to counteract each other.

While much work has been done on ozone effects at the leaf level, little is known about responses at the ecosystem level. A pioneering study in the San Bernadino Mountains of California with a chronic ozone exposure over 30 years showed leaf injury, decreased leaf photosynthesis rates, and premature leaf senescence in five tree species, *Pinus ponderosa* being the most sensitive (Miller *et al.*, 1982). All of the above led to a decreased carbohydrate content with a decrease in radial growth and height of the exposed trees (McBride *et al.*, 1975; Miller & Elderman, 1977). Early senescence and abscission resulted in a thick layer of accumulated pine needles which changed patterns of decomposition. The opening of the overstory and the lowered competitive capacity of the trees led to the development of an understory of shrubs and trees that were ozone tolerant. The weakened *P. ponderosa* became susceptible to root rot, predators (pine beetles) and pathogens (James *et al.*, 1980).

In a controlled field experiment, McLeod & Skeffington (1995) found that ozone had little or no impact on key ecosystem processes, as anticipated from previous growth-chamber and greenhouse experiments. Individual and interactive effects of free-air ozone and SO_2 fumigation on planted tree-stands of *Pinus sylvestris*, *Picea abies* and *Picea sitchensis* were studied in England. Although SO_2 alone, or in combination with ozone, had numerous effects on several ecosystem processes, ozone alone had no effect on growth of any species, foliar leaching or cation concentrations in throughfall, or on mycorrhizae (the latter based on fruit body counts and root harvests for morphotype analyses). In another field study with open top chambers, Boerner & Rebbeck (1995) found that for three deciduous tree species, only *Acer saccharum* showed lower specific leaf area, lower soluble carbohydrate concentrations, and higher lignin content as a result of the elevated ozone treatment; the other two species remained unaffected. However, there was no significant effect on the mass loss from litter over the first year of decay for all species, and N loss was higher only for *A. saccharum*. This species was also reported to reduce fine root growth at elevated ozone, which, in combination with the above changes, has the potential for altering the ecosystem C and N cycling (see also Sandermann *et al.*, 1997).

In summary, little is known about the effects of acute or chronic exposure of ozone at the ecosystem level. However, because species show very different ozone tolerance, it is expected that changes in ecosystem physiology will be ultimately mediated by changes in the species composition.

7.8 Modelling net ecosystem responses to multiple drivers of global change

The previous sections have discussed plant and ecosystem responses to individual global change drivers (CO_2, temperature, N-deposition, UV-B, and ozone). Little is known, however, about interactive effects of those drivers on ecosystem function (Kirschbaum, 1996). Part of the problem stems from the difficulty of carrying out multi-factorial experiments under realistic field conditions at the ecosystem level. The potential complexity of the interactions among the drivers is high, since many show nonlinear responses and nonadditive effects (Hättenschwiler & Körner, 1996; Gwynn-Jones *et al.*, 1996; Wedin & Tilman, 1996). Various modelling approaches have therefore been developed to gain new insights into the ecosystem response to multiple drivers of global change.

At present, however, there are no ecosystem physiology or biogeochemistry models that incorporate the full suite of environmental factors discussed above. One reason for this is the complexity of mechanisms that would need to be included, the tradeoffs between such complexity, and the need to apply and validate such models at the ecosystem or regional level.

The most comprehensive models can simulate many of the interacting effects of CO_2, temperature, precipitation, and nitrogen. Examples of these include the biogeochemistry models described in Table 7.3, and in Chapter 6. Such models include the effects of temperature and water on plant growth and soil properties, including decomposition, and they also incorporate mechanisms by which nitrogen supply controls plant growth both directly and indirectly through soil feedbacks (biogeochemistry models are discussed further in Chapter 10).

The CENTURY ecosystem model (Parton *et al.*, 1993 and users manual reference) and the G'DAY model (Comins & McMurtrie, 1993) were used to simulate the combined impacts of changing atmospheric CO_2 levels, increasing air temperature and N-deposition. Model outputs were compared for the Jasper Ridge annual grassland system in California (Field *et al.*, 1996), a wet Norway spruce forest site at Flakaliden, Sweden (Linder, 1995), and a dry pine forest system (BFG) in Australia (Benson *et al.*, 1992) (see Section 7.2.5 and Fig. 7.4). Ecosystem responses were evaluated for the 10 to 20 year period following the change in environmental conditions (Fig. 7.10). This modelling experiment was devised to simulate effects of doubled atmospheric CO_2 (350 to 700 ppm CO_2), increased air temperature (+ 2 °C), and atmospheric N deposition (+ 0.25 g N m^{-2} $year^{-1}$). These changes in temperature and N deposition

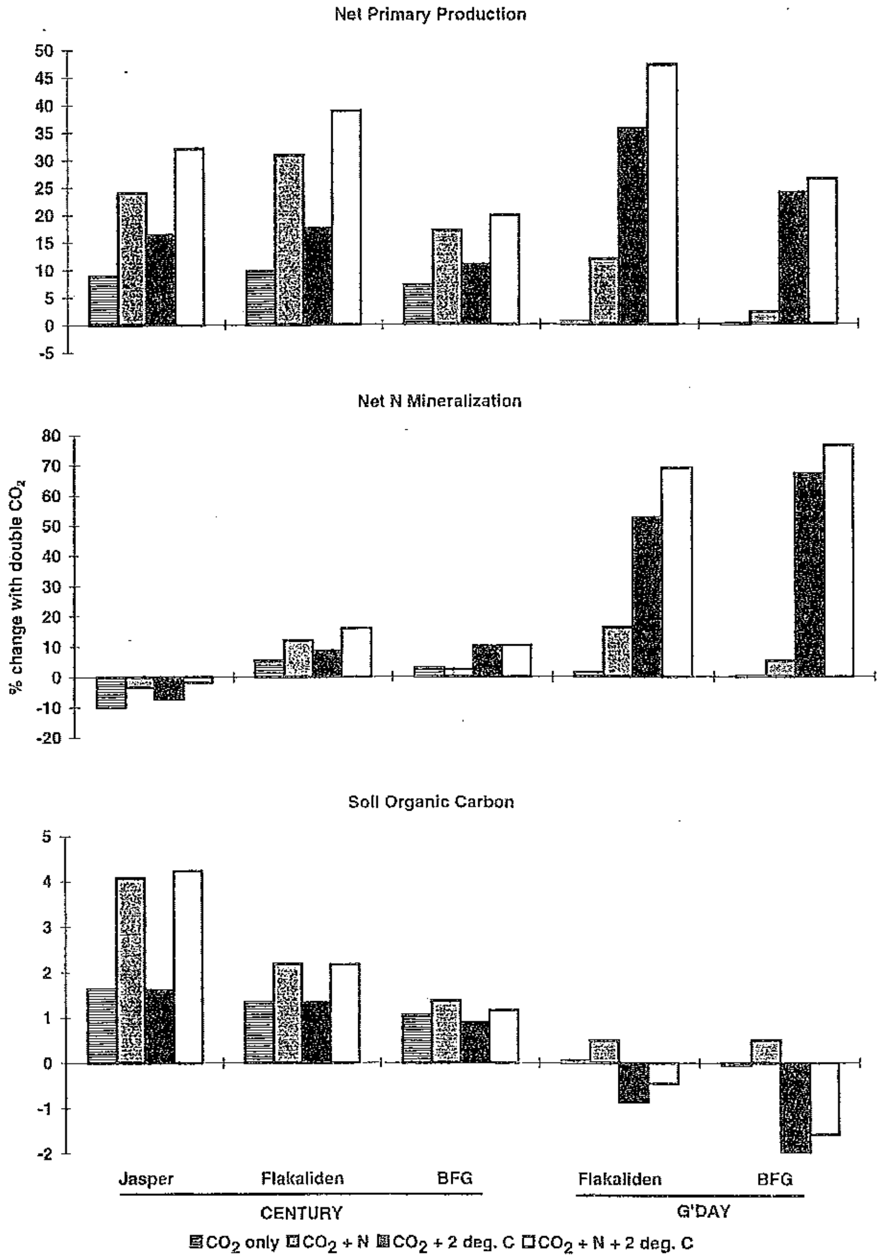


Figure 7.10 The simulated impact of doubled CO_2 (350 to 700 ppm), increased air temperature (+2 °C) and atmospheric N deposition (+0.25 g m^{-2} yr^{-1}) on net primary production, net N mineralization, and soil organic carbon on a wet Norway spruce forest site at Flakaliden, Sweden, and a dry pine forest system (BFG), Australia, using the CENTURY and G'DAY models. The CENTURY model was also run for an annual grassland at Jasper Ridge, California.

are consistent with current projections of GCMs and measured increases in N deposition in highly polluted areas, respectively. The two models were run to equilibrium using the same observed weather data before changes in environmental factors were imposed.

Comparison of the double ambient CO_2 and double CO_2 plus air temperature runs shows that increasing air temperature increases plant production and N mineralization rates for all sites, and decreases soil carbon levels. A similar comparison of the double CO_2 run with the double CO_2 plus N runs shows that adding N results in increased NPP, soil N mineralization rates and soil C storage. Although the results highlight the importance of differences in model formulation, the two models show similar trends, although the CENTURY model tends to have larger NPP responses to increased N deposition while G'DAY has larger responses to increased air temperature. Both models show that the combined effect of increased atmospheric CO_2 with higher air temperature and increased N deposition leads to increased N mineralization and NPP, while soil C storage is decreased by increasing the soil temperature. In summary, (i) increasing N, air temperature and CO_2 together have larger effects on ecosystem properties than increasing CO_2 levels alone, (ii) increasing N inputs results in increases in plant production, N mineralization and soil C storage, while (iii) increasing air temperature decreases soil C levels and increases plant production and N mineralization.

Acknowledgments

We thank Robert Scholes and Sune Linder for reviewing this chapter, Martyn Caldwell for providing information on the UV-B section, and Becky Techau for helping with the CENTURY model runs. We also thank the following people for contributing to Tables 7.1 and 7.2: Jay Arnone, Tim Ball, Peter Curtis, Bert Drake, David Ellsworth, Chris Field, Roger Gifford, Stephan Hättenschwiler, George Hendrey, Jacques Roy, Paul Jarvis, Franco Miglietta, Josef Nösberger, Paul Newton, Richard Norby, Walter Oechel, Clenton Owensby, Catherine Potvin, Jean-Francois Soussana, Boyd Strain, David Tingey, David Whitehead and Jennifer Wolfenden.