

AGROECOSYSTEMS

in a

Changing Climate



Edited by

PAUL C. D. NEWTON

R. ANDREW CARRAN

GRANT R. EDWARDS

PASCAL A. NIKLAUS



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AGROECOSYSTEMS

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Preface

This book is the 12th in the continuing CRC Series on Advances in Agroecology. While other volumes have discussed aspects of climate change, this is the first to deal directly with this topic. In this book we employ a broader definition of climate change to include changes not only in climatic factors per se (temperature and rainfall) but also in the composition of the atmosphere (carbon dioxide in particular but also ozone).

Climate change is an issue that engages many more participants than just the scientific research community. The issue is highly politicised and widely presented and discussed in a range of media and fora. It is therefore not surprising that the opinions people hold about climate change are informed by a range of material of which original scientific research might be only a small component. We are introducing this book into this lively arena because as experimental scientists our experience demonstrates to us that changes in temperature, precipitation, and atmospheric carbon dioxide have the potential to profoundly alter terrestrial ecosystems and the delivery of the services they provide. We do not have to wait for accurate projections of a future climate to make progress here. An important task is to develop our understanding of the effects of the climate change drivers and their interactions on biological systems; from this base of knowledge we will be much better placed to consider the range of future environments that may arise and the range of agroecosystems we will need to cover. Consequently, we have organised the book so that a fundamental understanding of processes is presented; we have then asked applied scientists to consider the consequences of a change in these processes for agroecosystems.

This book has taken a long while to prepare — a period sufficiently long for atmospheric CO₂ to increase by 6 ppm — but this event has allowed our authors to include the most recent findings and views and we would like to thank them for their patience and for sharing their ideas as well as their knowledge of their particular subject areas. We would like to thank the editor of the “Agroecology” series, Clive Edwards, and Taylor & Francis editor, John Sulzycki, for their invitation to prepare this book and for their advice and encouragement. Pat Roberson and Linda Manis have provided the essential publishing expertise and a number of colleagues gave up their time to referee chapters and we thank them all for these essential contributions.

**Paul C.D. Newton, R. Andrew Carran,
Grant R. Edwards, and Pascal A. Niklaus**

Editors

Paul C.D. Newton, Ph.D., is senior research scientist in the Land and Environmental Management group of AgResearch based in Palmerston North, New Zealand. After completing a diploma in communications studies at the Central London Polytechnic he worked in a number of areas including agriculture and entertainment. He then earned a degree in agricultural botany at the University College of North Wales, Bangor and subsequently earned a Ph.D. in a joint project between Bangor and the Weed Research Organisation. Dr. Newton moved to New Zealand in 1986 for a postdoctoral fellowship and has remained there, studying the effects of global change on grazed pastoral systems. His research has included locating and working at natural CO₂ springs and the construction of a Free Air Carbon Dioxide Enrichment (FACE) experiment in 1997. This experiment is continuing and his work concentrates on how the relationships between plant community structure and ecosystem function is modified by elevated atmospheric CO₂.

R. Andrew Carran, is a senior research scientist at AgResearch located in Palmerston North, New Zealand. After graduating with a M. Agric. Sci (Hons soil science) he worked at research stations of the Grasslands Division of the New Zealand Department of Scientific and Industrial Research until 1991. During this period, he researched soil processes including nitrogen fixation, acidification, and ammonia volatilisation in sheep production systems. Through 1990, he held a Visiting Researcher position at the Leopold Center for Sustainable Agriculture at Iowa State University. Since 1991 his research programme has expanded to include source sink studies of nitrous oxide and methane in soils, and the impacts of elevated CO₂ on soil processes influencing nutrient availability and loss in grazed pastures.

Grant R. Edwards, Ph.D., is a senior lecturer in Pasture Ecology in the Agriculture and Life Sciences Division, Lincoln University, New Zealand. He completed his undergraduate degree in Agriculture Science at Lincoln University, before being awarded a Rhodes Scholarship to study at Oxford University. He was awarded a DPhil from Oxford University in 1994 for his thesis titled: *The Creation and Maintenance of Spatial Heterogeneity in Grasslands: The Role of Plant-Herbivore Interactions*. Thereafter, he had two postdoctoral research positions at Imperial College, London and at AgResearch, Hamilton, New Zealand. From 2000 to 2004, he was a lecturer at Imperial College, London. In 2004 he obtained his present position at Lincoln University. His research interests include the ecology and management of temperate grasslands under a changing climate. Current research conducted by his group addresses how an understanding of livestock diet selection and plant population dynamics can be used to manipulate the botanical composition of pastures, be it for weed control or livestock production reasons.

Pascal A. Niklaus, Ph.D., is currently a senior scientist at the Institute of Plant Sciences of the Swiss Federal Institute of Technology in Zürich, Switzerland. He studied physical, inorganic, and organic chemistry at the University of Basel where he obtained his diploma in chemistry in 1992; investigating model systems for oxygenating enzymes. He obtained his Ph.D. in botany in 1997 at the Institute of Botany of the University of Basel with investigations of global change-effects on grassland ecosystems. During his postdoctoral years, he also was visiting scientist at the Institute of Arable Crops Research in Rothamsted, United Kingdom and at Landcare Research, New Zealand where he investigated soil trace gas relations.

A main focus in Pascal Niklaus' research is on the consequences of environmental change for plant communities and the biogeochemical cycling of nutrients and water in ecosystems; special emphasis is on interactions with soils and effects on the ecosystem's greenhouse gas balance (CO_2 , CH_4 , N_2O).

Contributors

Vincent Allard

INRA-Agronomie
Fonctionnement et Gestion de
l'Ecosystème Prairial
France

Daniel J. Archambault

Laurentian University
Sudbury, Ontario, Canada

Andrew Ash

CSIRO Sustainable Ecosystems
St. Lucia, Queensland, Australia

Joseph C. Blankinship

Department of Biological Sciences
Northern Arizona University
Flagstaff, Arizona

R. Andrew Carran

Land and Environmental Management
Group
AgResearch
Palmerston North, New Zealand

Sukumar Chakraborty

CSIRO Plant Industry
Queensland Bioscience Precinct
St. Lucia, Queensland, Australia

Jann P. Conroy

Centre for Plant and Food Science
University of Western Sydney
Penrith South, Australia

Grant R. Edwards

Agriculture Group
Agriculture and Life Sciences
Division
Lincoln University
Canterbury, New Zealand

Jürg Fuhrer

Air Pollution/Climate Group
Agroscope FAL Reckenholz
Swiss Federal Research Station for
Agroecology and Agriculture
Zürich, Switzerland

Oula Ghannoum

Centre for Plant and Food Science
University of Western Sydney
Penrith South, Australia

Stephen L. Goldson

AgResearch
Lincoln, New Zealand

Jo E. Hossell

ADAS Gleadthorpe
Meden Vale, Mansfield,
Nottingham
United Kingdom

Mark J. Hovenden

School of Plant Science
University of Tasmania
Hobart, Tasmania, Australia

Bruce A. Hungate

Department of Biological Sciences and
Merriam-Powell Center for
Environmental Research
Northern Arizona University
Flagstaff, Arizona

Jonathan A. Newman

Department of Environmental Biology
University of Guelph
Guelph, Ontario, Canada

Paul C.D. Newton

Land and Environmental Management
Group
AgResearch
Palmerston North, New Zealand

Pascal A. Niklaus

Institute of Plant Sciences
ETH Zürich
Zürich, Switzerland

Matthias C. Rillig

Microbial Ecology Program
Division of Biological Sciences
The University of Montana
Missoula, Montana

G. Brett Runion

Soil Dynamics Laboratory
USDA-ARS
Auburn, Alabama

William H. Schlesinger

Nicholas School of the Environment
and Earth Sciences
Duke University
Durham, North Carolina

Matthew J. Searson

Australian Greenhouse Office
Department of the Environment and
Heritage
Australia

Chris Stokes

CSIRO Sustainable Ecosystems and
CRC for Tropical Savannas
Management
Aitkenvale, Australia

Richard B. Thomas

Department of Biology
West Virginia University
Morgantown, West Virginia

Skip J. Van Bloem

Depto Agronomía y Suelos
Universidad de Puerto Rico
Mayagüez, Puerto Rico

Lewis H. Ziska

Crop Systems and Global Change
Laboratory
USDA-ARS
Beltsville, Maryland

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1 Introduction

*Paul C.D. Newton, R. Andrew Carran,
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1.1 THE CONTEXT

Agricultural systems (agroecosystems) are enormously diverse in their biological structure, in the climatic and socioeconomic drivers that shape them, and in the services they provide. Agroecosystems may be critical in sustaining social, economic, and cultural fabrics as well as playing a key role in community health. The challenge we face is to maintain these services and roles during a period of rapid environmental change — perhaps producing combinations of environmental conditions that modern agriculture has not previously experienced. In the first instance, this is an issue for biologists; it is essential to improve our understanding of the potential impacts of environmental change. However, it is also the case that agroecosystems are the site of intense interaction between humans and the natural world. In some situations this offers the prospect of effective adaptation to climatic change — either amelioration of negative effects or exploitation of positive effects; however, at the other extreme there will be many situations in which the effects of climate change will be exacerbated by socioeconomic factors such as income inequality or credit availability (Patt et al. 2005). As biologists we cannot ignore this reality, and if we want our work to be relevant, then we need to consider carefully who and how we are targeting with our knowledge. We consider some of these issues later in this chapter, but first we review the main drivers of environmental change.

1.2 THE ENVIRONMENTAL CHANGES

The changes in the environment we are most concerned with involve temperature, precipitation, and atmospheric CO₂ concentration. Here we consider some of the

issues surrounding these *drivers of change*, which we feel are of central importance in determining biological responses. In particular we draw attention to variation in current and predicted temperature and precipitation trends, and to the likelihood of further increases in atmospheric CO₂ concentration.

1.2.1 ATMOSPHERIC CO₂ CONCENTRATION

As well as its indirect effect on ecosystems through its role as a greenhouse gas, atmospheric CO₂ has a direct effect on the biosphere because it is the primary raw material for plant growth. Direct measurements of atmospheric CO₂ have been made since 1958 in Hawaii (Keeling et al. 1982), and new monitoring stations have been established since that time to give a more global coverage. The data from these stations (CDIAC 2005), together with historical records extracted from ice cores (CDIAC 2005), show the atmospheric concentration has increased exponentially since the late 19th century, that it increases each year, and that it is now at a level higher than at any time in the last 650,000 years (Siegenthaler et al. 2005).

Because CO₂ is such an important driver of biological systems, our picture of the future must include the rate of change in atmospheric CO₂ and the level at which the concentration will stabilize; these both depend upon the balance between CO₂ emissions and the rate at which CO₂ can be sequestered into sinks. A recent carbon (C) budget for the 1990s (Schimel et al. 2001) calculates emissions from fossil fuels to be 6.3 Gt C yr⁻¹, with an additional 1.7 Gt C added from land use change. Approximately half of CO₂ emissions are removed by oceanic and terrestrial sinks leaving an annual addition of approximately 3.2 Gt C to the atmosphere. During this period, the CO₂ concentration in the atmosphere increased at a rate of about 1.5 ppm or 0.44% per year. If this balance of sources and sinks were to continue, then by 2050 the concentration in the atmosphere would reach 460 ppm. As neither sink nor source activity is expected to stay constant over this period, prediction becomes a difficult task.

On the source side, prediction of future emissions depends upon a range of assumptions about technology change and population growth. Emissions projected for 2050 range from 11.0 to 23.9 Gt C (Prentice et al. 2001). To put emissions reduction in perspective, we can make a crude calculation: Assuming current emissions of 6.3 Gt yr⁻¹ (Schimel et al. 2001) and a world population of 6 billion, then our current emissions rate is 1 t of C per capita yr⁻¹. To maintain a balance with the sinks, which currently absorb only half of these emissions, and to have no net increase in the atmosphere, we need to have emissions of 500 kg per capita yr⁻¹. If we look at current rates of per capita emissions of C from fossil fuel use (Marland et al. 2004), we find that emissions from the United States and Western Europe are, respectively, 10 times and 4 times the 500 kg rate that would balance current sinks. The current per capita emission rate in China also exceeds the “stabilising” output level, and it is only in countries such as Africa and India that emissions are below the 500 kg per capita level. These figures suggest that major changes in our energy creation and use will be necessary to achieve significant reductions in emissions (Hoffert et al. 2002).

The second half of the equation is the activity and size of sinks. Again, we can make a rough calculation to establish the size of the problem by considering how much sink activity would need to change by 2050 to keep net emissions to the atmosphere at the current 3.2 Gt C level; that is, to constrain the annual increase to 1.5 ppm. Using the low prediction of CO₂ emissions for 2050 of 11 Gt C (Prentice et al. 2001) would require sinks to remove 7.8 Gt C to maintain net emissions at 3.2 Gt C. If half of the sink activity is oceanic and half terrestrial, then terrestrial sinks would need to absorb 3.9 Gt C or 2.8 times their current rate (assuming a current terrestrial sink of 1.4 Gt yr⁻¹, Prentice et al. 2001). The stimulation of plant growth due to the rising concentration of CO₂ offers the promise of enhanced sink strength; however, in the absence of significant changes in the ratio of C to nitrogen (N) in terrestrial pools, such an increase in C sequestration would require substantial increases in N availability, perhaps beyond the capacity of ecosystems to provide (Hungate et al. 2003). In fact, elevated CO₂ may exacerbate this constraint, as a common response appears to be a progressive decline in the availability of N to plants (Luo et al. 2004). The potential sink capacity of the terrestrial biosphere remains a critical value if we are to predict future CO₂ concentrations. However, a doubling of sink capacity would be required to absorb even current emissions, let alone those expected in the next decades, placing an unrealistic expectation on the absorbing capacity of this sink.

The average annual CO₂ concentration of the well-mixed atmosphere does not differ greatly among monitoring stations, although there is a slightly lower average in the Southern Hemisphere. However, at different scales there can be considerable variation in concentration, and it is relevant to consider whether these variations are likely to change in the future in response to the changing climate and atmosphere. The net CO₂ exchange of the biosphere results in marked seasonal differences (15 to 20 ppm, Keeling et al. 1996) in atmospheric concentration in the Northern Hemisphere; interestingly, the amplitude of this difference is increasing over time (Keeling et al. 1996), probably because of disturbance and a change in the identity and activity of the vegetation (Zimov et al. 1999). Regional differences in atmospheric CO₂ concentration can arise from urban development where large sources of fossil fuel use can dominate the concentration profile. For example, Ziska et al. (2004) measured average concentrations of 466 at 0.5 km from the city centre of Baltimore, Maryland — 401 ppm 10 km from the centre and 385 ppm at a distance of 50 km. Temperature gradients are also established by urbanization, and clearly both CO₂ and temperature gradients will be determined by future urban development and energy use.

Plants also experience large differences in CO₂ concentration between day and night (often > 100 ppm; e.g., Ziska et al. 2001); we are not aware of data considering trends in this difference, but certainly one aspect of climate change has been a reduction in the diurnal temperature range (Prentice et al. 2001), and it may be that this could influence the biological processes of C fixation and respiration that largely govern the differences in CO₂ concentration near the surface. These biological processes also result in considerable spatial variation in concentrations of CO₂ within plant canopies; plants growing close to the soil surface experiencing concentrations of CO₂ perhaps 100 ppm greater than plants with foliage higher in the canopy

(Bazzaz and Williams 1991). It is not certain whether this spatial variation will alter under climate change, but as soil respiration is sensitive to both temperature and elevated CO₂ (e.g., King et al. 2001) there is a strong likelihood of different canopy profiles in the future. The spatial and temporal variation occurs at scales relevant to plant growth and has been shown to influence plant responses to elevated CO₂ (Ziska et al. 2001).

1.2.2 TEMPERATURE AND PRECIPITATION

The global mean near-surface temperature record shows an increase over the 20th century of about 0.6°C (Folland et al. 2001), which is consistent with satellite data for tropospheric temperatures (Tett et al. 1999; Vinnikov and Grody 2003). Further evidence for a temperature change are the “fingerprints” of increasing temperature that can be seen in a range of biological data such as phenological records (Parmesan and Yohe 2003; Root et al. 2003). There are a number of *forcing agents* that can modify climate, some of which are natural (solar radiation and volcanic aerosols) and some anthropogenic, including greenhouse gases, tropospheric aerosols, cloud changes, and changes in the land surface characteristics altering albedo (Hansen et al. 1998). When climate models are run to simulate long-term temperature trends, the prediction for the latter part of the last century requires greenhouse gas effects be included in order to adequately simulate the observed changes (e.g., Karoly et al. 2003); studies such as these are part of the argument that anthropogenic emissions of greenhouse gases are resulting in a change in our climate (Mitchell et al. 2001). Predictions for the change in mean temperature over the next 100 years range between 1.4 and 5.8°C (Cubasch et al. 2001). Spatial variation in temperature and precipitation trends are widely observed and predicted. Rainfall has increased by 10 to 40% over the past 100 years in northern Europe, but has decreased by 20% in southern Europe. In the United States, soil temperatures (1 m over the period 1967 through 2002) show a positive warming trend at stations in the north and northwestern United States, but a strong cooling trend in the southeastern part of the country. Because part of the spatial variation is driven by land use (Pielke et al. 2002; Stone and Weaver 2003; Feddema et al. 2005), variation within regions is also apparent. For example, Pielke et al. (2002) examined the long-term records from a cluster of stations in eastern Colorado and found “enormous” differences, defying attempts to calculate regional trends.

Any trend in mean annual temperature or precipitation is unlikely to be evenly distributed across seasons. For example, in Australia there has been a trend since 1950 for an increase in minimum temperatures in all seasons in Queensland, but a cooling of maximum summer temperature in northwestern Australia (Anonymous 2005). Differences can be a matter of degree, such as the long-term increase in European summer temperatures over the past 100 years of 0.7°C compared to an increase of 1.1°C in winter temperatures; or can be quite strikingly different even in sign, such as the trends in soil temperatures (40 cm) at Irkutsk, Russia, where there was a marked positive trend in annual average temperature over the past 120 years, but a decline in the average summer temperature of 4°C over this time (Zhang et al. (2001).

Variation is also evident at shorter timescales with a reduction in the diurnal temperature range being frequently and widely observed (Prentice et al. 2001). As one of the major factors implicated in this change is soil moisture content (Stone and Weaver 2003), there is a direct link back to vegetation responses to the changing environment. Diurnal patterns in precipitation have been less thoroughly investigated, but here again trends have been identified (Dai 1999).

1.3 THE STRUCTURE OF THIS BOOK

In summary, we can anticipate a continuing increase in the global mean atmospheric CO₂ concentration, and in global mean temperature with a variety of changes in temperature, precipitation, and CO₂ occurring at different scales relevant to biological activity. How can we deal with this complexity?

We suggest that two aspects are particularly important. First, an improved understanding of the biological consequences achieved through greater integration of basic and applied knowledge; and second, a clearer focus on the audience for this research, as this should enable us to ask and address more targeted and relevant questions.

Our perception is that climate change impact research often occurs in two ways. On the one hand there are studies of the direct effects of a particular set of climate drivers on a specific crop, often concentrating on the agricultural outputs, such as yield and quality (e.g., Reddy and Hodges 2000). On the other hand, there is a more ecological literature that seeks to find some general principles of response (e.g., Körner and Bazzaz 1996, p. 4). In this volume we hope to draw these two approaches together so that ecologists can provide the “theoretical underpinning that informs them (agriculturalists) what might be happening, what to look for, and what to build on” (Lawton 1996, p. 4), and agriculturalists can interpret these ecological insights and general theory in relation to agroecosystem performance. Consequently, each section of this book combines general principles of response leading to applied consequences. We have sections considering (1) the supply of resources necessary to sustain agriculture in the future, which we identify from an understanding of how climate change will modify biogeochemical cycles and changes in plant nutrient demands; (2) the incidence of pests, weeds, and diseases and their control for which we need an understanding of how the population biology of organisms will change; and (3) the adaptations that might be possible, including plant breeding solutions, for which we need an understanding of the capacity for adaptation that exists in plant populations. In addition to the full chapters, we have included Special Example chapters that deal in more detail with specific issues.

Having collected the best information, we are then faced with the issue of communicating it effectively to interested groups and, in particular, to those groups that can act effectively in leading or implementing adaptive measures. On this basis we suggest that while farmers and landowners will likely be interested in projections that consider, for example, changes in yield or the incidence of pests, their behaviour is unlikely to be modified by such predictions, as they tend to be responsive to current conditions. Consequently, we imagine that the issues in this book will resonate most strongly with other researchers and with agribusiness because here are important messages about potential opportunities for the development of new

technologies. These are important sectors to reach, as it is through the development of new, adaptive technologies that we can imagine making a difference in agroecosystem performance in a changing environment.

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Part I

Resource Supply and Demand

2 Climate Change Effects on Biogeochemical Cycles, Nutrients, and Water Supply

Pascal A. Niklaus

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2.1 INTRODUCTION

The atmospheric CO₂ concentration has increased by ≈30% relative to the preindustrial concentration of 280 μL L⁻¹ and is projected to reach 540 to 970 μL L⁻¹ by the end of this century, depending on emission scenarios and climate feedback (IPCC [Intergovernmental Panel on Climate Change], 2001). CO₂ and other atmospheric gases of anthropogenic origin are radiatively active, and increases in global temperatures in the range of 1.4 to 5.8° C are predicted, depending on emission scenarios and climate sensitivity (IPCC, 2001). As a consequence of warming, changes in the global distribution of precipitation are anticipated, with projected increases at medium to high latitudes, but decreases in other areas (e.g., the European Mediterranean).

In this chapter, I analyse how these global changes might affect the biogeochemical cycling of nutrients and hydrology, and how this ultimately may impact on agricultural ecosystems.

An important distinction to be made is between agroecosystems with high fertiliser input and relatively open nutrient cycles on one hand, and low input and seminatural systems in which nutrient cycles are relatively closed on the other hand. In intensified agriculture, relatively large amounts of nutrients are removed from the ecosystem with the crop and need to be resupplied in the form of mineral or organic fertiliser. Effects of global change on soil nutrient cycling are less likely to be of importance in these systems. However, soil processes such as trace gas emissions may change, which can strongly feed back on the climate system. Also, the nutritional composition of crops may change, altering their nutritional quality and possibly requiring changes in fertiliser composition. In natural ecosystems as well as in extensively managed systems, such as low-input crop cultivation, pastures, rangelands, and low-intensity forestry, a significant fraction of plant nutrient demand is met by the internal mineral nutrient cycles of soils, and effects of climate change on soil processes may directly feed back on plant growth.

Despite several decades of global change research, available data on the effects on soil nutrient cycling are surprisingly limited, especially for agroecosystems and nutrients other than N. In many areas, we are still in the stage of pattern searching without having a very detailed understanding of the mechanisms underlying responses. In the attempt not to unnecessarily narrow the scope of this chapter to what is already well known, included is data from all available sources, including studies in natural ecosystems. Whether and to what extent these findings can be extrapolated to typical agricultural situations remains to be explored.

2.1.1 ESSENTIAL ELEMENTS

Plant tissue is primarily composed of carbon (C), hydrogen (H), and oxygen (O). These elements are derived from the fixation of atmospheric CO₂ and from the

uptake of soil H_2O , and are generally available in ample quantities. However, virtually all naturally occurring elements are also found in plants, and more than 10 are essential for growth (Welch, 1995). Mineral nutrients are generally classified into macronutrients, required by plants at relatively large concentrations (nitrogen [N], phosphorus [P], potassium [K], sulfur [S], calcium [Ca] and magnesium [Mg]; Epstein, 1965); and micronutrients, which are required in much lower quantities (chlorine [Cl], iron [Fe], boron [B], manganese [Mn], zinc [Zn], copper [Cu], molybdenum [Mo] and nickel [Ni]). Still other elements are beneficial to plants but probably not essential for growth (sodium [Na], silicon [Si], cobalt [Co] and selenium [Se]). Micronutrients are predominantly bound in enzymes, where they often have important functional roles at the active sites, whereas macronutrients are constituents of organic macromolecules (e.g., N, P, and S in proteins and nucleic acids) or act as osmotica (e.g., K).

Most studies of global change effects on nutrient cycling have so far focused on nitrogen. One reason may be that N is the nutrient required in the largest quantity; another reason may be the relative ease with which N can be measured. The nitrogen cycle is also clearly the most complex of all cycles of essential elements because N occurs at a wide range of oxidation states; is involved in a vast array of microbial transformations; and also occurs in gaseous, solid, and dissolved forms, endowing it with exceptional mobility. There is, therefore, a large potential for climate change to interfere with N nutrition. However, the N cycle is also special in that a biological pathway exists with N_2 fixation by which ecosystems can adjust to altered N demand. This is not the case for the other elements. Indeed, while N clearly is often limiting (Vitousek and Howarth, 1991), the level at which N becomes limiting in the long term is frequently determined by the availability of other mineral nutrients (e.g., P: Cole and Heil, 1981; McGill and Cole, 1981; Niklaus and Körner, 2004, Mo: Hungate et al., 2004).

Many animals, both wild and domestic, forage on plants and accommodate their mineral nutrient needs from plant sources. Animals require many of the same elements as plants, but additionally require various complex organic molecules. Plant chemical composition, therefore, can determine animal growth, but the limiting component is often not easy to determine. For example, herbivores are often more limited by N than by carbohydrates. An important consideration is that nutrient concentrations that are sufficient for plants may be too low for the animals that feed on them. For example, many New Zealand and Australian soils are very low in cobalt; cobalt is not essential to plants* and, thus, does not limit their growth. However, sheep foraging on these plants exhibit severe cobalt-deficiency symptoms (Lee et al., 1999). The accumulation of nonplant-essential elements in plant tissue (e.g., iodine or cobalt) and the accumulation of plant-essential elements beyond limiting concentrations, therefore, can be ecologically and economically important.

Human nutrition ultimately also depends on plant chemical composition, whether plants are consumed directly or indirectly as animals that previously fed on plants (Underwood and Mertz, 1987). Besides insufficient total energy and protein input, the World Health Organization (WHO) identified micronutrient deficiency as

* Except for N_2 fixation.

a major cause of malnutrition (WHO, 2000). Over 2 billion people are currently affected by deficiencies in iodine, zinc, iron, selenium, and calcium, but also of more complex phytochemicals such as vitamins A and E, niacin, and folate (Grusak and DellaPenna, 1999; WHO, 2000). Clearly, human malnutrition at the global level is a complex phenomenon involving political, sociological, and economic aspects beyond the scope of this chapter. However, these data emphasize that micronutrient effects of global change may have important implications beyond the functioning of plants (Allaway, 1987).

2.1.2 MECHANISMS AND KEY PROCESSES

In the following analysis, I focus on a number of key processes in nutrient cycles that are experimentally accessible. I review experimental evidence on how these respond to simulated climate change, and analyse, from a theoretical point of view, how they may be affected, directly or indirectly, by elevated CO₂, elevated temperatures and altered precipitation. While these drivers are quite different and the details of the mechanisms involved clearly are complex, two principal groups of mechanisms can be identified (Figure 2.1).

A first group of effects is related to changes in carbon cycling. A primary effect of elevated CO₂ is to increase photosynthesis and plant growth; warming also increases primary production of most ecosystems, but it also affects respiration and decomposition. Elevated CO₂ and warming, therefore, result in alterations of the carbon balance of plants, soils, and soil organisms.

The second group of effects is related to the hydrological cycle. Elevated CO₂ reduces stomatal conductance in virtually all vascular plant species, and this can reduce evapotranspiration and water use, at least per unit of plant biomass. Warming, on the other hand, increases evapotranspiration and generally results in a drier environment. Precipitation, finally, has a direct effect on the water balance of the

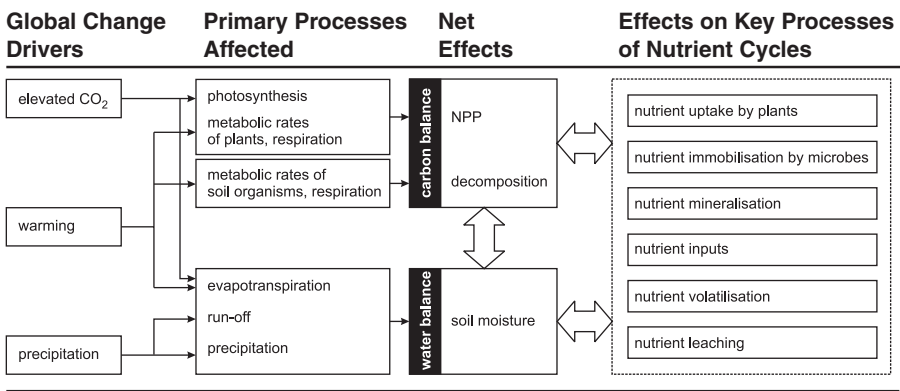


FIGURE 2.1 Schematic of effects of global change drivers via alterations of carbon and water balance. See text for a detailed discussion.

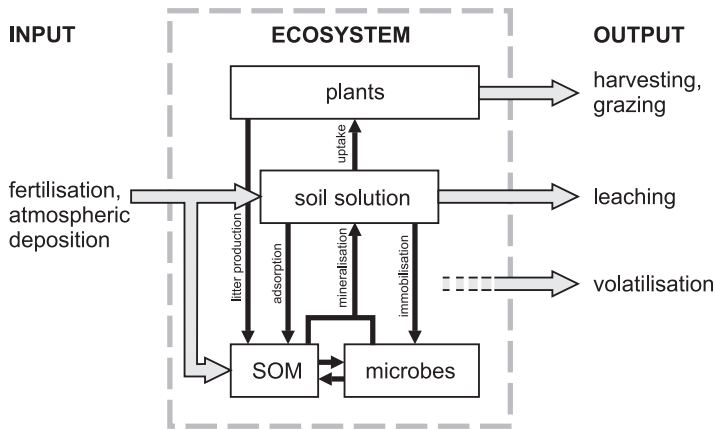


FIGURE 2.2 Key processes in nutrient cycles that might be affected by global environmental change (SOM = soil organic matter).

ecosystem. Alterations of the ecosystem water balance affect many processes including the diffusion of gases and nutrients, sorption processes, and leaching rates. Redox potential is also strongly affected by the soil water balance, primarily by controlling gas-filled pore space and, therefore, the diffusion of O_2 ; this can induce shifts in the activity of different microbial groups involved in nutrient transformations, but operating under different redox conditions, for example, between nitrifying and denitrifying bacteria.

Effects via carbon and water balance interact because in many ecosystems productivity and decomposition are limited by low soil water content (but by high soil moisture in water-logged soils). There are also more complex feedback mechanisms involved that will be discussed. Some key quantities and processes that are focused on in this chapter are schematically shown in Figure 2.2.

2.1.2.1 Nutrient Balance of the Whole Ecosystem

Summing all nutrient fluxes across an ecosystem's boundaries theoretically allows calculation of the nutrient balance of the whole ecosystem. If nutrient outputs are larger than inputs, nutrient stocks within the ecosystem will become depleted and productivity may decrease in the long run. Data allowing for a complete balance are scarce; however, there is a substantial body of literature reporting the main fluxes, and these may give an indication of the changes to expect in a future climate.

Climate change may affect the nutrient balance of ecosystems in several ways:

1. Nutrient deposition from the atmosphere could change with altered weather patterns (precipitation, range of transport, anthropogenic emissions of pollutants [N, S], etc.).
2. Biological fixation of atmospheric N_2 may change (addressed by Thomas et al., Chapter 4, this volume).
3. Weathering rates of minerals may change.

4. The amount of nutrients exported may change due to changes in amount and elemental composition of plant material.
5. Losses by leaching and erosion could change due to effects on nutrient cycling and alterations in climate, especially in precipitation.

In the long run, changes in the nutrient balance may necessitate a corresponding change in the elemental ratio of nutrient inputs to maintain the status quo.

2.1.2.2 Mineralisation of Soil Organic Matter

Plants take up nutrients from soil solution. One process delivering nutrients to soil solution is the mineralisation of organic matter. The mineralisation of different elements does not occur in concert because mineral nutrients differ in the way they are bound in organic matter (McGill and Cole, 1981). Nitrogen is predominantly covalently bound to carbon. Sulphur is covalently bound both directly to C and via ester linkages. Phosphorus is essentially ester-bound, while potassium does not bind covalently at all, but forms ionic bonds. The mineralisation of N is, therefore, largely coupled to that of C, while ester-linked P and S can be mineralised independently of C by the hydrolytic action of soil exoenzymes.

Cycling rates of mineral nutrients are controlled by complex interactions between plants, soil microbes, and abiotic factors (Schlesinger, 1996). These controls differ between mineral nutrients: The cycling rate of limiting nutrients will control plant productivity (e.g., N and P: Güsewell, 2004; Niklaus and Körner, 2004; Vitousek and Howarth, 1991; Vitousek et al., 1993), whereas plant productivity will generally control the cycling of nutrients that are available in excess (e.g., sulphur). The cycling of still other elements is predominantly geochemically controlled and relatively independent of plant growth (e.g., chlorine).

Global change can alter organic matter mineralisation rates in several ways. For example, the quality and quantity of organic matter produced by plants can be affected, resulting in altered decomposition. Microbial activity and decomposition can be affected by soil fluxes of plant-derived C (*priming effect*), and abiotic conditions such as temperature and moisture, which are important controls of decomposition rates, may also be changed.

2.1.2.3 Immobilisation in Soil Microbial Biomass

The soil microbial biomass is a highly dynamic organic matter pool and its nutrient content often exceeds that of plants. Changes in amounts of mineral nutrients bound in microbial cells can substantially alter the within-ecosystem nutrient distribution and affect plant growth. The soil microbial community is predominantly saprophytic and, therefore, depends on inputs of plant-derived organic material. As a consequence, soil microbial community biomass may respond to alterations in soil C fluxes under global change. Apart from C supply, soil microbial biomass is also controlled top-down by grazing by protozoa and microfauna (Blankinship and Hungate, Chapter 5, this volume), by the availability of nutrients such as P or N, which can (co-)limit microbial growth, and by soil conditions that can have strong

effects on microbial populations (e.g., soil moisture, temperature, freeze–thaw and drying–rewetting cycles, soil mineral, and aggregate structure).

2.1.2.4 Leaching and Volatilisation of Nutrients

Significant amounts of nutrients can be lost from ecosystems by leaching and, in the case of N, by volatilisation of NH_3 , NO, N_2O , and N_2 (Barnard et al., 2005). Leaching losses will generally be more important for compounds such as NO_3^- and K^+ , which are highly soluble and show low sorption to the solid phase. Leaching rates are related to many factors that are likely to change in a future climate, for example to soil solution concentrations of nutrients and the amount of water drained. However, water flow often follows preferential flowpaths in the soil, and leaching events are erratic, so that predictions are difficult.

2.2 EFFECTS OF ELEVATED CO_2 ON NUTRIENT CYCLING

Elevated CO_2 concentrations often stimulate plant growth. One mechanism for this response is that photosynthesis is stimulated by elevated CO_2 , at least in C_3 plants. A second mechanism is that in almost all species, stomatal closure is induced in response to the increased availability of CO_2 . Lower stomatal conductance can result in reduced evapotranspiration, which in turn can result in comparably higher soil moisture at any given plant biomass, or to the maintenance of higher plant biomass at any given level of soil H_2O (Jackson et al., 1998; Niklaus and Körner, 2004; Owensby et al., 1999). A recent analysis has demonstrated that this latter indirect effect (increased water use efficiency) accounts for much of the biomass stimulation observed in arid and semiarid but also in some mesic grasslands exposed to elevated CO_2 (Morgan et al., 2004b), and both C_3 and C_4 plants, therefore, generally exhibit growth responses to elevated CO_2 (Wand et al., 1999). Nutrient dynamics may be altered by both increased C fixation and increased soil moisture.

2.2.1 EVIDENCE FOR CHANGES IN SOIL CARBON FLUXES

Higher plant productivity under elevated CO_2 will ultimately increase organic matter inputs to soils unless all the extra production is removed as harvested plant material (hay, crop).^{*} The pathways by which extra C enters the soil under elevated CO_2 , however, still remain elusive. Only limited field data is available (see, for example, Hungate et al., 1997b; Niklaus et al., 2001a; Ross et al., 1995), in part due to methodological difficulties to assess plant–soil C fluxes *in situ* (Darrah, 1996; Hilbert et al., 1987; Hungate et al., 1996; Lund et al., 1999; Niklaus et al., 2000). Exudation is a major component of soil C inputs, but there are virtually no data on flux rates and chemical composition of exudates under field conditions. There have been early indications from laboratory studies, mostly conducted under hydroponic conditions, that rhizodeposition per unit root length would increase under elevated CO_2 (review

^{*} Even then, soil organic matter inputs will increase due to biomass turnover between harvests.

by Darrah, 1996), and this effect has been interpreted as plants being saturated with carbohydrates and passively leaking or actively “disposing” belowground the extra C not needed. However, this notion could not be corroborated in a number of field systems, probably because soil matrix effects and resorption of organic compounds reduce or eliminate the effects observed in hydroponics (Darrah, 1996; Jones and Darrah, 1996). Field data are mostly based on observations of fine root turnover (Arnone et al., 2000; Fitter et al., 1996; Pregitzer et al., 2000) and carbon tracer studies (e.g., Hungate et al., 1997b; Newton et al., 1995; Niklaus et al., 2001a). Nevertheless, even in the absence of a carbon overflow-type effect on rhizodeposition under elevated CO_2 , and in the absence of increased root-to-shoot ratios, increased plant productivity should result in increased soil C inputs. However, the ultimate magnitude of this effect is still unknown, and so are the pathways by which extra C enters the soil.

2.2.2 NUTRIENT IMMOBILISATION AND MINERALISATION RESPONSES TO ELEVATED CO_2

Increased soil C fluxes under elevated CO_2 could lead to higher soil microbial biomass and immobilisation of mineral nutrients. This *negative* feedback on plant growth has been demonstrated in a pot CO_2 experiment where microbial biomass N increased and plant responses to elevated CO_2 were negative (Diaz et al., 1993), presumably due to increased input of high C:N compounds to soils. Extra C inputs to soils can, however, increase microbial activity and, thus, prime the mineralisation of organic matter. This *positive* feedback on plant growth has been proposed by Zak et al. (1993). Priming effects on mineralisation and increased nutrient immobilisation in microbial biomass are not mutually exclusive and microbial biomass and the availability of nutrients to plants may increase concurrently (higher net immobilisation plus increased net mineralisation rates).

Experimental evidence of elevated CO_2 effects on microbial biomass is equivocal. While some greenhouse studies reported increases in microbial biomass, responses in field studies of grassland appear to be smaller and often even absent (Table 2.1). Various experimental protocols were used; nitrogen mineralisation, for example, was measured in the field or using isolated soil samples, with methods that ranged from buried bags, aerobic or anaerobic laboratory incubations, to short- and long-term ^{15}N isotopic pool dilution methods. Despite all these differences, some broad response patterns emerged.

Microbial C often does not respond to elevated CO_2 , even after several years of increased plant productivity. However, microbial N and N mineralisation increase in many studies, suggesting that microbial N responds more than C, and that this extra microbial N originates from increased mineralisation of soil organic matter rather than from immobilisation of soil mineral N. Two different mechanisms may explain these observations: First, microbial N may have been primed by extra C inputs under elevated CO_2 (mechanism proposed by Zak et al., 1993); second, increased soil moisture at elevated CO_2 may have led to increased N mineralisation, at least in (temporarily) H_2O -limited ecosystems. CO_2 effects may effectively be indirect, that is, soil moisture effects in disguise. It is very difficult to disentangle

these two components of elevated CO_2 unless an experimental design involves a factorial irrigation treatment.

I have previously argued that cases in which microbial sequestration of extra N under elevated CO_2 occurs may be restricted to systems where N supply is abundant and nutrient cycles are not in equilibrium with plant demand, that is, the cycling of C and N are not strongly coupled (Niklaus and Körner, 1996); others arrived at similar conclusions (Hu et al., 1999). The data that have become available in the meanwhile, however, indicate that increased net microbial N immobilisation occurs in many (though not all) systems exposed to elevated CO_2 . High N supply seems to favour this response, probably via increased plant growth under elevated CO_2 and associated increased soil inputs of C and N from plants; however, this increase in N is generally paralleled by an increase in N mineralisation rates, so that reductions in plant N availability (the negative feedback mechanism identified by Diaz et al., 1993) appear not to happen. One reason why this is not the case may be that overall the C:N in organic matter inputs to soils does not change much under elevated CO_2 .

Dynamics of P and S might respond to elevated CO_2 in a fashion similar to that of N; after all, increases in soil microbial biomass will be accompanied by the immobilisation of these nutrients as well, and the decomposition of soil organic matter will release the mineral nutrients that it contained. However, an important difference is that a significant portion of soil organic P and S is ester-bound and, therefore, can be mineralised independently of C as has been discussed above.

Microbial biomass P and S can be measured with techniques analogous to the ones used for N (e.g., chloroform fumigation-extraction; Brookes et al., 1982; Wu et al., 1994); however, to my knowledge, absolutely no data is currently available from elevated CO_2 studies. At first approximation, microbial P and S pools could be assumed to change in concert with microbial biomass, but this assumption can be poor, as data for N demonstrate.

An indicator of P status of plants and soil microbes is the activity of soil extracellular phosphatases; these enzymes are released in response to growth limitations by plants, and their activity is especially high in P-depleted zones in the immediate vicinity of plant roots (Barrett et al., 1998; Spiers and McGill, 1979). Experimental data under elevated CO_2 is quite limited. In a grassland, Ebersberger et al. (2003) found a 32% increase in alkaline phosphatase activity in a N–P-colimited calcareous meadow (Niklaus and Körner, 2004) exposed to elevated CO_2 for 6 years (but no increase in enzymes related to the N cycle). Moorhead and Linkins (1997) reported increased phosphatase activities in tussock tundra exposed to elevated CO_2 for 3 years, and Dhillon et al. (1996) found increased acid phosphatase activity in soil turves with the annual Mediterranean grass *Bromus madritensis* (but no change in extractable soil inorganic P and N). For trees and forest ecosystems, increases in acid phosphatase activity have been found in soil below *Quercus ilex* exposed to twice-ambient CO_2 for 5 years (Moscatelli et al., 2001), but no effects were found in a plantation of 16-year-old *Pinus taeda* exposed to elevated CO_2 for 2 to 3 years. Matamala and Schlesinger (2000) and de Lucia et al. (1997) reported signs of decreased phosphatase activity under ponderosa pine seedlings exposed to elevated CO_2 (but increased concentrations of P-chelating oxalate).

TABLE 2.1
Effects of Elevated CO₂ on Microbial Biomass C and N, N-Mineralisation and Nitrification

TABLE 2.1 Effects of Elevated CO ₂ on Microbial Biomass C and N, N-Mineralisation and Nitrification									
System/Species	CO ₂ Treatment Conc. (ppmv)	Years for Which Effects Are Listed	Fertiliser Inputs	Effects of CO ₂ Enrichment					Reference
				Microbial C	Biomass N	N- Mineralisation	Nitrification		
Grassland									
<i>Lolium perenne</i>	600	2	14 and 56 g N m ⁻² a ⁻¹	n.s.	n.s.		n.s. ¹	Schortemeyer et al. 1996	
<i>Trifolium repens</i>	600	2	14 and 56 g N m ⁻² a ⁻¹	n.s.	n.s.		n.s. ¹	Schortemeyer et al. 1996	
<i>Lolium perenne</i>	600	1 to 10	14 g N m ⁻² a ⁻¹			n.s. ²		Schneider et al. 2004	
	600	1 to 10	56 g N m ⁻² a ⁻¹			↑ ²		Daepp et al. 2000	
Annual grassland (sandstone soil)	A+350	2 to 5	unfertilised	↑/=		↑ ³		Hungate 1997a,b, 2000	
Annual grassland (serpentine soil)	A+350	2 to 5	unfertilised	↑/=		↑ ³			
Perennial pasture	475	1 to 5	0 kg N m ⁻² a ⁻¹ ; P,K,Mg,S supplied	n.s.	↑/=	(↑)	n.s.	Ross et al. 2004; pers. comm.	
Perennial meadow	600	6	unfertilised	n.s.	↑/=	↑/=	n.s. ⁵	Niklaus 1998; Niklaus et al. 2001d, 2003	
Planted perennial communities	600	5	disturbed,unfertilised	n.s.	n.s.	=	↓ ⁵	Niklaus et al. 2001b,c	
Alpine meadow	680	4	unfertilised	n.s.	n.s.			Niklaus and Körner 1996; Körner et al. 1997	
Alpine meadow	680	4	full fertiliser (equiv. 4.5 g N m ⁻² a ⁻¹)	n.s.	n.s.				

Tallgrass prairie	2 × A	2 to 8	unfertilised	↑/=4	↑/=4	Williams et al. 2000; Rice et al. 1994
Arid desert	550	3 to 5	unfertilised	n.s. ⁶	n.s.	Billings et al. 2004
Shortgrass steppe	720		unfertilised	n.s.		Stahl, pers. comm.; Morgan et al. 2004a
<i>Lotium perenne</i> <i>Holcus lanatus</i>	600	3	full fertiliser (equiv. 24 g N m ⁻² a ⁻¹)	n.s.	n.s. ⁵	Barnard et al. 2004
Woody Pine forest	A+200	1 to 5	unfertilised	n.s.	n.s.	Finzi and Schlesinger 2003
<i>Populus tremuloides</i> <i>Betula papyrifera</i> <i>Acer saccharum</i>	550	3	unfertilised	n.s.	n.s. ³	Holmes et al. 2003
<i>Liquidambar</i> <i>styraciflua</i>	565	2 to 3	unfertilised	n.s.	n.s. ³	Sinsabaugh et al. 2003
Crop Production <i>Oryza sativa</i>	A+200	1 to 2	8 to 9.4 g N m ⁻² a ⁻¹	↑	↑	Inubushi et al. 2001

Note: Data was only included from field studies for which effects on microbial N were reported. Effects listed in parentheses are marginally significant.

¹ Number of autotrophic ammonia oxidising bacteria.
² Measured by pool dilution using ¹⁵N-labelled fertiliser; effect increases with time.
³ Gross rates measured by ¹⁵N pool dilution.
⁴ No effect on average across all years; there was a significant increase of C in 1 and a significant increase in N in 2 out of 6 years.
⁵ Nitrification potential measured in incubations.
⁶ Data in wetted soils as required for chloroform-fumigation-extraction method (Sparling et al. 1990).

Soil P availability has been measured more directly in a number of studies, mainly by bicarbonate extraction (Olsen-P). For example, Johnson et al. (2003) reported reduced soil P availability in scrub oak forest exposed to elevated CO₂ for several years on some but not all sampling dates. However, no differences in P collected on anion exchange resins were found in the same study.

The interpretation of soil phosphatase data is not straightforward for several reasons. First, the production of extracellular phosphatases is supposedly induced by a lack of available P. Increased phosphatase activities could increase mineralisation rates and ameliorate this condition; however, if the production of phosphatases has been induced by a particularly low availability of P, mineralisation rates may effectively still be reduced. Elevated phosphatase activities, therefore, can be interpreted either as signs of increased P mineralisation (because this is the purpose for which they are produced) or of reduced supply to plants (because this is what induces their production). Second, P can also be rendered plant-available by other avenues; organic acids such as oxalate and citrate can effectively chelate phosphate and improve its solubility, mobility, and plant availability. Third, measurement of soil P pools by sequential extraction procedures yield indicators of plant-available forms of P. However, low concentration can be a result of increased uptake by plants, or the reason for low uptake, and active uptake mechanisms via organic acid exudation and mycorrhizal networks are important and not accounted for by these extractions for P (Rouhier and Read, 1998).

Enzyme activity and soil concentration measurements provide valuable information, but in order to achieve a more conclusive understanding of CO₂ effects on P cycling, several methods would ideally be combined. These include a complete assessment of ecosystem P pools (plants, soil microbial biomass, soil pool measurements by sequential extraction procedures) and isotopic measurements of exchange kinetics and microbial immobilisation (³²P/³³P).

Effects of elevated CO₂ on S-cycling have not received much attention so far. Mineralisation of S has been found to correlate with soil microbial activity in some studies (e.g., Eriksen et al., 1995) and effects of elevated CO₂ therefore appear possible. Ebersberger et al. (2003) measured arylsulphatase activity in a calcareous grassland and did not find any change under elevated CO₂, but enzyme activities may be poor indicators of S mineralisation rates. Supply of S has generally not been a concern for agricultural production because atmospheric inputs from air pollution are sufficient to cover plant demand, at least in industrialised areas. However, SO₂ emission control has now led to a negative S balance in many agricultural soils (e.g., Knudsen and Pedersen, 1993). Plant S supply from mineralisation and potential effects of elevated CO₂ may become more important in the future.

2.2.3 PLANT TISSUE QUALITY

A significant part of plant biomass is exported as yield in many ecosystems (hay, crop, animal biomass). The elemental composition of plant tissue is therefore a critical determinant of the nutrient balance of the ecosystem. A shift in elemental ratios under global change thus may shift the coupling of nutrient cycles and affect

nutrient limitations, also higher up the food chain. This may necessitate adaptations in fertiliser use, and also alter the nutritional quality of plants.

Elevated CO₂ affects plant tissue quality by several mechanisms:

1. Carbohydrate levels of green plant tissue increase, primarily in the form of starch (Penuelas and Estiarte, 1998; Wong, 1990).
2. Leaf nitrogen concentrations decrease in many studies, mainly due to increased carbohydrate contents and reduced amounts of photosynthetic enzymes in C₃ plants (e.g., Ainsworth et al., 2002; Rogers and Ellsworth, 2002; Sage et al., 1997; Sage, 2002; Seneweera et al., 2002; Stitt and Krapp, 1999).
3. Leaf P decreases often less than leaf N, presumably because more P is required in phosphorylated intermediates when photosynthetic capacity increases under elevated CO₂ (Ghannoum et al., Chapter 3, this volume; and Gifford et al., 2000).
4. Allocation to secondary compounds may increase under elevated CO₂ due to reduced C and N limitation (Herms and Mattson, 1992; Penuelas and Estiarte, 1998).

Not much is known about effects on elements other than N and P. What is the experimental evidence that shifts in elemental composition occur under elevated CO₂, especially for elements other than N? In a search for patterns, I have compiled data on pools and concentrations of nutrients in plants exposed to elevated CO₂ (Table 2.2). I have mostly focused on multiyear field studies and excluded experiments for which only N concentration was reported because the aim here is to assess differential responses of mineral elements.

A remarkable finding is that foliar K concentrations decreased under elevated CO₂ in many studies conducted under relatively infertile conditions: Newbery et al. (1995) reported decreases in shoot K concentration in *Agrostis capillaris* grown under low K supply; specific root absorption, measured as ⁸⁵Rb absorption of excised roots, increased by over 100%, indicating increased demand for K. Decreased shoot K concentrations were also reported by Schenk et al. (1997) for *Lolium perenne*/*Trifolium repens* swards. In trees, reductions in foliar K concentration were reported for *Quercus alba* and *Picea abies* (Norby et al., 1986) and in mixed stands of *Quercus germinata*/*myrtifolia* (Johnson et al., 2003). It is noteworthy that the decreases in K were often larger than the decreases in N. These reductions in K translated into reduced litter K concentrations where this was measured, and reductions in K again were larger than reductions in N (mixed stands of *Quercus germinata*/*myrtifolia*: Johnson et al., 2003; ombrotrophic *Sphagnum* bogs: Hoosbeek et al., 2002). This decrease in foliar K occurs less frequently in well-fertilised systems, though there are exceptions (e.g., cotton: Prior et al., 1998; *Picea sitchensis*: Murray et al., 1996).

It remains to be explored whether this decrease in K concentrations is ecologically significant. Soils differ greatly with respect to K availability. Fine-textured soils have generally larger exchange capacities, which prevent K leaching, and K is constantly resupplied from mineral weathering. In these soils, K is generally not limiting. However, sandy soils with low exchange capacity can result in significant K leaching,