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GCTE

Terrestrial Ecosystems in a Changing World

J. G. CANADELL
D. E. PATAKI
L. F. PITELKA
Editors

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Josep G. Canadell · Diane E. Pataki · Louis F. Pitelka (Eds.)

Terrestrial Ecosystems in a Changing World

With 104 Figures

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Preface

The GCTE project was born on the day the Berlin wall fell (November 10, 1989). It was the final day of the Planning Committee meeting for the IGBP, at Berlin's Wissenschaftskolleg. Co-ordinating Panel 4 had presented its recommendations to the IGBP Planning Committee during the preceding week, and on that day they were accepted as the basis for GCTE, ratified later at the general IGBP inaugural meeting in Paris, in 1990.

The first full meeting of GCTE was its Open Science meeting in Brighton, England, in February 1991. Much good science was defined and put into effect at that meeting. But one point remained unresolved – an appropriate name and acronym. Everyone was agreed that GCTE was dreadful and could never work. The topic was debated at (the end of) each subsequent meeting of the Steering Committee, and no agreement on a better (publishable) name and acronym was ever reached. Its clumsiness eventually made it distinctive and so, 15 years later, it is finally put to rest, with the project.

From its inception GCTE was marked by, and most fortunate in having, a group of outstanding scientists to lead its defined Activities. They constituted the GCTE Steering Committee and their performance and stature attracted the best researchers joining what has been an exemplary (yet essentially voluntary) scientific effort.

The evolution of GCTE is an interesting reflection of scientific progress and increasing awareness of what is needed to understand the functioning of the Earth System. It began with three "Foci", ecophysiology (at various scales), vegetation dynamics (again at scales from patches to the globe) and agro-ecosystems. A fourth Focus, on biodiversity, but also involving linkages across the other three, was added as results from initial studies and models began to emerge. The evolution to a more integrated approach continued and the results presented in this volume show the level of awareness that has now been achieved.

Perhaps the most important achievement of GCTE has been to demonstrate the critical role that terrestrial ecosystems play in the functioning of the Earth System. When GCTE began, it was widely assumed that Earth System dynamics were dominated by the ocean-atmosphere system, and that terrestrial systems were just the recipients of changes in the dynamics of these two great fluids. Now the picture is much different, as the following examples demonstrate.

Terrestrial processes in the carbon cycle. Until very recently, projections of future atmospheric CO_2 concentration were determined only by estimated emissions from fossil fuel combustion and land-use change. Research within GCTE and elsewhere has elucidated the important role that feedback processes in terrestrial ecosystems – heterotrophic respiration, wildfires, permafrost melting – will play in determining the trajectory of atmospheric CO_2 concentration over the next few decades and centuries. This work has contributed to the issue of 'sink saturation' and the possibility that the terrestrial will switch later this century from being a net sink to a net source of carbon.

Nonlinearities in the Earth System. Within the IGBP framework, GCTE took the lead in analyzing the nature of nonlinear change in Earth System functioning. This work played a central role in the emergence of abrupt change, surprises and extreme events as unifying themes in the second phase of IGBP research.

Dynamic Global Vegetation Models (DGVMs). When GCTE began its implementation in 1991, the terrestrial surface was treated as a 'big leaf' or a 'green slime' in global climate models. One of the project's highest priorities was to change this situation. Several research groups associated with GCTE produced prototype DGVMs by the mid-1990s, a model intercomparison was implemented later in the decade, and now DGVMs are recognized as an essential component – as important as the oceans and the atmosphere – in Earth System models.

Complementing this Earth System perspective, the last phase of GCTE also placed emphasis on the consequences of global change for the things that matter to people – captured in this book in the section on "Ecosystem Services". These consequences are mostly reflected at regional scales and the regions under most stress are discussed in the final section of the book.

We are delighted and honored to have been asked to write this Preface. Brian was GCTE's first Chair and Will the first full time Scientific Officer, before he took over as IGBP Director. We both greatly enjoyed our involvement, benefiting from it enormously, and this was in large measure thanks to all the fine people who were involved. We cannot mention them all but we want to acknowledge one person in particular, Rowena Foster, for the prodigious effort she has put in, throughout the 15 years of its existence, to making GCTE work. We know that every scientist who was involved in one of the many workshops organized by Rowena will join us in thanking her.

GCTE's research over the past 15 years provides a sound base for the new Global Land Project, and the community that GCTE has built will make many further contributions to the GLP. This book highlights the exciting work that was carried out during the second half of GCTE and points towards the new challenges to be undertaken under the GLP banner. We congratulate the authors and editors on a fine effort. We thank the GCTE community for its many achievements and wish the GLP all the best for the future.

Brian Walker and *Will Steffen*
November 2006
Canberra

Acknowledgments

The implementation and success of GCTE was possible thanks to the commitment and contributions of many scientists from around the world who have volunteered for leading roles to drive activities, established networks, and run workshops and synthesis efforts for almost 15 years. Over 100 scientists played roles as members of the scientific steering committee, and as activity and task leaders. To all of them we want to show our appreciation and gratitude for their valuable time and intellectual contributions. Their willingness to contribute well beyond their own interest provided an invaluable service to the development of a globally coordinated understanding of science. Particular thanks go to the chairs of GCTE: Brian Walker, Ian Noble, and Louis Pitelka; and Harold Mooney for being such a motivating and inspiring leader.

We also want to thank to a smaller group of individuals who invested their careers in the roles of executive and project officers to support the implementation of the GCTE science plan. Without those individuals who were able to be full time facilitators, coordinators, and leaders, the GCTE would have not been able to operate successfully. Those individuals include: William Batista, Pep Canadell, Sara Duke, Pablo Inchausti, John Ingram, Elisabeth Huber-Sannwald, George Koch, Diane Pataki and Will Steffen. We also want to thank Rowena Foster who supported with great proficiency the International Project Office (IPO) in Canberra for the entire life of the project.

No GCTE activity or office would have been possible without the engagement and long term commitment of the many funding agencies which supported the offices and the development of networks, workshops, and synthesis efforts.

These long term funding relationships were key to the success of GCTE, enabling the establishment of an IPO and several focus offices that continuously supported the operations of GCTE. The IPO was based in Canberra, Australia and funded by the Australian Greenhouse Office (AGO) of the Department of the Environment and Heritage, and the Australian Commonwealth Scientific and Research Organization (CSIRO); initially in the Division of Sustainable Ecosystems and later on in the Division of Marine and Atmospheric Research. Both AGO and CSIRO Marine and Atmospheric Research are continuing their invaluable support to international research coordination through their support to the Global Carbon Project, a joint project of the Earth System Science Partnership (IGBP, IHDP, WCRP, and Diversitas).

The US-National Science Foundation (NSF), the National Aeronautics and Space Administration (NASA), Stanford University, and the University of Utah in Salt Lake City supported the focus 1 office on ecosystem physiology and biogeochemistry; the US-Department of Energy (DOE) funded many activities related to ecosystem physiology. The Natural Environment Research Council (NERC) through the Centre for Ecology and Hydrology in Wallingford, UK supported the focus 3 office on agroecology and production systems. The Inter-American Institute for Global Change based in Brazil, the University of Buenos Aires, and the CNRS-Ecole Normale Superieure in Paris supported the focus 4 office on functional biodiversity.

On behalf of the GCTE and its sponsor program, the International Geosphere-Biosphere Program, we want to express our appreciation and thanks for the long term commitment and significant contributions to the coordination of international science. This support has enabled the GCTE to leave behind a legacy of improved understanding of the effects of global change on terrestrial ecosystems, and a large community with the scientific capacity to continue this work into a new phase.

Finally we want to thank all the authors of chapters in this book for their time and valuable contributions towards this final GCTE effort.

Josep Canadell, *Diane Pataki*, *Louis Pitelka*
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Chapter 1

Global Ecology, Networks, and Research Synthesis

Louis F. Pitelka · Josep G. Canadell · Diane E. Pataki

1.1 Introduction

The Earth System, including its terrestrial and marine ecosystems, is being altered as a result of human activities. These global changes have been well-documented (e.g., Vitousek et al. 1997; Mooney and Canadell 2001; Steffen et al. 2004). They include changes in the composition of the atmosphere, including increasing concentrations of greenhouse gases; changes in global and regional climate; habitat destruction and land cover change; increases in the amounts of reactive nitrogen compounds in the biosphere; increases in species extinction rates; and increases in the number and impacts of exotic invasive species. The extent and magnitude of human-caused changes has led Nobel laureate Paul Crutzen (2002) to propose that the Earth has entered a new geologic era, the Anthropocene – an era of human domination of the Earth System, in contrast to the previous billions of years of Earth's history when natural forces dominated the Earth.

Nowhere are the impacts of human activities more apparent than in terrestrial ecosystems, with even the most remote and pristine terrestrial systems experiencing the effects of global change. The terrestrial portion of our planet obviously supplies many of the important ecosystem services upon which our society depends, including fresh water and much of our food and fiber. Because global change has the potential to significantly alter the structure and functioning of terrestrial ecosystems, considerable resources have been invested over the past decade on research to understand the effects of global change on ecosystems. In addition, since terrestrial systems are active components of a dynamic Earth System, research has also focused on whether those changes in terrestrial ecosystems are resulting in positive or negative feedbacks to the atmosphere and physical climate system.

Since 1991, the Global Change and Terrestrial Ecosystems (GCTE) core project of the International Geosphere-Biosphere Program (IGBP) has played a leadership role in developing and coordinating an international agenda on the two research areas mentioned above (Steffen et al. 1992). Over 100 synthesis papers and 25 special issues and books were published as a result of GCTE activity, not counting the primary research-data papers that stemmed from the various efforts. A synthesis of the first five years of GCTE research was published in 1999 (Walker et al. 1999) which followed an initial project-wide effort to further define the scientific scope of GCTE (Walker and Steffen 1997). This new volume, unlike the previous ones, describes examples of research conducted under the umbrella of GCTE during the second half of the project and does not intend to provide a comprehensive overview of all research. This chapter places these contributions in a historical context and explains how they fit into the broader GCTE endeavor.

This volume also marks the end of GCTE. After more than a decade of focusing on linkages between geophysical and biological research, the IGBP has entered a new, second phase aimed at describing and understanding the interactive physical, chemical, biological, and socio-economic processes that regulate the total Earth System and the changes that are occurring in this system. Because of the tremendous advances in disciplinary research on specific components of the Earth System made during phase I of IGBP, the global change research community is well poised to undertake the types of more interdisciplinary research that will be required to advance to the next level of understanding of the Earth System. As part of the transition to IGBP II, major restructuring of the core projects has taken place. A number of projects have ended, while new projects that bring together elements of the original projects have been initiated. GCTE is now closed, but IGBP research on terrestrial ecosystems will continue under the new Global Land Project (GLP), a joint project of IGBP and IHDP (the International Human Dimensions Project), built upon the foundations of GCTE and the Land-Use and Land-Cover Change (LUCC) project. The science objectives of the GLP are described in Chap. 25 (Ojima et al. 2007, Chap. 25 of this volume).

The overarching goals of GCTE were

- to predict the effects of changes in climate, atmospheric composition, and land use on terrestrial ecosystems;
- to determine how these effects lead to feedbacks to the atmosphere and physical climate system.

GCTE addressed these goals primarily by playing a coordinating and networking role among new and existing research projects of individual investigators. This role took a variety of forms. Through workshops and conferences involving broad representation from the international global change science community, GCTE developed and implemented a research agenda to address the goals of the project. Another successful strategy used by GCTE to advance global science was to facilitate the development of international research networks to enhance communication and integration. Workshops organized by these networks have produced a large number of synthesis books and journal articles. Still other GCTE activities have included model inter-comparisons and the development of critical databases.

GCTE was originally comprised of four foci: Ecosystem Physiology; Ecosystem Structure; Agriculture, Forestry, Soils; and Biodiversity. It is worth reflecting on the fact that, in the early 1990s, it was necessary and made sense for these four foci to operate fairly independently. At that point, there were models and experiments that focused only on responses of ecosystem physiology (e.g., NPP) to global change (e.g., elevated CO_2). Researchers were interested in how ecosystem structure (e.g., vegetation type) would respond to a changing climate without simultaneously considering effects on ecosystem physiology. Research on agricultural and forestry systems was distinguished from research on more natural ecosystems. And research on the interactions between biodiversity and ecosystem functioning (physiology) was just beginning. A measure of the progress made over the past decade is the extent to which research activities now integrate across two or more of these previously separate subdisciplines, and we will highlight examples in this chapter.

1.2 Carbon and Water Cycles in the 21st Century

Research on the effects of rising atmospheric CO_2 concentrations on terrestrial ecosystems has been a component of GCTE since its inception. At the time GCTE was founded, much of the literature on elevated CO_2 effects focused on individual plants grown under ideal conditions of adequate water and nutrient availability (Mooney et al. 1999). To promote and synthesize ecosystems-based research on the effects of elevated CO_2 on whole communities in the field, the Elevated CO_2 Network began to hold a series of workshops on the role of community responses, belowground processes, interactions with environmental stress, and other key uncertainties in understanding the responses of the terrestrial biosphere to elevated CO_2. An increasing number of experiments have addressed these uncertainties in a variety of biomes from grasslands and forests to drylands, agroecosystems, and more. As a result, our understanding of the variability and complexity of ecosystem responses to elevated CO_2 has improved dramatically over the past decade, particularly with regard to water and nutrient limitations to CO_2 responses, belowground carbon pools, and community scale dynamics (see Chap. 2 by Körner et al.).

Changes in atmospheric CO_2 concentrations in the 21st century will occur in concert with changes in temperature, precipitation, nitrogen deposition, and other aspects of global change. Studies of ecosystem responses to perturbations such as elevated CO_2 or temperature can improve future projections of critical attributes of the terrestrial biosphere such as the carbon balance (see Chap. 6 by Canadell et al.). In addition to the Elevated CO_2 Network, the Network of Ecosystem Warming Studies greatly added to our understanding of global change ecology by synthesizing the results of experimental manipulations of temperature in a variety of ecosystems (Rustad et al. 2001; Shaver et al. 2000; Chap. 3 by Norby et al.). However, interactive effects among multiple disturbances may not be additive and merit further investigation in the next generation of manipulative and modeling experiments. In Chap. 3, Norby et al. review ecosystem responses to warming, interactive effects of CO_2 and temperature, and effects of multiple of aspects of global change as assessed by experimental and modeling results. Relative to responses of individual perturbations, our understanding of interactive effects of multiple global change drivers is at a fairly early stage, and will continue to remain a critical aspect of understanding terrestrial ecosystems responses in the coming decades.

Another important contribution of GCTE was the initiation of the Biosphere-Atmosphere Stable Isotope Network (BASIN), which is still ongoing. As described by Pataki et al. in Chap. 4, the application of measurements of the isotopic composition of atmospheric trace gases in ecosystem-scale studies has provided new information about ecosystem physiology and its role in ecosystem, regional, and the global carbon cycle. Isotopes integrate physical and biological processes over space and time, and are increasingly measured in a variety of ecosystems ranging from virtually unmanaged to highly managed and human dominated. In general, human dominated ecosystems are increasingly of interest to the ecological and global change communities due to their large influence on the atmosphere and climate system, resource availability, and ecosystem services and human welfare. The effects of urbanization on biogeochemistry are reviewed by Pouyat et al. in Chap. 5 as an emerging area of critical importance in quantifying impacts of land use and land cover change, as well as the dynamics of coupled human and natural systems, which will be a focus of the new Global Land Project (see Chap. 25 by Ojima et al.).

1.3 Changing Biodiversity and Ecosystem Functioning

The interest in establishing relationships between biodiversity and ecosystem function arose from the realization that rates of species loss are accelerating due to human activities, particularly due to habitat lost and fragmentation among others. Given that species have different functional traits, major changes in biodiviersity could result in significant changes in biogeochemistry and other processes that regulate the Earth System (Loreau et al. 2001; see Chap. 7 by Diaz et al., and Chap. 10 by Naeem et al.). This GCTE activity quickly moved to include the effects of atmospheric composition and climate change on biodiversity (see Chap. 9 by Potvin et al.), and the effects of rapid expansions of exotic species which can profoundly change the structure and function of many terrestrial and freshwater ecosystems (see Chap. 8 by Vilà et al.).

The GCTE established a focus on this topic in partnership with the emerging program of Diversitas, leading the development of what was a completely new field of research early in the 1990s. It soon became clear that functional changes due to species loss, addition or replacement could have significant impacts on ecosystem properties such as productivity, decomposition rates, nutrient cycling, and resistance and resilience to perturbations. Numerous reviews were instrumental in the development of this new field (Sala et al. 1999; Loreau et al. 2001, 2002; Hooper et al. 2005). These syntheses described some fundamental patterns (Hooper et al. 2005): *(i)* Certain combinations of species are complementary in their patterns of resource use and can increase average rates of productivity and nutrient retention, *(ii)* Susceptibility to invasion by exotic species is strongly influenced by species composition and, under similar environmental conditions, generally decreases with increasing species richness, *(iii)* Having a range of species that respond differently to different environmental perturbations can stabilize ecosystem process rates in response to disturbances and variation in abiotic conditions.

Finally, GCTE also led the development of new biodiversity scenarios with a first attempt at mapping changes in the global distribution of species due to climate and land use change (Sala et al. 2000).

1.4 Landscapes under Changing Disturbance Regimes

Disturbances such as fire, pests, windthrow, and harvesting are important in determining the structure and functioning of terrestrial ecosystems. Global warming and other forms of global change will further perturb ecosystems over the next decades, and will interact with the other forms of disturbance in complex ways. The chapters in this section are examples of research conducted over the past decade to better understand how changing disturbance regimes will interact with and affect ecosystems.

One of the key effects of climate change on ecosystems will be adjustments in the ranges of plant and animal species, and accordingly, of communities and biomes. It is well known from the paleoecological literature that species have migrated in the past in response to changes in climate (e.g., Davis and Shaw 2001), and relatively recent evidence demonstrates that species ranges are already beginning to change in response to contemporary climate change (Parmesan and Yohe 2003; Walther et al. 2002). A critical question given the expected rate of climate change over the next decades is whether and which species will be able to migrate fast enough to keep pace with the changing climate. The answer to this question is relevant to issues as diverse as the conservation of species and the carbon balance of ecosystems. It has been recognized for some time that models of ecosystem response to climate change must include migration, but the challenges of incorporating these effects into models are immense. A GCTE activity was devoted to this issue (Pitelka et al. 1997; Neilson et al. 2005), and in Chap. 11, Midgley et al. review our current understanding and the hurdles that still face ecologists in understanding and predicting future migrations of plants.

Migration is actually a two-part process, with one being dispersal and the second successful establishment and population growth. Disturbance by fire could be one of the most important mechanisms that would facilitate and speed up the successful establishment of migrant species. Because fire occurs across much of the Earth's land surface, it also has great significance for the carbon budget of terrestrial ecosystems. Thus, it is critically important for ecologists to understand how fire regimes might change with global change and incorporate this understanding in models of ecosystem response, especially to climate change. Keane et al. (Chap. 12) review models of vegetation dynamics that incorporate fire and describe our current understanding of global fire dynamics.

A major concern throughout global change science is the potential for non-linearities in responses of ecosystems or other components of the Earth System (Steffen et al. 2004). Fire is an example of a process that can spread non-linearly across space and generate cascading effects (see Chap. 14 by Peters et al.). Unless scientists can identify where and when non-linear responses are likely, human society will like be unprepared for their occurrence, and thus the consequences are likely to be far greater than if the response had been identified and anticipated. In Chap. 14, Peters et al. describe a general framework for understanding and predicting spatially non-linear responses to global change.

A GCTE activity that built on the understanding developed in other areas of GCTE research, including the efforts referred to above, is the development of Dynamic Global Vegetation Models or DGVMs. Early in the history of GCTE entirely different classes of models were employed to simulate how climate change affects ecosystem structure and composition vs. ecosystem processes. These models were equilibrium models that could not predict how long it would take to reach a future state or the vegetation dynamics of the process. The next development was a simple linking of vegetation and ecosystem models such that the ecosystem models used the future vegetation distribution predicted by vegetation models as inputs (VEMAP Members 1995). Meanwhile, ecosystem modelers recognized the need to fully couple vegetation and ecosystem models and make them dynamic, i.e., to develop DGVMs. Prentice et al. (Chap. 15) provide a review of DGVMs, including their successes in simulating various phenomena, as well as their limitations.

DGVMs and most other types of models described in this section do not simulate individual plant species but rather group species into a relatively small number of *plant functional types*, or PFTs, with similar morphological and physiological traits. Lavorel et al. (Chap. 13) describe the efforts to develop useful and logical classifications of plants into PFTs.

1.5 Managing Ecosystem Services

Many of the GCTE activities directly contributed to a better understanding of the provision of goods and services for the well-being of human societies, and how those goods and services were being altered by changes in atmospheric composition, climate and land use. However, the single biggest contribution came from the focus on "agroecology and production systems" which dealt with the effects of global change on the production of food as a key component in global food security. A number of networks and consortia were established to study individual crops including wheat (see Chap. 16 by Porter et al.), rice, potato, pastures, and forest plantations. Key outcomes from this research were a better understanding of the benefits of increasing atmospheric CO_2 on crop production and how warming, nutrients, and water modulate that response, either by dampening it or by enhancing it depending on the particular combination. Temperature thresholds for crop failure were also identified for some of the rice varieties growing under elevated CO_2 and warming. This research naturally included the role of agricultural pests in reducing food production and how climate change is likely to alter pest-plant dynamics (see Chap. 17 by Sutherst et al.).

The work in agroecosystems also extended to the integration of food/fiber production and biogeochemistry to fully account for plant-soil feedbacks, and with that the study of soil carbon sequestration which yielded one of the important legacies of GCTE, a global soil organic matter database and a number of carbon sequestration assessments under different climate and management scenarios (SOMNET; see Chap. 18 by Smith et al.).

A key development which required higher level integrative research was the one on complex agroecosystems and farm-level integration of the management of single units of land with multiple crops, as separate subsystems, or as a single interconnected complex systems. The latter are still the systems that much of the world's population relies on for food and fiber despite an overall push for intensification and simplification.

Two additional chapters complement what is perhaps one of the most critical trade-offs in managing ecosystem goods and services, that between carbon and water. Chap. 19 by Jackson et al. focuses on this trade off in conversions to forests and shrublands, and Chap. 20 by Reynolds et al. focuses on a new paradigm to explain the natural and human dimensions of land degradation in arid and semi-arid regions.

1.6 Regions under Stress

The GCTE made a substantial effort to initiate research on the effects of global change on terrestrial ecosystems in parts of the world where little research or capacity existed despite playing key roles in the functioning of the Earth System.

Early in the 1990s the GCTE developed the transect approach for global change research, establishing 15 transects in critical regions of the world to cover most environmental conditions and biomes/ecotones with special attention to highly sensitive regions (e.g., high latitudes and tropical regions) (Canadell et al. 2002).

The transect approach has evolved over the years to comprehensive regional studies building upon the initial research undertaken during the 1990s. In this book we present research focusing on several key sensitive regions in the world including tropical Asia (see Chap. 21, Murdiyarso et al.), regions affected by the Monsoon climate (see Chap. 22 by Zhou, and Chap. 23 by Kohyama et al.), and high latitude ecosystems (see Chap. 24, McGuire et al.).

1.7 The Way Forward

As noted earlier, the GCTE has now ended, but clearly there is still much to do to understand the effects of global change on terrestrial ecosystems. Research on terrestrial ecosystems will continue under the auspices of the new Global Land Project (GLP), a joint project of the IGBP and the International Human Dimensions Program (IHDP). The GLP will integrate research elements from both GCTE and the Land-Use and Land-Cover Change (LUCC) project, the latter already jointly sponsored by the IGBP and IHDP. A major goal is to treat human activities and decision-making as an integral part of the terrestrial system, the so called human-environment system. The final chapter of this book, Chap. 25 by Ojima et al., describes the science objectives of the GLP and the innovative research agenda on land for the next decade (GLP 2005).

In addition, GCTE has also contributed a great deal to the development of the scientific agendas of the Global Carbon Project (GCP) and the Global Environmental Change and Food Systems (GECAFS), both joint projects of the new Earth System Science Partnership (ESSP). The ESSP has brought together IGBP, IHDP, the World Climate Research Program, and Diversitas, and has developed a highly interdisciplinary and integrative research agenda to support Earth System sustainability.

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Part A

Carbon and Water Cycles in the 21st Century

Chapter 2

CO_2 Fertilization: When, Where, How Much?

Christian Körner · Jack Morgan · Richard Norby

2.1 Carbon a Limiting Plant Resource?

Among the certain facets of global change, the steady CO_2 enrichment of the atmosphere affects plants directly. CO_2 is a substrate for photosynthesis, and for most (C_3) plant species CO_2 concentrations will remain below saturation levels of photosynthesis even at twice-current concentrations. Thus, the photosynthetic CO_2 response curve (a saturation function with a near-linear initial part and a plateau reached at close to 1 000 ppm) became the corner stone of modeling the biological consequences of rising of CO_2, because it was assumed to represent the degree of CO_2-fertilization in plants. In fact, models built around this response function forecast an approximately 290 Gt carbon sequestration into the terrestrial biosphere (biomass and soils) within the 21st century (e.g., Cao and Woodward 1998; IPCC 2001), raising hopes for a significant biotic mitigation of atmospheric CO_2 enrichment, which currently measures 3–4 Gt C yr^{-1}.

Thirty years of research, the most active part in the GCTE decade (1993–2003), have produced an estimated more than 4 000 publications (Körner 2000) in essence testing this or related hypotheses. It turned out that the rate of CO_2 uptake per unit leaf area is a rather unreliable predictor of plant growth and the cascade of follow up ecosystem processes. This limits predictions of future plant growth and crop production and it also restricts the credibility of estimates of the amounts of carbon that could be sequestered to the biosphere as a result of 'CO_2-fertilization'.

Still not fully resolved, the discrepancy between photosynthetic stimulation by elevated CO_2, which is almost always observed, and actual plant growth responses, which vary considerably, became a central problem in predicting both the biosphere's future in a CO_2-rich world and the potential of biological mitigation of atmospheric CO_2 enrichment. A related quandary has been the observed stimulation of growth in the less common but important C_4 class of plants through elevating CO_2 above present ambient levels (Wand et al. 1999; Ghannoum et al. 2000), since C_4 photosynthesis was thought to be saturated at present atmospheric CO_2 concentrations (Bazzaz 1990; Bowes 1993). A weak quantitative linkage between photosynthesis and growth (or yield) has long been known among crop breeders (Evans and Dunstone 1970; Saugier 1983; Wardlaw 1990), and there are many reasons for the mismatch between the CO_2-stimulation of photosynthesis and the actual biomass responses, but the most important ones are:

(1) The photosynthetic uptake of CO_2 depends on the total photosynthetically active surface of a plant and its integrated CO_2 flux activity over time (not easily quantified in discontinuous leaf-level gas exchange measurements) relative to its respiratory losses by heterotrophic tissue, (2) CO_2 release by respiration, which likewise depends not only on tissue specific rates but on the contribution of various, differentially active tissues to total plant biomass, and (3) the unknown export of assimilated carbon through roots, either directly to the rhizosphere microbe community or to mycorrhizal fungi.

With these and some other minor components of the internal carbon housekeeping, plants co-control their carbon investment in addition to their control over photosynthesis. The relationship between carbon uptake (source activity) and carbon investment (sink activity) drives the net outcome in terms of growth and biomass production.

It is obvious that these carbon investments also depend on resources other than CO_2, in particular mineral nutrients. A common effect of short-term plant exposure to elevated CO_2 is a reduced consumption of nutrients, but also water, per unit of biomass produced (Drake et al. 1997) or a constant consumption at greater biomass per unit land area (Niklaus and Körner 2004). In cases where total nutrient uptake is increased under elevated CO_2 (Finzi et al. 2002) this will deplete soil resources in the long run. In cases where tissue nutrient concentrations are depleted, this will induce cascades of negative ecosystem level feedbacks, which eventually may also cause initial rates of carbon gain to diminish. In many cases, it became questionable whether carbon is a limiting resource at the whole plant or ecosystem level (Körner 2003a). It is worth recalling that all taxa of today's biosphere grew and reproduced successfully with only 180–190 ppm, half the current CO_2

concentration, 18 000 years before present (peak of last glaciation). Based on this reference period, current biota operate already in a double CO_2 atmosphere. In addition, the observed reduction of water consumption per unit land area is likely to induce climatic feedbacks (through a drier atmosphere), not yet accounted for in experiments. Furthermore, any CO_2 enrichment effect on plants will depend on their developmental stage, with younger plants more responsive than older ones (Loehle 1995). Most of the CO_2-enrichment responses for woody species available to date are – for very practical reasons – for young, rapidly expanding life stages, during which carbon is more likely a limiting resource.

All together these interdependencies are making predictions of the biosphere's overall response to elevated CO_2 far more difficult than was thought initially in view of the straightforward photosynthetic CO_2 response of leaves. The experimental evidence exemplified here, points at the need to reconsider the largely source activity dominated model parameterisation and to account for the constraints to carbon sink activity. Using current atmospheric carbon relations, Schimel et al. (2001) find the biosphere roughly in balance, i.e., deforestation being balanced by new C-fixation, part of which is due to forest expansion, hence leaving a much smaller leeway for CO_2-driven C-sequestration compared to what was anticipated during the 1980s.

In contrast to theoretical models, experiments are limited in space and time, and manipulations may disrupt ecosystem processes and thus, can create artifacts, though directions of responses are commonly still identified correctly in such situations (Norby et al. 1999). A major limitation, however, is that more than 80% of the Earth's life biomass is stored in wood, but trees are too big to be studied in conventional test systems, and it is nearly impossible to put a mature forest into an enclosure. Free air CO_2 enrichment (FACE) at such scales entails exorbitant costs, so that tests remained restricted to a few places and mostly fairly young trees. FACE refers to a CO_2-release system that does not need any enclosures, but freely releases (controlled by a computer in connection with an infrared gas analyser) CO_2 over test plots. The situation is far better for grassland and agricultural crops, where the low stature vegetation permits smaller CO_2-enrichment plots and where enclosures create fewer artifacts.

In this summary we will highlight what we think were major achievements during the last decade and we will restrict our considerations to the most realistic field tests, largely but not exclusively, using free air CO_2 enrichment *in situ*. Given the urgent need for forest data, these will receive particular attention. We will not re-review this vast field, but will try to illustrate the major lines of evidence and future needs in this arena of global change research.

2.2 Long-Term Biomass Responses and Carbon Pools

Whether a measured biomass gain under a step increase of CO_2 and otherwise unchanged life conditions reflects a change which might be seen in the real world, depends on three factors: time, nutrients and water. In addition, global change factors in the real, future world like temperature change (apart from effects on water, see Norby et al. 2007, Chap. 3 of this volume), light (change in cloudiness), and biotic interactions, will co-determine CO_2 effects. There have been few attempts at deciphering such interactions under realistic test conditions (see e.g., Rawson 1992; Shaw et al. 2002; Vonder et al. 2004; Wan et al. 2004) and the answers so far are inconclusive, with no clear interactive effect (Pendall et al. 2004). The general impact of a warming climate on the carbon balance of ecosystems will be dealt with elsewhere in this volume (Norby et al. 2007, Chap. 3 of this volume). We will, however, refer to the significance of interactions between CO_2 and light for tree seedlings and lianas in shaded habitats.

2.2.1 Time Matters

Plants with determinate growth (annuals, many crops) may grow faster initially at elevated CO_2, but end up with similar biomass accumulation per individual a couple of days or weeks earlier than controls, except under very fertile conditions. This was so for most of the 25 species of semi-desert winter annuals from the Negev desert of Israel, grown for their full life cycle in elevated CO_2, with only one species, namely one of the five legumes (the most 'mesic' one), taking great advantage of CO_2 enrichment, causing the whole sward to end up with more biomass (Grünzweig and Körner 2001, Fig. 1). In seedlings or saplings of woody species, such initial responses (when space and nutrients are ample and plants are very leafy) will cause future growth to capitalize on size differences induced by CO_2 very early in their life (analogous to compound interest in economics), which has nothing to do with ongoing CO_2 stimulation. Such initial responses simply shift the growth curve in time (Norby et al. 1995; Loehle 1995; Körner 2000; Spinnler et al. 2002) and cause the date of harvest to determine the difference in biomass gain.

Among the many other time dependent drivers of plant and ecosystem CO_2 responses, changes in community composition are important, and soil responses are particularly critical, given the size and slow turnover of soil C pools. Most of the humus carbon stored in soil is of very old age (often >1 000 years) and only a small fraction (commonly <1% in steady state systems) participates in year to year C-turnover. Mass based assessments of soil carbon are thus near to impossible. On the other hand, carbon tracer experiments with true control (also the ambient CO_2 system being labeled at the same rate) are restricted to small scale, highly disturbed test systems (e.g., Leavitt et al. 2001; Niklaus et al. 2001). So, experiments provide rather limited access to the long-term fate of C in soils, but may point at some likely trends.

2.2.2 Nutrients and Water Determine Biomass Responses at Elevated CO_2

Grassland biomass responses to elevated CO_2 reported in the literature (Körner 2002) are clearly related to the fertility of the test conditions as well as to soil water availability. In mesic grasslands, CO_2-induced biomass increases are greater under more fertile conditions (e.g., Hebeisen et al. 1997). Alpine grassland seems to be an exception, since there was no positive growth response to elevated CO_2 even when mineral nutrients were added (Schäppi and Körner 1996). In native and semi-natural grasslands with no fertilizer amendments (Fig. 2.1), the seasonal biomass response to elevated CO_2 appears to be more pronounced in dry years, as a result of the CO_2-induced stomatal reduction of transpiration. This indirect water relations response to CO_2 enrichment increases leaf and canopy-level water use efficiency, extends the effective growing season in drier grasslands, and enhances nutrient availability (Morgan et al. 2004a). Most grasslands are characterized by periods of water shortage (Stephenson 1990; Campbell et al. 1997) and thus experience this indirect water relations benefit. A serious constraint on the usefulness of grassland biomass data produced under elevated CO_2 is the extrapolation of these indirect CO_2 effects to future environments because such water relation responses to CO_2 may not be seen in reality. At the landscape scale, reductions in leaf conductance to water vapor will lead to a drier and warmer atmosphere, which in turn would increase evaporative losses. Warmer future ambient temperatures will enhance such evaporative losses, while predicted higher humidity in some locations might reduce them (IPCC 2001). The final outcome will depend on complicated interactions between the atmosphere and the biosphere that are difficult to predict, and will vary geographically. Thus, much of the presumed direct CO_2 effects on grassland biomass (Fig. 2.1) are in fact indirect water relations responses (Morgan et al. 2004a) that will have to be corrected for future atmospheric humidity conditions and humidity driven biosphere/atmosphere feedback – a major forthcoming challenge for modeling.

With these caveats, the seasonal gain in harvestable biomass of seven different grassland systems is between 0% and 30%, with the Californian grassland showing the largest and the alpine the smallest response. Removing the CO_2-induced moisture effect on biomass, the remaining effect will most likely be smaller than +10% for a doubling of CO_2 in most cases. Here and in the following, it is important to distinguish between net biomass accretion (what is left for harvest at peak season or after a season) and the total biomass which had been produced during a year, irrespective of whether it was preserved or had been recycled i.e., lost before harvest. The latter is called net primary production (NPP), and is much larger than, and not to be confused with, the standing stock of biomass.

Mature forest trees have been exposed to elevated CO_2 only in a few cases, with the majority of data coming from young trees in enclosures. A particularly valuable source of data has come from trees growing around natural sources of CO_2 (Miglietta et al. 1993; Amthor 1995). Oak trees (*Quercus ilex*) grown around natural CO_2 springs in Italy, showed a significant stimulation of tree ring growth during their years of re-growth after coppicing (Hättenschwiler et al. 1997), very similar to the responses seen in scrub-oak after fire (Dijkstra et al. 2002). Such re-growth situations after complete losses of above

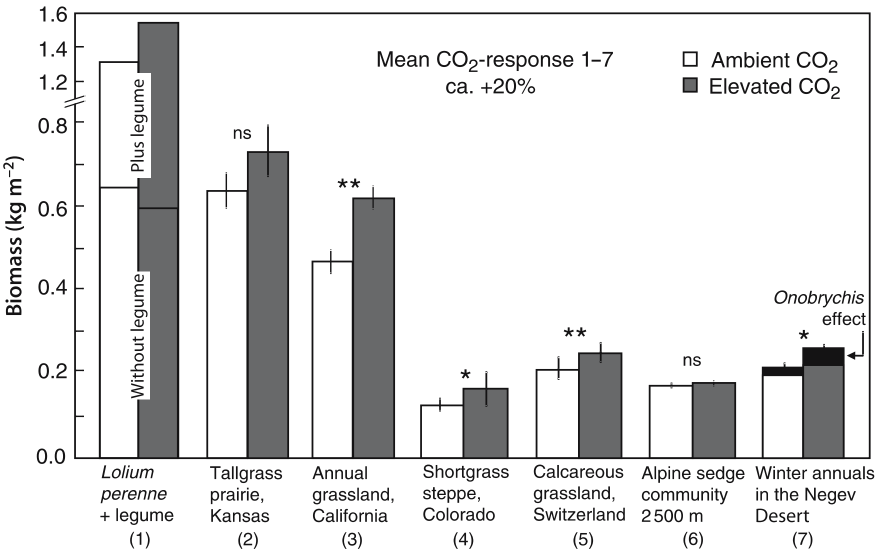

Fig. 2.1.
A comparison of biomass responses to elevated CO_2 in 6 natural grassland ecosystems (all grown on unfertilized ground) plus one artificial *Lolium perenne/Trifolium repens* stand (*1*). The prairie (*2*) and calcareous grassland (*5*) data are multi-year averages, with the positive effect largely introduced by dry years. Bars indicate plus/minus one standard error. References: (*1*) Hebeisen et al. (1997a), 5 cuts per year, 12 g N m^{-2} a^{-1}, (*2*) Owensby et al. (1997), (*3*) Shaw et al. (2002), (*4*) Morgan et al. (2001), (*5*) Niklaus et al. (2001), Körner (2000), (*6*) Körner et al. (1997), (*7*) Grünzweig and Körner (2001)

ground structures represent a life phase for these trees with unlimited nutrient supply and ample space and light, conditions where carbon-assimilation may be the prime limitation of growth. Later, as stands close, the biomass relationships are re-established and excess nutrients are used up, the gain would be expected to vanish. Indeed, the gain in growth of Mediterranean oaks around CO_2 springs was greatly diminished compared to controls after about 25 years of growth under elevated CO_2 (Hättenschwiler et al. 1997).

Trees growing in older stands, which had reached a closed canopy before the onset of CO_2 enrichment may thus show much smaller CO_2 stimulation or more rapid re-adjustment to previous growth rates than was found in seedlings and saplings. Total foliage area (LAI) of fully developed canopies has not increased in response to CO_2 enrichment in any closed canopy system studied so far (Körner and Arnone 1992; Hättenschwiler and Körner 1996; DeLucia et al. 2002; Norby et al. 2003); hence, any growth response must derive from an enhancement of growth per unit leaf area.

Three FACE experiments have been operating in tree stands starting with fully developed canopies: a pine (*Pinus taeda*) stand in the Duke forest in North Carolina, a sweetgum (*Liquidambar styraciflua*) stand at the Oak Ridge National Laboratory in Tennessee, and a mature multi-species deciduous forest near Basel, Switzerland. The young monospecific stands have shown a sustained increase in productivity in response to elevated CO_2, but the trajectory of growth response has differed. Increased productivity in the pine stand has resulted in more stem growth and more leaf litter production (Hamilton et al. 2002; DeLucia and Moore 2005, Fig. 2.2a). Analysis of an additional plot at the Duke FACE site, however, suggested that an N limitation would cause this growth stimulation to disappear (Oren et al. 2001). Productivity in the deciduous sweetgum stand has been 22% higher in elevated CO_2, but the initial stimulation of aboveground growth disappeared after the first year (Norby et al. 2002; Fig. 2.2b). Instead, the additional carbon assimilated in elevated CO_2 has supported a large increase in fine-root production (Norby et al. 2004). The inherent difference in fine-root turnover rates in the pine and sweetgum stands (Matamala et al. 2003) may be an important determinant of whether a CO_2 stimulation of productivity results in increased growth or increased turnover, and this difference affects the long-term fate of C in the ecosystem.

The Swiss forest FACE experiment as been run for 4 years only, and the 30 m tall trees belong to several species, requiring a careful analysis of long tree ring chronologies to overcome obvious replication problems in the case of such large 'experimental units' and their restricted number. However, accounting for pre-treatment differences in vigor of individual trees (via tree ring analysis), the stem growth trajectory is similar to the one seen in the Oak Ridge FACE, showing a stimulation of radial growth in 100 year old beech in the first year which disappeared thereafter (Fig. 2.2c; Körner et al. 2005). Surprisingly, leaf photosynthetic capacity showed no down

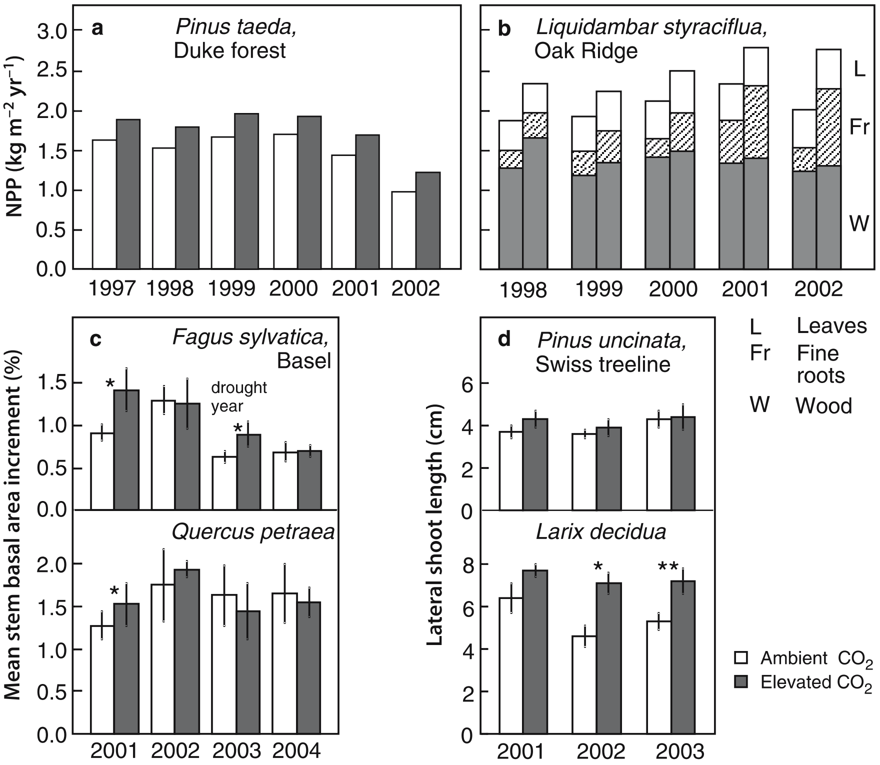

Fig. 2.2.
A synthesis of in situ biomass responses of mature trees to Free Air CO_2 Enrichment (FACE). Net primary production (NPP) estimated from basal area increment, leaf litter collection, and minirhizotron analysis for **a** a *Pinus taeda* (loblolly pine) plantation in North Carolina (DeLucia et al. 2005), and **b** for a uniform stand of *Liquidambar styraciflua* (sweet gum) in Tennessee, in this case separated by biomass compartments. Note the exclusive effect on fine roots (Norby et al. 2004). **c** Mean stem basal area increase (+ s.e.) in 2001–2004 of oak and beech at the Swiss Canopy Crane site (Asshoff et al. 2006). **d** as in **c**, but for shoot growth response to three consecutive years of free air CO_2 enrichment in 30 year old larch and pine trees growing at treeline (Swiss Alps, 2200 m). Mean shoot length was based on five lateral branches per tree ($n = 5$ trees per species/CO_2 level; Handa et al. 2005)

ward adjustment (Zotz et al. 2005), but soil CO_2-emission suggests enhanced carbon throughput in this system as well (Steinmann et al. 2004), which is in line with earlier findings for complex model ecosystems (Körner and Arnone 1992; Hättenschwiler and Körner 1996, 1998). The only case where woody plants showed a near homoeostatic downward adjustment of photosynthesis under elevated CO_2 is the desert FACE experiment in Nevada (Hamerlynck et al. 2002). One may speculate that this has to do with a lack of significant below ground biological activity (e.g., mycorrhiza). A fourth FACE test established at the Swiss high elevation climatic treeline in 30 year old 1.5 to 2 m tall pines (*Pinus uncinata*) and larches (*Larix decidua*) also revealed an initial pine response, which disappeared by year three, but so far, a positive response in larch is persisting (Handa et al. 2005, Fig. 2.2d).

In summary, these data suggest a rather limited growth stimulation in mature trees, after the initial effect of a step-increase in CO_2 concentration is surpassed. However net primary production and the associated carbon turnover become enhanced in a high CO_2 environment, explaining in part the discrepancy between photosynthetic stimulation and biomass responses. The challenge for the future is to identify the fingerprints of enhanced carbon flows through undisturbed soils.

The available data for tall, closed canopy forests contrast with the significant stimulation often reported for seedlings or saplings grown under favorable experimental conditions. However, seedlings growing in deep forest shade, will take great advantage from the reduced light requirements for photosynthesis under elevated CO_2 under natural conditions, as was documented in situ for both a tropical (Würth et al. 1998) and a temperate forest (Hättenschwiler and Körner 2000). Under such conditions, elevated CO_2 is likely to affect tree recruitment in favor of particularly responsive species, and likely could affect future forest composition (see also the effect on lianas below).

2.2.3 Scaling from Growth to Carbon Pools

Great care is advised when translating such plot-based data into landscape carbon gains (Amthor 1995). At these larger scales the mean residence time of carbon per unit land area influences carbon stocks. If trees would grow faster and mature earlier, tree turnover would be greater, but not necessarily the mean C-storage in biomass. In fact, a faster forest rotation may reduce the forest C-pool. There is evidence for accelerated maturation in pine trees grown in elevated CO_2: cones were produced earlier and in greater masses than in controls (LaDeau and Clark 2001). The above described transient nature of tree growth responses to elevated CO_2 and the contribution of CO_2-induced water savings, which may in part be artifacts, because of a lack of atmospheric feedback, set rather stringent limits to expected growth stimulations in a CO_2-rich world. Accelerated development may reduce mean forest carbon stocks (Körner 2003b, 2004), but enhanced C-turnover may also feed more carbon into the humus compartment, a rather uncertain projection, given the high demand for nitrogen and other minerals to form the complex humus aggregates.

Thus, an important message to users of experimental findings is that growth or productivity, i.e., a rate of carbon incorporation, as they are documented in some cases, should not be confused with the amounts of carbon stocked per unit land area. It is the latter which matters for sequestering carbon away from the atmosphere. In terms of carbon storage policy, a high stocking rate (e.g., old growth forests) is desirable rather than a faster forest rotation, as it may become facilitated by elevated CO_2 in plantations on fertile ground. Such growth stimulations, however, can add to the substitution of fossil by renewable fuels and products.

2.3 Carbon to Nutrient Ratios and Consumer Responses

2.3.1 The C to N Ratio Widens

It has been documented many times that exposure of plants to elevated CO_2 causes an increase in non structural carbohydrate concentrations (NSC; e.g., Körner and Miglietta 1994 for natural CO_2 springs, underlining the long term nature of this response) and a reduction in leaf nitrogen concentrations (Cotrufo et al. 1998; King et al. 2004). However, N-depletion is not a universal effect and often is a dilution effect caused by NSC accumulation, disappearing on an NSC-free dry matter basis. In tissues other than leaves, such changes have been seen less frequently. But seeds have also been found N-(protein)depleted in plants grown under elevated CO_2 under natural growth conditions (Fig. 2.3a), and in wheat when not heavily fertilized, with far ranging nutritional consequences (see below). Secondary compounds do respond as well, but in unpredictable direction (Penuelas and Estiarte 1998). An increase in desired mobile carbon compounds could be an asset. For instance the rubber tree might be expected to produce more latex and thus channel excess carbon assimilates in this non-structural biomass compartment. A growth chamber test with a relative of the rubber tree, *Euphorbia lathyris*, one of the so-called Diesel-plants, from which one hopes for fossil fuel substitutes, ended with a big surprise (Häring and Körner 2004). Elevated CO_2 significantly reduced latex production (Fig. 2.3b), unless plants received a lot of N-fertilizer. So far, stem wood produced under elevated CO_2 has not yet been found to contain less N or more NSC. Hence the idea that a widening of the C/N ratio in wood could allow more wood carbon to accumulate in the landscape with a given N supply has so far not been supported by data.

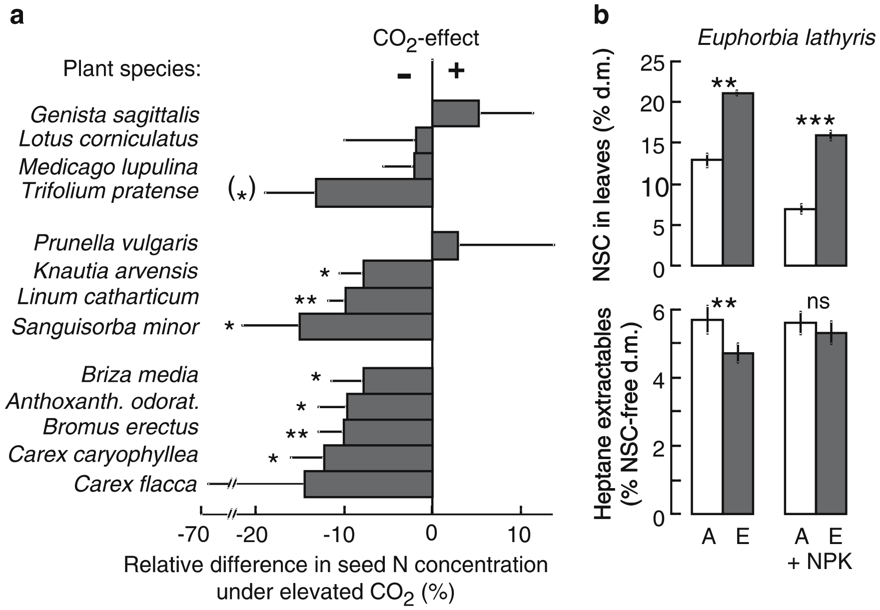

Fig. 2.3.
Elevated CO_2 influences plant chemical composition. **a** Relative difference in seed nitrogen-concentration under elevated compared to ambient CO_2 concentration in a calcareous grassland community (Thürig et al. 2003). **b** Effect of elevated CO_2 on non-structural carbohydrate concentration and concentration of heptane extractable hydrocarbon (latex) in *Euphorbia lathyris* leaves (Häring and Körner 2004)

2.3.2 Consequences for Herbivory, Decomposition and Plant Nutrition

A shift from protein to carbohydrates or more generally a wider C/N ratio is commonly considered negative for consumers (herbivores) and litter break down (decomposition). Some animals feed at equal rates and thus have reduced protein uptake rates, some feed less when faced with the N-depleted food, others compensate by feeding more, and others shift to other host plants. One important conclusion is that animals behave differently when given a choice of food plants (for reviews see Lincoln et al. 1993; Kinney et al. 1997). Reduction in forage quality due to CO_2 enrichment is a common theme in grassland CO_2 enrichment work (Owensby et al. 1996; Milchunas et al. 2005), and will likely have important consequences for many grazers. Altered grazing of CO_2-enriched forage may also feed-back on forage quality since re-growth tissue often differs in quality from non-defoliated tissue (Milchunas et al. 1995), and ultimately interacts with the environment to determine plant community composition. The change in seed quality (Fig. 2.3a) propagates effects to the next generation, but seedling success did not reveal strong influences when tested. Cereal grains, besides the nutritional effect as such, had been found to be of reduced baking quality in cases where elevated CO_2 was applied without extra fertilizer (e.g., Kimball et al. 2001).

Initial thoughts that leaf quality changes may translate into litter quality changes and a slowing of decomposition have not been supported by the majority of tests (O'Neill and Norby 1996; Norby et al. 2001; but there are a few exceptions). Effects may depend on the maturity of the test system and timing of the trial. Another key aspect is the export of excess carbohydrates to rhizosphere microbes, which then become competitors for nutrients (e.g., Zak et al. 1993) and may even draw down productivity (Díaz et al. 1993; Hättenschwiler and Körner 1996; Shaw et al. 2002).

2.4 Plant Water Relations and Hydrological Implications

As briefly addressed in the biomass section, elevated CO_2 influences plant water relations through its effect on stomata. In turn plant water consumption influences soil moisture and atmospheric humidity, both feeding back on plants. Soil moisture feedback can be controlled and documented, or even simulated experimentally, but atmospheric feedback cannot. Hence all assumptions on influences of atmospheric CO_2 on hydrology depend on the nature of this feedback, which needs large-scale climate models to estimate. We recall, that between 65 and 70% of all vapor loss from vegetated land masses passes through leaf stomates (Maniak 1988; Gerten et al. 2005), thus causing any CO_2-driven effects to have substantial impact on the water balance.

Currently available data for natural ecosystems suggest a remarkable balance between stomatal responses and aerodynamic resistance which operates in a way so that water savings for a doubling of preindustrial CO_2 (ca. 550 ppm) are surprisingly similar for grassland, deciduous forests and conifer forests, despite large differences in stomatal responsiveness (Fig. 2.4). Although, signals differ a lot with species, with some responding strongly and others not at all, average stomatal conductances in grassland and crops may drop by 30 and 50% of controls (Knapp et al. 1996; Lauber and Körner 1997; Ainsworth et al. 2003; Kimball et al. 2002; LeCain et al.

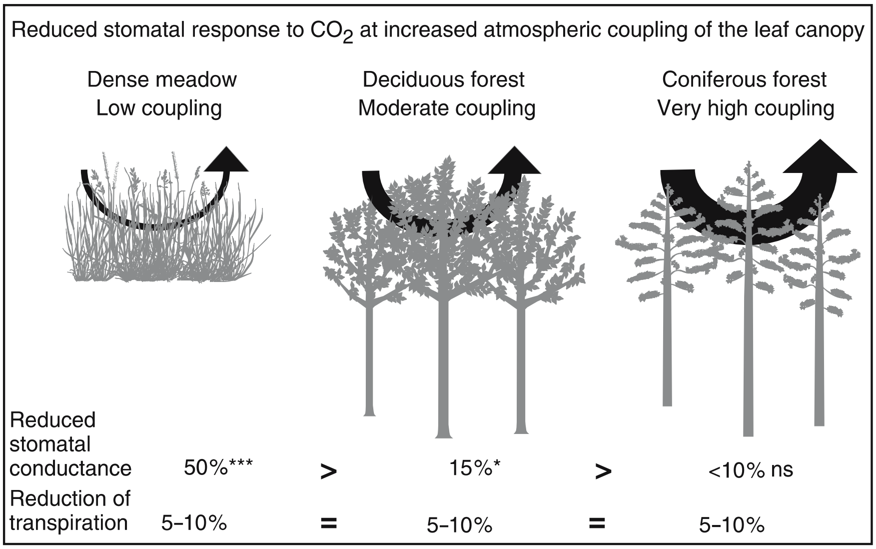

Fig. 2.4.
A synthesis of water relations responses to elevated CO_2 for three types of vegetation. *Round arrows* symbolize the degree of canopy ventilation (a distillate from various sources, references in the text)

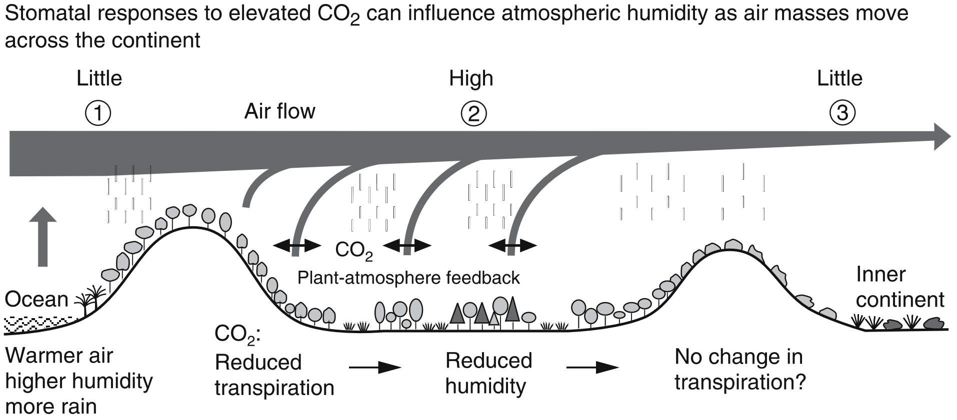

Fig. 2.5. Schematic landscape scale vegetation-atmosphere interaction resulting from stomatal responses to elevated CO_2 (Fig. 2.4). Coastal regions *(1)* are exposed to ocean driven atmospheric humidity (no or little vegetation-climate feedback). As air masses move across the continent, they take up moisture from transpiring vegetation, but based on available experimental data 5–10% less (Fig. 2.4) when elevated CO_2 reduces stomatal opening, with cascading downwind consequences for humidity *(2)* which feed back on transpiration to a point, where transpiration becomes very low in the semiarid continental interior *(3)* with minor vegetation influence on the atmosphere. Horizontal arrows symbolize regions of intense CO_2-driven interactions between vegetation and climate

1993; Bunce 2004). In deciduous forest trees, signals average at around −20% (Saxe et al. 1998; Medlyn et al. 2001). It was a big surprise that none of the adult conifers ever tested produced the theoretically expected stomatal signal, which means, if there is a response, it would be within measurement error, i.e., smaller than 10% (e.g., Barton et al. 1993; Pataki et al. 1998; Ellsworth 1999).

This sequence of responsiveness at the stomata level is the reverse of atmospheric coupling, with dense grassland most strongly decoupled and conifers very well coupled to air circulation. Actual water flux studies in non-chambered grassland (e.g., Stocker et al. 1997) and cereals (e.g., Pinter et al. 1996), in deciduous forest trees (Wullschleger et al. 2002; Hungate et al. 2002; Cech et al. 2003) and in conifers (Schäfer et al. 2002), almost all arrive at seasonal savings between 5 and 10%, more close to 5%. Such a uniform effect is good news for model parameterization and is in line with an earlier proposition of such a balance of stomatal and aerodynamic controls of transpiration (Meinzer and Gantz 1991; Meinzer et al. 1993). Effects have been larger in some closed or semi-closed systems in which atmospheric coupling may have been enhanced, (e.g., Owensby et al. 1997). At the canopy scale, a best current guess is a reduction of evapotranspiration in this range, yet, without accounting for atmospheric feedback, which will reduce the effect. So, a realistic signal for hydrological considerations may be a 5% reduction in transpiration for twice pre-industrial CO_2 concentrations, irrespective of plant functional type. It is noteworthy that for plants it matters *when* these savings happen. Otherwise small differences in water consumption can improve drought survival. In wet conditions they may also enhance runoff. An important consensus from experimental results is that effects are strongest under high humidity and decline rapidly as the vapor pressure deficit exceeds 10–15 hPa (Wullschleger and Norby 2001; Cech et al. 2003), an observation confirmed by earlier measurements in trees around natural CO_2 vents (Tognetti et al. 1996). Transferred to a landscape or continental scale, any reduction of vapor loss will change atmospheric moisture loading, which in turn, would affect (increase) vapor loss from vegetation (Fig. 2.5).

2.5 Stress Resistance under Elevated CO_2

Exposing plants to elevated CO_2 can have beneficial effects under conditions of stress such as water shortage and air pollution, but it can also diminish frost resistance.

Since stomates lose less water for a given amount of CO_2 absorbed when CO_2 concentrations are elevated, plants may do better under drought. More than 100 controlled experiments have explored this field and nearly all found drought mitigating effects of elevated CO_2 (e.g., Tolley and Strain 1984; Hibbs et al. 1995). However, as several authors have shown (e.g., Samarkoon and Gifford 1995; Volk et al. 2000) the secondary effects of high CO_2 on soil water (as discussed above) exert a strong confounding influence, particularly in pot studies with limited rooting volume. Wullschleger et al. (2002) consider the actual benefits in the field as minor. In the desert FACE experiment in Nevada, it was the moist period which permitted the greatest CO_2 effect on shrubs and none during a drought period, somewhat dampening perspectives for a greening of dry lands in a high CO_2 world (Smith et al. 2000). No conclusive benefits for Mediterranean shrubs around CO_2 springs could be detected during drought (Tognetti et al. 2000), but crops grown under FACE profited more from elevated CO_2 (in relative terms) when passing through a drought (Conley et al. 2001). Future research will have to clearly separate effects of soil moisture savings from actual drought × CO_2 effects.

In the light of the greater carbohydrate supply of leaves grown in elevated CO_2 (including osmotically active sugar), it came as a surprise that frost resistance declines in plants exposed to a CO_2-rich atmosphere. This was found independently in plants as different as a temperate herbfield community (Obrist et al. 2001), Australian eucalypts (Lutze et al. 1998) and Douglas fir (Guak et al. 1998). The changes may be within the natural safety margin (Repo et al. 1996) and roughly match predicted global warming, but nevertheless affect one of the basic determinants of global plant distribution.

Elevated CO_2 concentrations have also been shown to mitigate the impact of ozone and other airborne pollutants, in part by reducing diffusive uptake (stomata) and in part by compensating damage (reviews by Sullivan 1997; Volin et al. 1998; Poorter and Perez-Soba 2001). A combined $O_3 \times CO_2$ FACE experiment with aspen confirmed these earlier findings and showed that certain realistic ozone levels may offset positive CO_2 effects (Isebrands et al. 2001). In summary, CO_2 enrichment has the potential to mitigate certain environmental stresses.

2.6 Biodiversity Effects May Outweigh Physiology Effects

We want to close this brief assessment by highlighting the key significance of species identity for the long-term outcome of atmospheric CO_2 enrichment (see also Potvin et al. 2007, Chap. 9 of this volume). Beyond the well known differential influence of elevated CO_2 on C_3 and C_4 species, recent studies have revealed a far more subtle differentiation of species that does not relate to any conventional groupings of plants into functional types and for which we often have no plausible explanation. We will illustrate this problem with a few examples.

2.6.1 Hydrology Implications of Elevated CO_2 Depend on Species Abundance

Imagine a mixed forest in a catchment, with some species saving water under elevated CO_2 and others not. This had been documented in a pine-sweetgum forest in N-Carolina (*Liquidambar* responding, *Pinus* not; Schäfer et al. 2002) and in a deciduous forest in Switzerland (*Carpinus* responding, *Fagus* not; Cech et al. 2003). The relative contribution of these species to the total forest canopy will determine whether the forest is saving water and how much. Furthermore, if one species saves, their non-saving neighbors may profit, which will alter the competitive balance and is most likely to induce a long-term change in community structure.

2.6.2 Biodiversity Effects on Forest Carbon Stocking and Grassland Responses

The longest term CO_2-enrichment experiments to data, the one in a wetland ecosystem, a sub-estuary of the Chesapeak Bay (Maryland; Hymus et al. 2003), all other grassland CO_2 studies (some examples in Fig. 2.1), the two forest FACE experiments in N-Carolina and Tennessee, but also two newer tree FACE experiments in Switzerland (Fig. 2.2), clearly demonstrate that CO_2 exerts species specific effects. The two US forest FACE studies, for instance, arrived at similar responses of net primary production, but in the case of pine, the additional biomass largely ended up in stems, whereas in the case of sweet-gum, it ended up in fine root turnover.

As mentioned in Sect. 2.2, accelerated growth may enhance tree turnover and lead to a lower rather than greater steady state C-pool in the landscape. One functional type of plants, lianas, the life cycle of which often

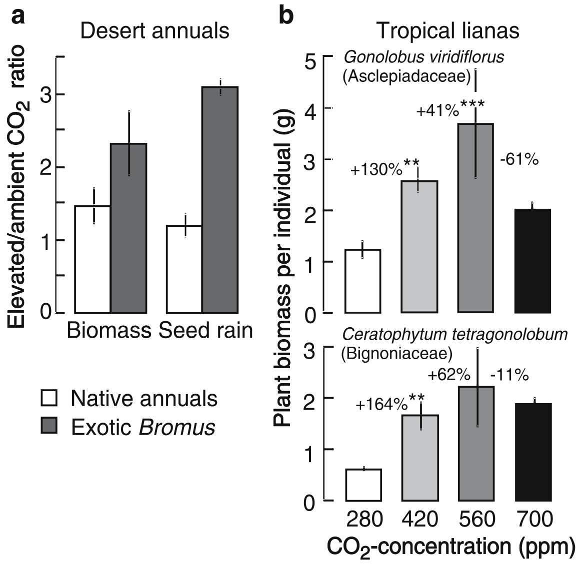

Fig. 2.6. Biodiversity–CO_2 interactions. **a** Mojave Desert native winter annuals and the exotic *Bromus madritensis* ssp. *rubens* (Nevada desert FACE, Smith et al. 2000). **b** the plant functional group of lianas. *Bars* indicate plus/minus one standard error (data by Granados and Körner 2002)

commences in deep shade, turned out to be particular responsive to elevated CO_2 (Granados and Körner 2002; Fig. 2.6). This has to do with a generally greater relative effect of elevated CO_2 on photosynthesis in deep shade. In the case of lianas, however, this stimulation greatly enhances their chance to reach the top of the forest. Well known to be the major driver of forest dynamics in the humid tropics (Schnitzer and Bongers 2002), such a greater vigor of lianas may cause the whole system to become more dynamic and store less C because trees do not live as long (Körner 2004). Demographic evidence suggests that such a process may be under way in Amazonia (Phillips et al. 2002) and had recently been reported for Panama as well (Wright et al. 2004). This example illustrates that there is no straightforward way to predict forest responses to elevated CO_2 from photosynthetic response curves without accounting for such biodiversity effects.

Similar examples have been shown in non-forest systems. For instance in the Mojave desert, an exotic annual *Bromus* grass species responds more strongly to CO_2 than native annuals (Fig. 2.6) enhancing the risk of fire (Smith et al. 2000). In the Negev winter-annuals' productivity (Fig. 2.1), it was a single species' response, which drove the whole community response. In the Colorado shortgrass steppe, recruitment of a single species under elevated CO_2 was largely responsible for a 41% production response (Morgan et al. 2004b). What if these species had been absent or were studied alone? Quite clearly species identity and species abundance have a major influence on the impact of elevated CO_2 on ecosystems.

2.7 Summary and Conclusions

Experimental CO_2 research with plants and whole ecosystems has made it clear that there is no straightforward relationship between the generally observed stimulation of leaf photosynthetic rates by elevated CO_2 concentrations and growth or productivity. The large number of tests with a broad spectrum of species and growth conditions have made it obvious that the extent to which greater availability of carbon to plants will translate into more structural growth depends on nutrient availability, either directly or via soil moisture conditions. The realism of projections derived from experimental works thus depends on the realism of nutrient and water regimes provided during tests (Körner 2003c). For the vast majority of non-agricultural ecosystems it seems that resources other then CO_2 control growth and productivity to such an extent that CO_2 concentrations above current levels exert little or no long-term stimulation. The major influence of atmospheric CO_2 on biota comes in (1) via differential responses of plant taxa or plant functional groups, (2) effects on water relations, and (3) soil feed back induced by greater C-input, the latter least understood.

Biodiversity effects have been found to be significant, with single species or plant functional types potentially driving whole system responses, and with no good explanations to date why this is so. The example of enhanced vigor of tropical lianas illustrates that functional group responses may in fact reverse the stimulatory effect of CO_2 enrichment into a reduction of carbon stocking in the single greatest biological C-reservoir on the globe. Water feedback may mimic growth stimulations in experiments, which may not be seen in reality when landscape wide feedback by climate and climatic changes are accounted for – a major future challenge for modelers. Nevertheless, the hydrological implications of elevated CO_2 are still a key global change aspect. Among the greatest surprises emerging from experimental works is that the differential responses of leaf stomates seen across taxa seem to level out to a common ca. 5–10% reduction of water loss at the ecosystem scale (evapotranspiration), a signal largely produced during humid periods.

Soil feedbacks other than through moisture include consequences of greater root turnover and microbial stimulation, but whether there will be a long term net input into the recalcitrant humus C pool is still very uncertain. Humus formation also strongly depends on nutrients, N in particular, and thus, competes directly with plant production and new C-input.

Overall, experimental CO_2 research has led to a wider appreciation of feedback constraints at the ecosystem level and the significance of plant taxa for ecosystem behavior (Fig. 2.7). At the ecosystem level, shifts in the presence and abundance of species may outweigh CO_2 effects seen at leaf or single species level. Taken together,

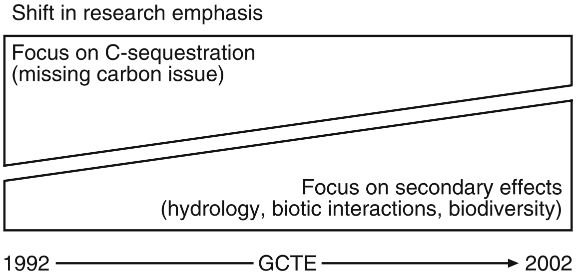

Fig. 2.7. The shift in research emphasis during the GCTE decade

the experimental findings suggest very cautious projections of CO_2 fertilization effects seen in short term tests with nutrient rich systems. Given that the few tests which used lower than current CO_2 (pre-industrial) concentrations as a reference to current or future concentrations revealed the strongest CO_2 effects (Fig. 2.6), the world may have seen or is midway into the most effective phase of CO_2 effects on biota, with a further rise perhaps exerting less additional effects. However, it will take many decades for the past and ongoing CO_2 effects to materialize, for instance, in the form of new plant assemblages.

Major questions to be explored in future biological CO_2 research are:

1. The translation of greater ecosystem carbon throughflow (growth rate, productivity, soil carbon fluxes) into steady state carbon pool sizes (biomass carbon, soil humus). CO_2 experiments revealed a lot of evidenced for enhanced carbon flux under elevated CO_2, but they are intrinsically constrained in estimating related changes in C-stocks. A worthwhile arena to be explored empirically is ecosystems of varying fertility, which exhibit contrasting carbon turnover for reasons unrelated to elevated CO_2. What are the mechanistic links between rates of carbon turnover (both at annual and centennial time scales) and the related pool sizes of biologically tied up carbon?
2. What are the long term consequences of plant species or functional type specific responses to elevated CO_2? It was a major outcome of GCTE related experimental research that biodiversity effects can outweigh physiology based 'average' plant responses at community level, and these consequences need to become focal areas of both further experiments and modeling. Based on this insight, it seems imperative, that future test systems include aspects of biodiversity, also in the light of the enormous costs involved.
3. There is an urgent need to implement realistic feedback between plant and ecosystem water relations under elevated CO_2 and atmospheric feedback in models. This is an arena were regional climate modeling and experimental research have to merge. Given the extent to which secondary effects of elevated CO_2 on water relations affect biomass responses and the potential hydrological implications, we need to arrive at a clear separation of direct, photosynthesis driven CO_2 effects and indirect, water driven CO_2 effects, which reflect certain climatic conditions.
4. Among the many secondary effects of exposing plants and ecosystems to enhanced availability of carbon, those on herbivory, mycorrhiza and rhizosphere food webs and all sorts of other interactions between plants and other organisms will have to remain focal areas.

A grand vision from an experimental point of view, would be an international research consortium which taps resources representing a small fraction of outer space research funding in order to establish three major forest research facilities, one in the boreal zone, one in the temperate zone and one in the tropics. These facilities would test complex forest responses to our future atmosphere, capitalizing on the experience accumulated over the last decades on simpler test systems. These large scale tests would employ the latest CO_2 enrichment technology, applicable for tall and diverse tree stands; would gradually elevate CO_2 concentrations, provide the needed canopy access technology; take a broad interdisciplinary approach; and guarantee long test periods under common protocols. They would represent international focal points of experimental global change research and tap resources from national partner agencies, which otherwise may continue to be diluted into smaller scale enterprises.

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Chapter 3

Ecosystem Responses to Warming and Interacting Global Change Factors

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3.1 The Multiple Factor Imperative in Global Change Research

Increases in atmospheric CO_2 concentration in the coming decades will be accompanied by other global changes. Higher air temperatures, altered precipitation patterns, increased tropospheric ozone concentrations, and N deposition are among the most prominent of the predicted changes that, along with elevated CO_2, have a high potential to affect ecosystem structure and function. Although the effect of elevated atmospheric CO_2 on ecosystem function was the primary focus of much of the GCTE effort in ecosystem physiology, each of these additional factors presents the possibility of altering the response of ecosystems to elevated CO_2 – perhaps negating the CO_2 response, enhancing it, or completely changing the nature of the response. Predictions of future ecosystem metabolism based solely on changes in a single factor are likely to be misleading. Hence, in addition to the elevated CO_2 network, GCTE fostered the development of a network to stimulate and coordinate research on ecosystem responses to climatic warming. Through all of its activities, GCTE promoted an agenda that embraced the mandate for understanding multi-factor interactions.

In the past, many model simulations of ecosystem response to global change were based on changes in climate alone, in part because the effects of elevated CO_2 were considered insignificant or too uncertain (Solomon 1986). Now, ecosystem and global models include multiple factors, particularly climate and CO_2, and the predicted responses can differ significantly from predictions based on changes in a single factor (Melillo et al. 2001; Cramer et al. 2001). It is important to the international global change research agenda that progress in experimental approaches keeps pace with model development. While many of the fundamental relations between ecosystem processes and temperature are well known, it is more difficult to have confidence in predictions of the combined responses to temperature and CO_2. Some interactions have a strong theoretical and empirical foundation: the optimum temperature for photosynthesis increases with increasing CO_2 (Long 1991). Temperature affects all biological processes, however, and the net response of an ecosystem to the combined effects of warming and elevated CO_2 are not so simply described (Norby and Luo 2004). Furthermore, ecosystem responses to CO_2 and temperature are likely to be modified by other environmental factors, especially the availabilities of water and nitrogen, which in turn are modified by CO_2 and temperature (Medlyn et al. 2000; McGuire et al. 2001).

Here, we explore recent experimental approaches to understanding ecosystem responses to global change, focusing on approaches that span an increasing range of complexity. First we will consider warming as a single factor, followed by an example of an experiment investigating interactions between warming and elevated CO_2 (Sect. 3.3). Temperature is more difficult to manipulate in field experiments than is CO_2, and the difficulties – both conceptual and operational – increase when temperature and CO_2 treatments are combined (Norby and Luo 2004). Hence, experiments on CO_2-temperature interaction have been at a smaller scale and in less complex biological systems than larger-scale FACE experiments, particularly those in forest ecosystems. Smaller stature systems, however, do permit more ambitious, whole-ecosystem, multifactor experiments, such as the Jasper Ridge Global Change Experiment, which is discussed in the Sect. 3.4. Results from such studies can be complex and perplexing, and there is a strong need for experimental results to be linked to ecosystem models so that the responses can be better understood and projected over longer time frames, as will be described in the fourth section.

3.2 Ecosystem Responses to Experimental Warming

It is now widely accepted that human-induced increases in greenhouse gas concentrations have already raised mean global temperature by ~0.6 °C during the last century, and unless these emissions are significantly curtailed, will likely result in a continued increase in mean global temperature of ~1.4 to 5.8 °C during the next century (IPCC 2001). Because temperature is one of the fundamental regulators of all chemical and biological processes, climatic warming in combination with other global change drivers – elevated atmospheric CO_2, changes in the quantity and timing of precipitation, and alterations in the global N cycle – is likely to have profound effects on the structure and function of terrestrial ecosystems (Rustad and Norby 2002). For example, in undisturbed systems, temperature is a key factor that regulates many terrestrial biogeochemical processes, such as soil respiration (Raich and Nadelhoffer 1989; Raich and Schlesinger 1992; Raich and Potter 1995; Kirschbaum 1995), litter decomposition (Meentemeyer 1978; Jansson and Berg 1985; Hobbie 1996), N mineralization and nitrification (MacDonald et al. 1995), denitrification (Malhi et al. 1990), CH_4 emission (Crill et al. 1988, 1991; Johnson et al. 1996), fine root dynamics (Boone et al. 1998; Pregitzer et al. 2000; Gill and Jackson 2000), plant productivity (Warren-Wilson 1957; Morison and Lawlor 1999), and plant nutrient uptake (BassiriRad et al. 2000). However, despite this extensive literature, the longer-term response of whole ecosystems to warming remains elusive. This is due, in part, to the complex array of direct and indirect responses of ecosystem processes to changes in temperature, the variable time-scale of response of different ecosystem processes and components to changes in temperature, and the importance of initial conditions (Shaver et al. 2000).

To help disentangle these complex issues and to establish cause-and-effect relationships between warming and ecosystem effects, a growing number of ecosystem warming experiments have been initiated around the world over the past few decades. The accumulating evidence from these experiments has greatly increased our understanding of short-term (i.e., 1–10 yr) responses of terrestrial ecosystems and their components to experimental warming. In this section we highlight results from two syntheses of experimental results (the GCTE-NEWS synthesis, Rustad et al. 2001; and the ITEX synthesis, Arft et al. 2000) and one longer-term study (the Harvard Forest soil warming experiment, Melillo et al. 2002).

3.2.1 The GCTE-NEWS Synthesis

Rustad et al. (2001) used meta-analysis to synthesize results on the response of soil respiration, net organic horizon N mineralization, and aboveground plant productivity to experimental warming from 32 ecosystem warming experiments, representing four broadly defined biomes – high arctic, low arctic (including a Minnesota bog and fen and a Colorado alpine dry tundra), forest, and grassland – associated with the GCTE Network of Ecosystem Warming Studies (GCTE-NEWS). GCTE-NEWS was established in 1999 in response to a perceived need for better synthesis and integration of results from ecosystem warming experiments. The goals of this network are to integrate and foster research on ecosystem-level effects of rising temperature, both alone and in combination with other vectors of global change. Warming methods used in the studies in the meta-analysis included electrical heat-resistance ground cables (Peterjohn et al. 1994; Rustad and Fernandez 1998), infrared heaters (Harte et al. 1995; Bridgham et al. 1999), greenhouses (Shaver et al. 1998; Jonasson et al. 1999), open-top chambers (Marion et al. 1997; Norby et al. 1997), climate-controlled chambers (Tingey et al. 1996), and passive nighttime warming (Alward et al. 1999). The relative merits of these different approaches have been discussed (Shaver et al. 2000). The duration of the experimental studies in the meta-analysis ranged from 2 to 9 years, and the experimental increases in soil or air temperature ranged from 0.3 to 6.0 °C, with a mean increase of 2.4 °C across all 32 studies.

Results for individual sites showed considerable variation in response to warming, as illustrated by the range in effect sizes [*d*] (Fig. 3.1). However, when all sites were considered together, results from the meta-analysis showed that experimental warming significantly increased rates of soil respiration by a weighted mean average of 20% (with a 95% confidence interval of 18 to 22%; $n = 17$), O horizon net N mineralization by a weighted mean average of 46% (with a 95% confidence interval of 30 to 64%; $n = 12$), and plant productivity by a weighted mean average of 19% (with a 95% confidence interval of 15 to 23%; $n = 20$) (Fig. 3.1). Although the number of studies was limited, the response of soil respiration to warming was generally greater in forested ecosystems compared to low arctic and grassland ecosystems ($P < 0.10$), and the response of plant productivity was generally greater in low arctic ecosystems than in forest and grassland ecosystems ($P < 0.01$). With the exception of aboveground plant productivity, which showed a greater positive response to warming in colder ecosystems, meta-analysis did not reveal any other significant relationships between the magnitude of the response of these three ecosystem processes to experimental warming and the other geographic (latitude, longitude), climatic (mean annual and growing season temperature and precipitation, mean frost-free days), or environmental (soil and foliar chemical properties, dominant vegetation type, soil classification, successional status) variables evaluated in this analysis.

These results appear to be consistent with the hypothesis that warming, at least in the short term, directly increases rates of microbial processes including litter decomposition and N mineralization, thereby increasing the availability of nutrients, and, particularly in nutrient-limited ecosystems, increasing plant productivity. Unfortunately, the observations of increased N mineralization and increased plant productivity largely came from different experiments; few experiments took a whole-ecosystem approach with integrated analysis of both above- and belowground responses. Hence, available experimental data cannot be used to evaluate a hypothesis linking warming, nutrient availability, and productivity.

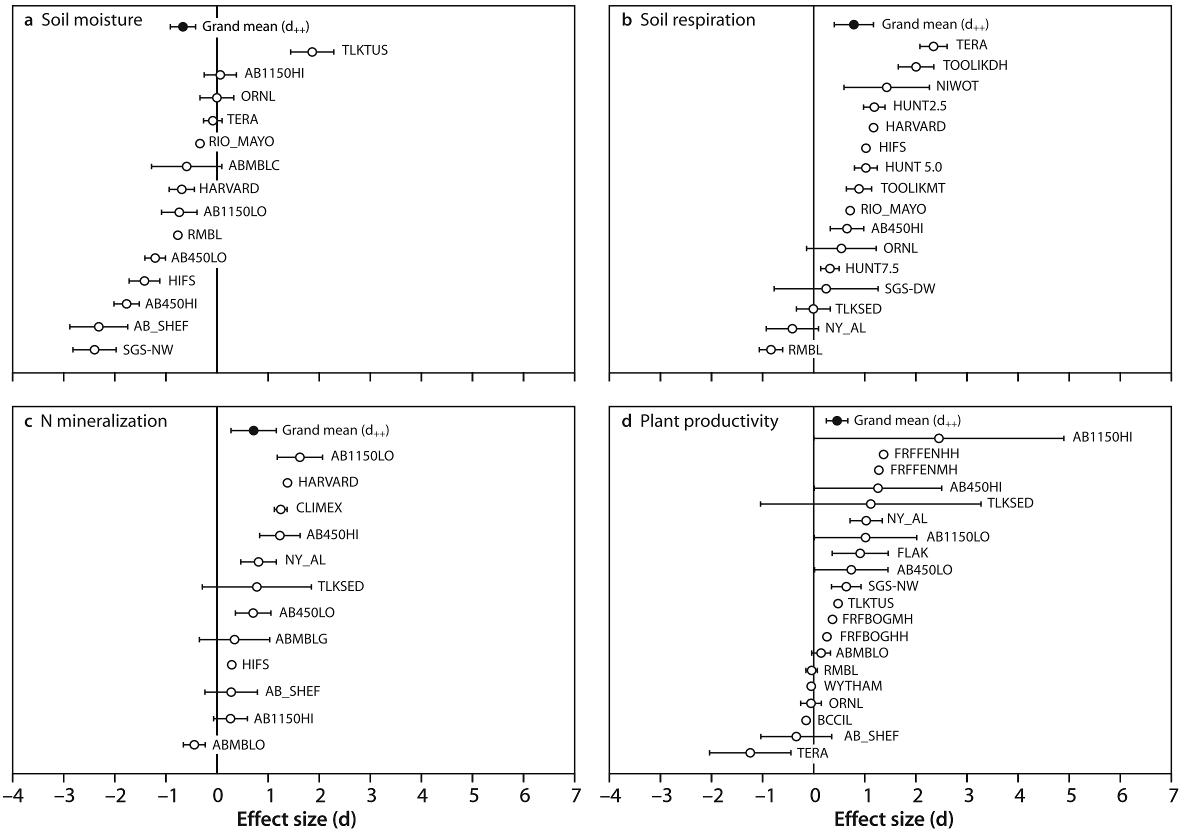


Fig. 3.1. Mean effect size, *d*, and 95% confidence intervals for different experimental sites used in a meta-analysis of responses to ecosystem warming. Measures of response are soil moisture, N mineralization, soil respiration, and plant productivity. If the 95% confidence interval of the grand mean does not include $d = 0$, the effect is considered statistically significant. The key to the different sites and a full analysis of the data are presented in Rustad et al. (2001) (reprinted with permission from Fig. 2 in Rustad et al. 2001)

The stimulation of plant productivity may also be a direct effect of warming on rates of photosynthesis (Lewis et al. 2001) or a warming-induced extension of the growing season (Dunne et al. 2002). However, the absence of strong relationships between the magnitude of the effect size of warming on the soil respiration, O horizon net mineralization, and aboveground plant productivity and the various geographic, climatic, and environmental variables considered in this analysis underscores the need to better understand the relative importance of specific factors (such as temperature, moisture, site quality, vegetation type, successional status, land-use history, etc.) at different spatial and temporal scales.

3.2.2 The ITEX Synthesis

Arft et al. (2000) also used meta-analysis to examine the response of plant phenology, growth, and reproduction to 1–4 years of experimental warming at 13 circumpolar sites associated with the International Tundra Experiment (ITEX). ITEX is a collaborative, multi-site experiment using a common open-top chamber experimental design to evaluate variability in species response to warming in tundra ecosystems. Results showed that (1) key phenological events including leaf bud burst, flowering, and seed dispersal generally occurred earlier in warmed plots compared to control plots throughout the four years of the study; (2) plant productivity was greater in the warmed plots than the control plots only during the first 2–3 years of the experiments (probably due to a depletion of belowground resources); (3) reproductive effort and success increased in later years, particularly in year 4 (probably due to the fact that flower buds are typically formed from one to several seasons before flowering); (4) the vegetative response to warming differed among plant life forms, with the response being generally greater in herbaceous than in woody species; (5) warmer, low arctic sites showed the strongest growth response to warming, and (6) colder, high arctic sites showed the strongest reproductive response to warming. Overall, the responses to warming observed at the ITEX study sites were consistent with those observed in the GCTE-NEWS study sites, and the two syntheses reinforce the observation that although terrestrial ecosystem processes are very sensitive to warming, the magnitude and even direction of response can be highly variable in time and space.

3.2.3 The Harvard Forest Soil Warming Experiment

Results from the aforementioned syntheses and individual warming experiments have greatly increased our understanding of the short-term responses of terrestrial ecosystems and their components to experimental warming. Nevertheless, concern exists that the majority of the existing or completed ecosystem warming experiments are of relatively short duration (i.e., <10 years) and that the initial reported responses may differ in magnitude and even direction compared to longer-term responses, thereby invalidating our ability to extrapolate short-term results to infer longer-term responses. An example of such a shift in response patterns over time is provided by the Harvard Forest soil warming experiment. Peterjohn et al. (1994) initially reported an approximately 40% increase in soil respiration during the first 6 months of the experiment. However, the magnitude of this initial increase diminished over time such that after 10 years of warming soils at 5 °C above ambient, soil respiration rates in the heated plots were not significantly different from rates in the control plots, probably due to depletion over time of temperature-sensitive, labile soil C (Fig. 3.2; Melillo et al. 2002). Net nitrogen mineralization rates, however, remained elevated for the duration of the experiment, resulting in a cumulative release of 41 g N m^{-2}. Assuming that 12.7% of this added N would be taken up by woody tissue (based on results from an associated long-term nitrogen fertilization experiment) and that C/N ratios of woody tissue are ~300/1, then warming-induced nitrogen mineralization could have resulted in a sequestration of ~1560 g C m^{-2} during the course of the experiment, thereby off-setting the estimated 944 g m^{-2} of labile soil C lost from the upper 60 cm of the soil profile. Results from this study underscore the needs for (1) long-term (i.e., >10 year) studies to evaluate changes in response patterns over time, and (2) understanding both direct and indirect effects of warming on ecosystem processes.

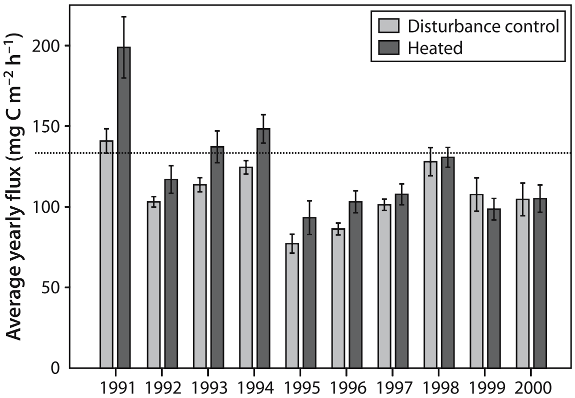


Fig. 3.2. Average yearly fluxes of CO_2 from the heated and disturbance control plots of the Harvard Forest soil warming experiment. Electrical resistance heating cables were buried 20 cm apart at 10 cm depth in the 6 × 6 m plots, and average soil temperature in the heated plots was maintained at 5 °C above ambient. Measurements were made from April through November for the period from 1991 through 2000. *Error bars* represent the standard error of the mean ($n = 6$ plots) between plots of the same treatment (reprinted with permission from Melillo et al. 2002)

An additional consideration should be how the results would have differed in the presence of an elevated atmospheric CO_2 concentration, given that the warming scenario being simulated in this experiment will in reality be associated with a significantly CO_2-enriched atmosphere. CO_2 enrichment of deciduous forests can significantly enhance the flux of C below ground (Norby et al. 2004) and soil respiration (King et al. 2004). Pendall et al. (2004) speculated that the effects of elevated CO_2 and warming on C substrate availability would moderate each other. In the Harvard Forest soil warming experiment the depletion of labile soil C and diminution of the soil respiration response (Melillo et al. 2002) might well not have occurred under a more realistic scenario combining warming and elevated CO_2.

3.3 Temperature and CO_2 Interactions in Trees: the TACIT Experiment

As discussed above, the climatic warming that is predicted for the future will be associated with increased atmospheric CO_2 concentrations, and there are strong reasons to suggest that CO_2 will alter the response of plants to temperature. The response of trees to a warmer, CO_2-enriched atmosphere is an important component of integrated analyses of forest response to global change and, therefore, of analyses of the feedbacks between the terrestrial biosphere, the global carbon cycle, and the climate system. Hence, it is important to understand not just the separate effects of elevated CO_2 and warming, but their combined effects and interactions as well.

3.3.1 Experimental Design

A 4-year experiment on temperature and CO_2 interactions in trees (TACIT) was designed to describe the effects of elevated CO_2 and temperature on ecosystem-level processes that control or influence C sequestration in ecosystems and to test specific hypotheses about the differential response of related species in relationship to their geographic ranges and ecological characteristics. TACIT explored the responses to a 4 °C increase in air temperature and a 300 ppm increase in CO_2 concentration in young *Acer rubrum* and *A. saccharum* trees growing in open-top chambers.

The experimental trees were grown in small stands for four growing seasons in open-top field chambers on the Oak Ridge National Environmental Research Park in Roane County, Tennessee (35°54' N; 84°20' W). Twelve

3-meter diameter chambers were modified to control air temperature to be the same as ambient air or to maintain a constant 4 °C elevation in air temperature (Norby et al. 1997). The temperature treatments were combined with ambient or elevated (+300 ppm) CO_2 concentrations. The temperature treatments were maintained throughout the year, but the CO_2 treatments were suspended during the winter (November–March) when the trees were leafless. The four treatments, comprising a 2 × 2 factorial arrangement of the two levels of temperature and CO_2 concentration, were replicated three times in a randomized complete block design. One-year-old seedlings were planted into the soil within the chambers in spring, 1994, and additional seedlings were planted in spring, 1995, for a total of 10 plants per species per chamber. The trees were harvested in September, 1997, ending the experiment. More details about the research site, chamber operation, and environmental conditions were provided by Norby et al. (1997, 2000).

3.3.2 Growth Responses

When the trees were harvested after four growing seasons (3.5 years) in the different combinations of CO_2 and temperature, they were in dense stands 4 m tall and with a leaf area index between 5 and 7 (Fig. 3.3). Elevated CO_2 enhanced growth: stem dry mass was increased by CO_2 enrichment by 34% in ambient temperature and 88% in elevated temperature. Warming, however, retarded growth by 35% in ambient CO_2 but only 9% in elevated CO_2 (Fig. 3.4). The main effects of CO_2 and temperature were statistically significant ($P = 0.001$ and $P = 0.025$, respectively), but the interaction between CO_2 and temperature was not ($P = 0.198$) (Norby and Luo 2004). Fine root biomass at the end of the experiment showed a similar pattern: a 60% reduction caused by the warming treatment in ambient CO_2 and a 27% reduction in elevated CO_2, but the CO_2–temperature interaction was not statistically significant (Wan et al. 2004).

Fig. 3.3. *Acer saccharum* and *A. rubrum* trees in an open-top chamber at the conclusion of the TACIT experiment. The plastic panels of the chambers and lower portions of the shade cloth, which were present throughout the four growing seasons of the experiment, have been removed to facilitate harvesting of the trees

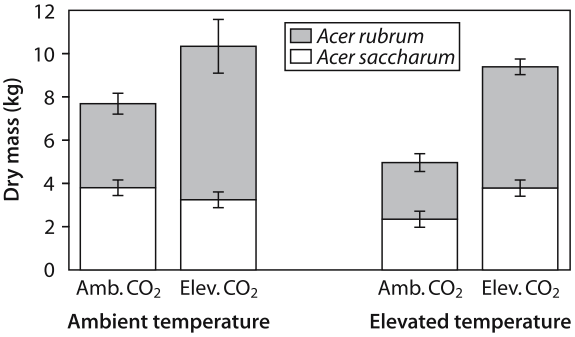


Fig. 3.4. Aboveground woody dry mass of *Acer saccharum* and *A. rubrum* trees after exposure for four growing seasons in open-top chambers with ambient or elevated CO_2 (+300 ppm) in combination with ambient or elevated (+4 °C) air temperature. The data are presented as biomass per chamber and are the means of three chambers per treatment ±SE (reprinted from Norby and Luo 2004 with the permission of New Phytologist Trust)

These biomass values at the end of the experiment mask a great deal of complexity. The final harvest data are the net result of both positive and negative effects that changed through time. Although elevated temperature suppressed instantaneous rates of photosynthesis (Gunderson et al. 2000), it also lengthened the growing season by 2–3 weeks (Norby et al. 2003). Relative growth rates were depressed in elevated temperature only during the second year of treatment when a severe hot period caused heat stress, but since the trees were undergoing exponential growth during the course of the experiment, this negative effect on dry matter accumulation during the stress period had a continuing effect on absolute growth rate for the remainder of the experiment despite a recovery in relative growth rate. Similarly, observations of fine root production and mortality during the third year of treatment did not predict fine root biomass at the final harvest. Both production and mortality were significantly increased by CO_2 enrichment and warming. The discrepancy between these observations of root dynamics and the harvest data are probably associated with drought-induced differential responses of productivity and mortality during the latter half of the growing season (Wan et al. 2004).

3.3.3 Higher-Order Responses

Higher-order responses also were addressed in this experiment. A premise of the experiment was that the two species would respond differently based on their presumed adaptations to temperature. The experimental site was close to the southern limit of the range of *A. saccharum*, whereas the range of *A. rubrum* extends much farther to the south. Although temperature effects were similar in the two species, *A. rubrum* was stimulated by CO_2 enrichment much more than *A. saccharum*. This observation is consistent with the premise that when temperatures are close to optimal, the relative biomass increase caused by increases in CO_2 enrichment is greater than when temperatures are sub- or supra-optimal (Poorter and Pérez-Soba 2001). The species also differed with regard to biotic interactions. Elevated CO_2 reduced growth of gypsy moth larvae feeding on *A. rubrum*, but not *A. saccharum* leaves (Williams et al. 2000). Warming shortened insect development but had no effect on pupal weight (Williams et al. 2003).

3.3.4 TACIT Summary

This relatively simple experiment illustrated many of the issues that must be considered when addressing multi-factor interactions, as well as many of the difficulties in taking up those issues in experimental studies (Norby and Luo 2004). Temperature affects many processes in plants and the net effect of a warmer atmosphere on tree growth will be difficult to predict when both negative and positive responses can occur together. Stochastic events, such as a late-spring frost that altered normal phenology (Norby et al. 2003) and the period of especially hot and dry weather that altered the growth trajectory, can play an important role in the integrated response. The duration of the experiment is an important consideration in this regard: the influence of a single unusual event should decrease with time, but the likelihood of an event occurring at all should increase. The specific combination of factors that influenced final dry mass in this experiment are not likely to be reproduced exactly in another experiment or in the real world, making it more difficult to extrapolate these results directly to an ecosystem scale. Different species – even closely related ones – may respond differently to global change factors, although some of those differences may be predictable based on the species' characteristics. In this experiment the effects of CO_2 and warming were additive; hence, their combined effects were predictable from knowledge of their single-factor effects. However, as will be apparent in the next section, unexpected interactions can also occur.

3.4 More Than Two Factors: the Jasper Ridge Global Change Experiment

Few ecosystem experiments have examined responses to more than two global change factors. Results from a four-factor study, the Jasper Ridge Global Change Experiment (JRGCE), demonstrate the need for this approach if we are to develop a comprehensive understanding of community and ecosystem responses to global environmental changes.

3.4.1 Experimental Design

Starting in 1998, the JRGCE exposed grassland plots in the San Francisco Bay Area (California, USA) to a factorial combination of warming, elevated CO_2, increased precipitation, and increased nitrogen deposition (Fig. 3.5). Circular grassland plots (2 m diameter) experienced either ambient conditions, ~1 °C of warming from infrared heat lamps, CO_2 enhancement of ~300 ppm via a FACE system, or warming and CO_2 enrichment together. Each plot was divided into four quadrants, which received am-

Fig. 3.5. An experimental plot in the Jasper Ridge Global Change Experiment. Four infrared heat lamps suspended over the 2-m diameter plot increase the canopy temperature by ~1 °C. Pure CO_2 is released from a circle of tubing surrounding the plot, enriching the CO_2 concentration in the air by about 300 ppm. Subplots comprise different combinations of precipitation and N deposition

bient or increased precipitation (+50%, including a 20-day extension of the growing season) combined with ambient or increased nitrogen deposition (+7 g N m^{-2} yr^{-1} as $CaNO_3$). Fiberglass barriers below the soil surface prevented roots and resources from escaping the quadrants. Because annual grasses and forbs dominate the grassland, species composition and standing biomass can respond quickly to the step changes in environmental variables. In addition, evolutionary responses to the treatments can occur within the course of a relatively short-term experiment.

3.4.2 Net Primary Productivity

Shaw et al. (2002) described responses of grassland net primary productivity (NPP) to the global change treatments after three years of exposure. At this time, warming, precipitation, and nitrogen all tended to stimulate NPP. The authors did not present a direct test of whether treatment responses were additive, but qualitatively described the interactions. NPP responses to some treatment combinations appeared approximately additive (warming and N deposition), while others were intermediate between treatments (warming and precipitation). The response to elevated CO_2 was even more complex. CO_2 enrichment increased aboveground biomass when all other factors were at ambient levels (paired *t*-test, $P = 0.0003$), but significantly suppressed NPP responses to other global change factors (paired *t*-test, $P = 0.048$). Much of this suppression occurred in the root biomass, which declined by 22% in response to CO_2 across all treatments.

Although this strong interaction appeared in the 2001 season, interactions involving CO_2 or warming were less common in other years. Dukes et al. (2005) found that, over the first five years of the experiment, the only consistent interaction occurred between increased precipitation and N deposition, with each treatment making the response to the other more positive in annual-dominated grassland (repeated measures mixed-model ANOVA, precipitation–N interaction, $P < 0.01$). NPP and aboveground biomass increased significantly in response to N deposition in four of the five years (by 21–42%, mixed-model ANOVA, $P < 0.05$). Precipitation tended to increase shoot growth, but decreased root growth, causing a shift in allocation but no net effect on NPP across the five years. Effects of CO_2 and warming were not significant, with warming tending to slightly increase NPP on average and CO_2 tending to increase NPP in two years and decrease it in three.

In this Mediterranean-climate system, plants germinate in October or November and senesce during May and June, after which they no longer use soil moisture. Zavaleta et al. (2003a) found that warming accelerates this senescence, leaving wetter soils in late spring and early summer. Elevated CO_2 also increased soil moisture during late spring, and the individual effects of warming and CO_2 were approximately additive over the first two years of the experiment (CO_2 effect on volumetric spring soil moisture: 1.6 ±1.0%; warming effect: 1.1 ±0.95%; combined warming and CO_2 effect: 2.7 ±1.0%).

3.4.3 Community Composition

Zavaleta et al. (2003b) found that some of these global changes affected the species richness of the grassland over the first three years of the JRGCE. Elevated CO_2 and nitrogen deposition both decreased species richness by reducing the number of forb species present in the plots, while more forb species were present in the plots receiving increased precipitation. In this case, treatment effects on species richness were almost perfectly additive, as indicated by both a lack of significant interactions in the ANCOVA model and by a "striking" correspondence between observed responses to treatment combinations and predicted responses based on the effects of single factors.

Global change treatments also affected the production and relative abundance of grasses and forbs (Zavaleta et al. 2003c). Although individual species responses were weak, responses of these groups could be more clearly characterized. Few responses were consistently strong across the first three years of the experiment, but a split-plot ANCOVA model identified some general patterns. Nitrogen deposition favored grasses at the expense of forbs. Forbs benefited from increased precipitation and from warming, but grass production was unresponsive to these treatments. Finally, elevated CO_2 had little effect on production of either functional group. Interactions among the treatment effects were even less consistent than the main effects. The treatment combination that featured warming, elevated CO_2, and increased precipitation caused the greatest change in relative abundance of the functional groups, a 50% increase in forbs.

Because these functional groups differ in their chemical makeup, shifts in community composition can affect litter quality. Henry et al. (2005) found that global change treatments affected lignin and nitrogen concentrations in litter, but that some of these direct effects were counteracted by the shifts in community composition. Direct effects included CO_2-induced increases in lignin (which were attenuated by warming in grasses and increased precipitation in forbs) and increases in litter nitrogen concentration in response to nitrogen deposition. This latter effect was dampened by increased precipitation. Although litter quality responded predictably to the global change treatments, the effects on litter quality did not markedly affect decomposition rates over the short term.

Litter decomposition and many other ecosystem functions could be altered by shifts in microbial community structure. Horz et al. (2004) observed shifts in the abundance and community composition of ammonia-oxidizing bacteria in response to some global change treatments. In this case, all responses depended on the level of other factors. Nitrogen deposition affected community structure, but only at ambient temperature and precipitation, and elevated CO_2 affected bacterial abundance, but only under increased precipitation.

3.4.4 JRGCE Summary

Thus far, results from the JRGCE suggest that treatment responses of production, community composition, and other measured variables are not tightly linked. Supplemental nitrate deposition has affected more of these variables than other factors, consistently increasing NPP, decreasing species richness by favoring grasses over forbs, and, under certain background conditions, influencing litter quality and bacterial community structure. The modest warming treatment has had few effects, most notably an acceleration of phenology that led to a small and unexpected increase in spring soil moisture. The precipitation treatment caused shifts in biomass allocation (from belowground to aboveground) and plant species composition (increasing forb diversity and abundance), and had interactive effects on litter quality and bacterial communities. Elevated CO_2 has had small, mostly nonsignificant effects on biomass production (with exceptions in 2001), and positive effects on spring soil moisture. Responses of plant and microbial community composition to elevated CO_2 have mostly been subtle, and CO_2-driven increases in litter lignin concentration were sometimes ameliorated by other treatments. Overall, the complexity of responses in the JRGCE confirms that multifactor, multi-year experiments are critical to forecasting global change responses, and highlights the challenge of determining the mechanisms behind such responses.

3.5 Modeling Temperature, CO_2 and N Interactions in Trees and Grass

The complexity of the ecosystem- and community-level responses to multiple changes in environmental conditions as observed in the JRGCE increases the need for a modeling framework to assist in drawing useful generalizations that are applicable to different ecosystems and over longer time frames. Models are needed to explore questions that cannot be addressed in experiments. Whereas climate-change experiments impose step changes in CO_2 concentration and temperature over periods of several years, models can be used to simulate either a step change or gradual change on the longer (decadal) timescales that are of primary relevance to policy makers.

In one modeling study, six dynamic global vegetation models were used to simulate future global terrestrial net primary production (NPP) and net ecosystem production (NEP) (Cramer et al. 2001). Under gradual CO_2 change alone NPP was predicted to increase by 60% on average by 2100, and NEP was predicted to increase to an average value of approximately 6 Pg C yr^{-1} by the end of the century, with little evidence of terrestrial carbon-sink saturation. Under rising CO_2 plus climate change, the models still predicted a sustained carbon sink, but with smaller increases in NPP (+50%) and NEP. There were, however, wide discrepancies among the six models. Explaining model discrepancies was difficult because of the models' complexity and the global scale of simulations with dynamic vegetation distributions and complicated climate-change scenarios. One factor contributing to discrepancies was that only two of the six models included soil nutrient feedbacks.

It is more straightforward to interpret results from models of individual stands that use simplified climate-change scenarios and simulate ecosystem processes, but not vegetation dynamics. Two ecosystem models that have been used in stand-scale simulations of experimental sites are DAYCENT (Del Grosso et al. 2001; Kelly et al. 2000; Parton et al. 1998) and G'DAY (Comins and McMurtrie 1993; Medlyn et al. 2000). The responses of NPP, NEP, and C storage to gradually increasing CO_2, temperature, and nitrogen input have been simulated for grasslands and forests.

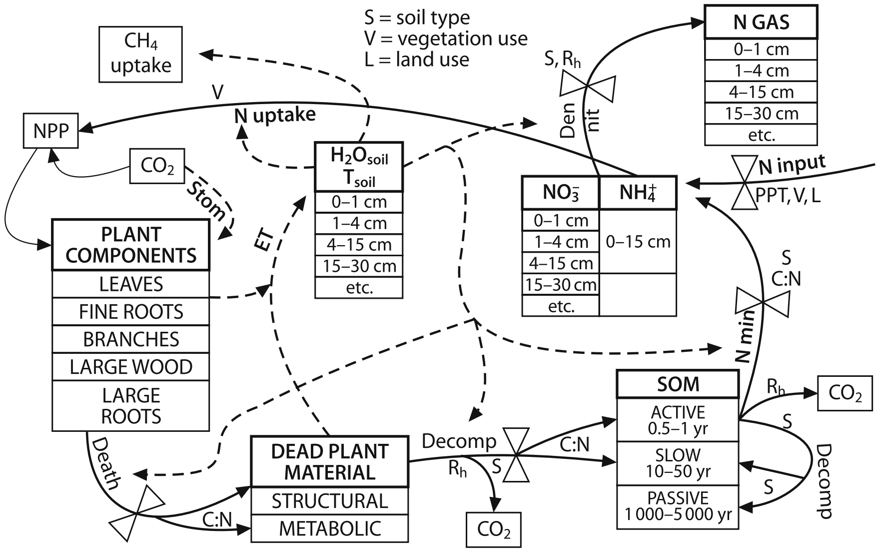
3.5.1 Global Change Simulations for a California Annual Grassland

The Jasper Ridge experiment provided a unique opportunity to compare model results with field data for a complex situation with multiple global change drivers. To have confidence in model projections that are unconstrained by data, it is important that the models can adequately recreate observed responses. Here, we describe how the DAYCENT model was used to simulate responses to increased atmospheric CO_2 concentration, N deposition temperature and precipitation for this site and compare the simulations with data collected during 1999–2002.

3.5.1.1 *DAYCENT Model Description*

DAYCENT is the daily time-step version of the CENTURY model (Parton et al. 1994). DAYCENT simulates exchanges of carbon, nutrients, and trace gases among the atmosphere, soil, and vegetation (Fig. 3.6). The model is of intermediate complexity and requires relatively simple inputs. Site-specific model input data include climate (daily maximum and minimum temperature and precipitation), soil texture and physical properties, vegetation

Fig. 3.6.
Pools and fluxes simulated in the DAYCENT model (Parton et al. 1998; Kelly et al. 2000; Del Grosso et al. 2001)



cover, and land management. Maximum plant growth rate is a function of vegetation type and solar radiation, which is calculated from latitude and day of year. Maximum NPP is down-regulated to account for nutrient, water, and temperature limitation. C allocation patterns, C/N ratios of biomass components, and senescence of plant components are functions of plant type, phenology and nutrient and water stress. Decomposition of dead plant material and SOM are driven by the amount of material and C/N ratios of different pools, as well as water and temperature limitation. Decomposition results in N mineralization, which makes N available for plant uptake, NO_3 leaching, and the processes (nitrification and denitrification) that result in N gas losses. DAYCENT includes a fairly complex soil water and temperature submodel (Parton et al. 1998) and also simulates CH_4 uptake in non-saturated soils. The effects of increased CO_2 concentration are implemented in three ways in DAYCENT. Maximum potential NPP rates can increase, C/N of above ground biomass can increase, and transpiration demand can decrease.

3.5.1.2 *DAYCENT Simulations and Results*

DAYCENT was used to investigate the effects of changes in precipitation, temperature, CO_2 concentration, and N deposition on plant growth and soil water content at the Jasper Ridge annual grassland. Model drivers (CO_2 concentration, precipitation, air temperature, and N inputs) were varied to mimic the experiments conducted at this site. Effects of elevated CO_2 were operationally defined for this site as a 10% increase in maximum NPP and C/N of leaf biomass, and a 50% decrease in transpiration demand. To better match observed NPP data, parameters had to be adjusted to decrease late-season belowground C allocation.

These effects capture the major biogeochemical interactions between CO_2, rainfall, heat and N fertilization. The experimental analysis and the model simulations indicate the role that water use and nitrogen availability have in affecting the net response to global change factors. Comparisons between mean simulated and observed changes in ANPP showed that the model did well for the single factor treatments but not for the interactions (Fig. 3.7a). The data showed a larger positive response for CO_2 alone than when CO_2 interacted with the other factors, whereas the model showed an additive response between CO_2 and the other factors.

Both simulated and observed aboveground productivity at the Jasper Ridge study was more dynamic relative to belowground productivity. The observed and simulated interannual and treatment variability tended to be much higher in the aboveground biomass. However, model results for mean BNPP did not agree with the data (Fig. 3.7b). In contrast to the data that showed a negative BNPP response for some treatments, DAYCENT showed a positive BNPP effect for all of the treatments because the model assumes that increased ANPP leads to higher nutrient and water demand so BNPP is enhanced. This indicates that ecosystem responses to global change are sensitive to environmental conditions modifying the belowground allocation, and the model needs improvement in how it represents allocation. Variability in observed data also contributes to the difficulty in modeling this system. Figure 3.7c shows the 4 years of data points that were averaged to obtain the bars in Fig. 3.7a along with the standard errors of the observed data. Both the spatial and temporal variability in the observed data are large and the model shows substantial error for some treatments during some years.

Simulation results indicate that environmental conditions and allocation patterns interact and have indirect effects on N mineralization and N-use efficiency,

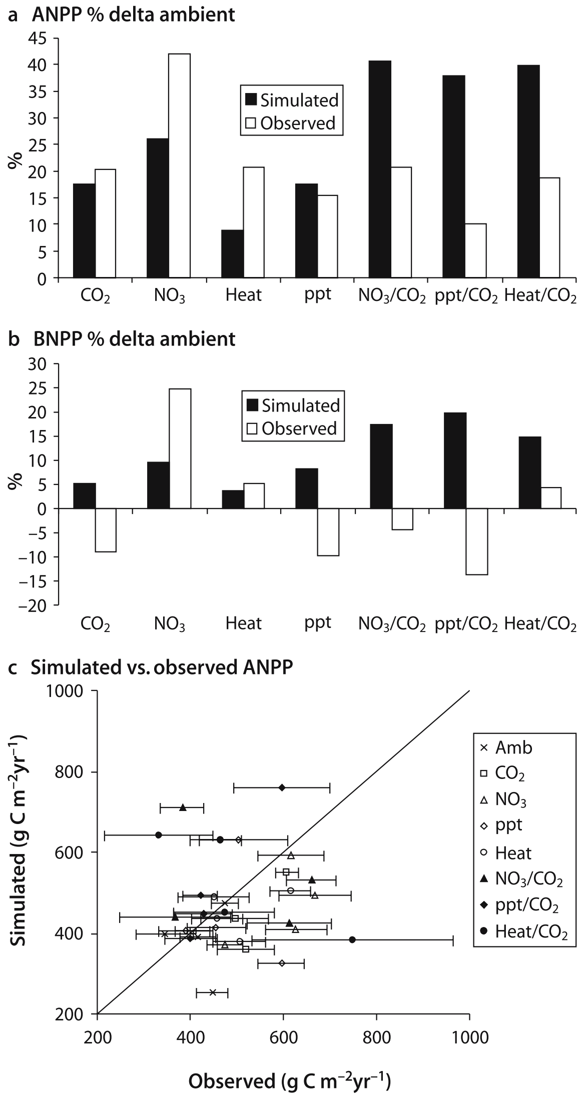


Fig. 3.7. Simulations and measurements of the relative effect of elevated CO_2, rainfall, heat and N fertilization on mean **a** aboveground and **b** belowground net primary productivity (ANPP and BNPP) during 4 years of the Jasper Ridge Global Change Experiment. The relative effect was calculated as (treatment – ambient) / ambient. **c** Simulated vs. observed annual ANPP, standard errors of observations, and the 1–1 line

which alter root-to-shoot allocation of new production. This effect has both short-term and long-term impacts on carbon biogeochemistry of these systems. The long-term storage of carbon will depend on the amount structural carbon formed, and changes in N-use efficiency may favor formation of less labile carbon materials and promote sequestration of carbon.

3.5.2 Comparing Forest and Grassland with G'DAY

DAYCENT and G'DAY were used to simulate responses of NPP, NEP, and C storage to gradually increasing CO_2, temperature, and nitrogen input for a short-grass steppe and a boreal forest site (Pepper et al. 2005). Here we will discuss NPP and NEP results from the G'DAY model. G'DAY (Comins and McMurtrie 1993; Medlyn et al. 2000) is a mechanistic model of C and N cycling and water balance in plant ecosystems. The model simulates plant physiological and soil processes: canopy photosynthesis, respiration, C and N allocation within the plant, and soil N feedbacks associated with decomposition of litter and soil organic matter. Processes included in the water-balance model are canopy interception and soil-surface evaporative water loss, drainage, runoff and transpiration modified by the CO_2 effect on water-use efficiency.

The sites considered are a short-grass steppe in Colorado, USA (40°8' N, 104°45' W; 1625 m a.s.l.) where the perennial C_4-dominant grassland is strongly water- and N-limited (Uresk et al. 1996), receiving 320 mm mean annual precipitation with a 4-month growing season. The forest plantation site is located at Flakaliden, Sweden (64°7' N, 19°27' E; 310 m a.s.l.) where stands of Norway spruce, planted in 1963, are N-limited but not water-limited (Bergh et al. 1999), receiving approx. 600 mm annual precipitation with a 4-month growing season. Both ecosystems are the subject of major long-term (>8 yr) climate-change experiments with CO_2-enrichment treatments at both sites and soil-warming at Flakaliden.

G'DAY was parameterized for each site and then simulated to equilibrium under current climate. Treatments simulated at each site were: gradually (linearly) increasing [CO_2] from 350 to 700 ppm over 100 years (Treatment C); gradually (linearly) increasing daily maximum and minimum air temperatures and soil temperature by 1, 3, and 2 °C, respectively, over 100 years (T), and nitrogen addition that increases linearly from 0 to 1 $g\ m^{-2}\ yr^{-1}$ over the century. The four treatments shown in Fig. 3.8 are denoted C, T, CT (rising CO_2 and temperature), and CTN (rising CO_2, temperature and N input). The CT treatment approximated the IS92a IPCC scenario (Houghton et al. 1995). Key results from multi-factor simulations are summarized below.

3.5.2.1 *Simulations with Rising Temperature and CO_2*

The NPP-response to treatment CT is similar in percentage terms at the grassland and forest, but comprises a large CO_2 effect and small negative T-effect at the water-limited grassland, compared with a small CO_2 effect and large temperature effect at the N-limited forest (Fig. 3.8). The explanation for these differences between grassland and forest is that the CO_2-effect is amplified under water limitation but diminished under N limitation, whereas warming enhances water stress at the grassland but stimulates N availability at the forest. NPP-responses to

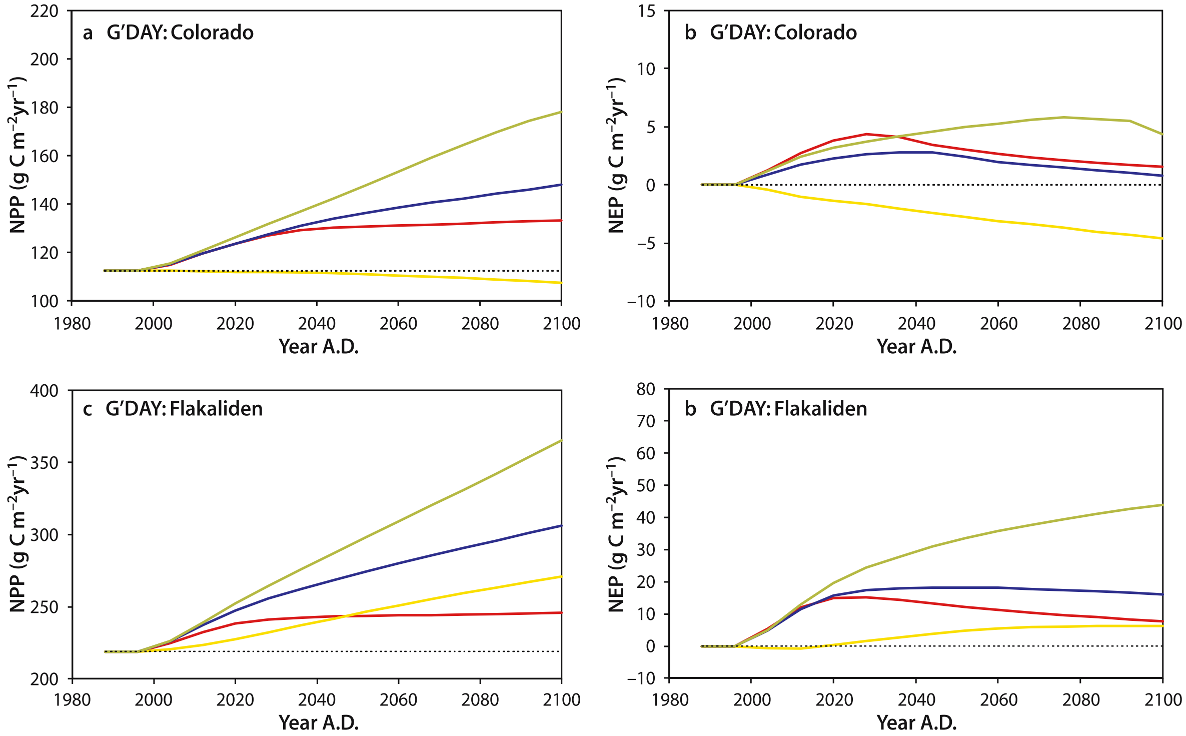


Fig. 3.8. Simulated **a** NPP and **b** NEP for Colorado short-grass steppe and **c** NPP and **d** NEP for Flakaliden boreal forest under single- and multi-factor treatments, where the *dotted line* denotes current equilibrium, *C* (*red*) denotes gradually increasing CO_2 concentration, *T* (*yellow*) denotes warming, *CT* (*blue*) the combination of *C* and *T*, and *CTN* (*green*) denotes the combination of *C* and *T* and increasing N inputs

CO_2 and T are approximately additive for forest, but not for grassland. The modeled CO_2–T interaction is strong at the grassland because of a synergistic effect whereby elevated CO_2 alleviates water-stress that is the major limitation on the grassland's temperature response.

Simulations of NEP under rising CO_2 show evidence of C-sink saturation (NEP declining towards zero) at both sites, probably because of developing N limitation. Under rising CO_2 and temperature, however, the forest shows little evidence of C-sink saturation because warming causes a gradual N transfer from soil with low C/N ratio to wood with high C/N ratio, which promotes C storage.

3.5.2.2 *Simulations with Increased N Input*

CTN simulations for both grassland and forest (Fig. 3.8) show that a relatively modest cumulative N fertilization (50 g m^{-2} over 100 years) is sufficient to sustain large NPP and NEP responses that are comparable in percentage terms to results of Cramer et al. (2001). This modest N addition overcomes the negative soil-N feedback that otherwise occurs at high CO_2 when increased litter input to the soil leads to increased N immobilization and reduced plant N availability. The CTN simulations show no evidence of C-sink saturation for at least 80 years (Fig. 3.8).

3.6 Summary and Conclusions

It is undeniable that ecosystems of the future will be subjected to multiple atmospheric and climatic changes. Research planning documents recognize this certainty and strongly promote the understanding of multi-factor interactions as a research imperative for the future (Committee on Global Change Research 1999). The research that we have highlighted here illustrates many of the challenges of addressing this imperative, but it also shows the importance of attempting to meet those challenges.

The net response to increased CO_2 concentration, warming, altered precipitation, N deposition, and other changes may be a simple additive effect of the separate influences, but experimental results also demonstrate the possibility of complex interactions. Single-factor experiments, such as those in the GCTE Elevated CO_2 network, are highly valuable for advancing understanding of the primary responses and how they are modified by other environmental factors. However, such experiments cannot be interpreted as providing predictions for ecosystem responses in a future climate. Single-factor ecosystem warming experiments are especially problematic, given the temporal and spatial variability of air temperature and the greater uncertainty (compared to CO_2) in future trajectories. Realistic warming treatments also are more difficult to carry out in experiments, especially in forests, and it has been harder to attain an integrated, ecosystem-scale understanding of all of the factors that will influence how ecosystems will respond to a warmer climate. Coupling the uncertain responses to warming to the simultaneous changes in other global change factors would seem to be a daunting task.

The experiments and modeling efforts highlighted in this chapter do not lead to a clear prediction of how ecosystems will be affected by various combinations of global change factors. They do, however, support several general principles about responses to climatic warming and multi-factor interactions:

1. Warming alone affects multiple pools and processes with different rate constants. Hence, responses are likely to change over time, as occurred in the response of soil respiration to soil warming at the Harvard Forest.
2. Whole-ecosystem warming experiments are necessary to address the complex interactions between belowground and aboveground responses. Without a whole-ecosystem perspective, critical hypotheses such as the linkage between warming effects on N availability and aboveground production cannot be evaluated.
3. Stochastic events can strongly alter the trajectory of response to warming. In the TACIT experiment a severe summer heat spell led to a loss in productivity after 4 years despite generally positive effects of warming. Short-term experiments may over emphasize the importance of such events while under representing the possibility of their occurrence.
4. Elevated CO_2 can sometimes ameliorate deleterious effects of warming, and since higher CO_2 concentrations are certain to be associated with future warming scenarios, it is imperative that their combined effects be considered when interpreting data. However, we cannot assume that the responses to elevated CO_2 always are positive, as evidenced by the Jasper Ridge experiment.
5. The responses to combinations of factors often equal the simple additive effects of the individual factors. That being the case, single-factor experiments continue to be very informative and can be the basis for model simulations. However, complex interactions do occur, and they may or may not be predictable. Multi-factor experiments are important for reminding us of this complexity.
6. Ecosystem models that incorporate our best understanding of the modes of actions of the individual factors will also capture many of the major biogeochemical interactions. Discrepancies between experimental data and model projections, such as for belowground productivity in the Jasper Ridge experiment, indicate areas where model improvement is needed. The influence of stochastic events and unexplained year-to-year variation in the nature of interactions suggest that simulations should be expected only to provide an envelope of possible future responses.
7. The long-term net effect of elevated CO_2 and temperature may be similar in different ecosystems, but the relative importance of the two global-change factors varies with site factors (e.g., water and N availability). Relatively modest N additions can overcome the soil-N feedback that can otherwise lead to C-sink saturation and loss of continued stimulation of NEP. These model results demonstrate why experiments must be conducted in a range of ecosystems under different conditions.

Acknowledgments

The experiments presented here are but a few of the many that contributed to GCTE Focus 1 activities, and we gratefully acknowledge the participation of all of the researchers who contributed their data, analyses, and ideas to GCTE workshops and syntheses. This paper was prepared at the Oak Ridge National Laboratory, which is managed by UT-Battelle, LLC, for the U.S. Dept. of Energy under contract DE-AC05-00OR22725.

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Chapter 4

Insights from Stable Isotopes on the Role of Terrestrial Ecosystems in the Global Carbon Cycle

DianeE. Pataki · Chun-Ta Lai · Charles D. Keeling · James R. Ehleringer

4.1 Introduction

The use of isotopic tracers in organic matter, water, and atmospheric gases has become an important component of the study of ecology and global change. Physiological and physical processes discriminate against heavy isotopes in predictable ways, so that measurements of isotopes at natural abundance, i.e., naturally occurring concentrations as opposed to artificial labeling experiments, can provide useful information about biological and physical processes at various spatial and temporal scales. Here we review recent progress in the application of naturally occurring stable isotopes in understanding ecosystem physiology and its role in biogeochemistry at ecosystem and global scales, with an emphasis on analyses of isotopes of carbon and oxygen in atmospheric carbon dioxide, a key component of the GCTE core project.

First, it is useful to review the basis for the application of stable isotopes in ecology and to provide some definitions of commonly used terminology. Isotopes of a single element contain differing numbers of neutrons. Some isotopes are stable while others are radioactive. We will focus here on two commonly used stable isotopes in the biological sciences: carbon-13 and oxygen-18. The most abundant isotope of carbon is ^{12}C which constitutes 98.9% of terrestrial carbon atoms; 1.1% of carbon is found as ^{13}C. In oxygen, 99.8% is ^{16}O, and the next most abundant form is ^{18}O constituting 0.2% of oxygen atoms (Fritz and Fontes 1980).

Isotopes are useful in ecology because they influence the physical and chemical properties of molecules. Light isotopes form weaker chemical bonds than heavy isotopes, so chemical reactions with substrates containing light isotopes occur more rapidly than with substrates containing heavy isotopes. This results in a difference in the abundance of heavy isotopes between the substrate and product of the reaction, and is called kinetic fractionation. In an equilibrium reaction, such as equilibration between liquid and gaseous water, the gaseous phase contains more of the light isotope and the liquid phase contains more of the heavy isotope, which results in equilibrium fractionation. There is also diffusive fractionation, which reflects the observation that molecules containing light isotopes diffuse more quickly than their heavier counterparts. A mechanistic understanding of fractionation in biological and physical processes is the basis of using isotopes as tracers of ecosystem processes (Fritz and Fontes 1980; Kendall and McDonnell 1998).

Isotopic measurements are generally expressed as the molar ratios of heavier isotopes to lighter ones (R). Such ratios are difficult to resolve in an absolute sense, and are usually expressed as relative ratios in delta (δ) notation:

$$\delta = (R_{\text{sample}} / R_{\text{standard}} - 1) \tag{4.1}$$

where R_{sample} and R_{standard} are the heavy-to-light molar ratios of the sample and of an international standard. If $R_{\text{sample}} < R_{\text{standard}}$ then δ is negative. For example, plants utilizing the C_3 photosynthetic pathway (the majority of terrestrial plants) typically have values of $\delta^{13}C$ that range from −21 to −35‰, where the symbol ‰ denotes per mil (parts per thousand), while atmospheric CO_2 is currently about −8.0‰ (Keeling et al. 2005) relative to the common standard for carbon stable isotopes, a belemnite from the Pee Dee formation in South Carolina (PDB).

A change in isotopic composition as a result of fractionation can be expressed as a discrimination (Δ):

$$\Delta = (\delta_{\text{source}} - \delta_{\text{product}}) / (1 + \delta_{\text{product}}) \tag{4.2}$$

where δ_{source} and δ_{product} are the isotope ratios of the source and product, respectively. With these definitions as a reference we can explore recent progress in the application of stable isotopes to understanding the role of terrestrial ecosystems in the carbon cycle.

4.2 Ecosystem Carbon Cycles

Measurements of the isotopic composition of air sampled near soils and plant canopies can provide information about ecosystem carbon cycles. The isotopic composition of respiration can be applied toward understanding physiological and environmental controls on the flow of carbon through various pools by applying a mechanistic understanding of carbon isotope fractionation. In addition, when different ecosystem pools or fluxes have distinct isotopic signatures, carbon isotopes can be used as a tracer to distinguish between components of the ecosystem carbon cycle.

Currently, a common protocol at a number of sites around the world is to repeatedly sample canopy air at night to obtain estimates of the isotopic composition of ecosystem respiration (see http://basinisotopes.org). We will denote the carbon isotope composition of CO_2 from ecosystem respiration as $\delta^{13}C_R$, and the oxygen isotope ratio of ecosystem respiration as $\delta^{18}O_R$. $\delta^{13}C_R$ is estimated by extracting the isotopic composition of plant- and soil-respired CO_2 from background air with a numerical method derived by Keeling (1958, 1961).

Consider CO_2 inside a forest canopy as a mixture of background CO_2 (not derived from any local sources) and CO_2 released by plant and soil respiration:

$$C_a = C_b + C_R \tag{4.3}$$

where C represents CO_2 concentration (mole fraction of dry air), and subscripts a, b and R represent the total CO_2, the background CO_2 and the ecosystem respired sources, respectively. Based on conservation of mass, we can write:

$$\delta^{13}C_a C_a = \delta^{13}C_b C_b + \delta^{13}C_R C_R \tag{4.4}$$

where $\delta^{13}C$ denotes δ of carbon-13 relative to carbon-12. Substituting $C_R = C_a - C_b$ from Eq. 4.3 to 4.4,

$$\delta^{13}C_a = \frac{C_b(\delta^{13}C_b - \delta^{13}C_R)}{C_a} + \delta^{13}C_R \tag{4.5}$$

Equation 4.5 is a linear function of $1/C_a$, allowing us to estimate $\delta^{13}C_R$ as the intercept of a linear regression with $1/C_a$ as the independent variable. A number of studies have investigated $\delta^{13}C_R$ over a wide range of ecosystems (Buchmann et al. 1997a; Buchmann et al. 1997b; Fessenden and Ehleringer 2002; Flanagan et al. 1996; Harwood et al. 1999; Quay et al. 1989; Sternberg et al. 1989). Pataki et al. (2003b) synthesized measurements from 33 sites and discussed the assumptions inherent in the collection and interpretation of $\delta^{13}C_R$, which include the critical assumption that $\delta^{13}C_b$ and $\delta^{13}C_R$ remain constant during the sampling period. Miller and Tans (2003) also illustrated uncertainties associated with measurement and analytical errors regarding the two-source mixing approach.

Advances in isotope ratio mass spectrometry have increasingly permitted analysis of CO_2 isotopes in smaller air volumes with greater automation, allowing for more frequent sampling (Ehleringer and Cook 1998; Schauer et al. 2003; Tu et al. 2001). Intensive measurements of $\delta^{13}C_R$ over short time-periods, as well as longer-term monitoring on a weekly basis, have led to recent advances in our understanding of ecosystem carbon cycling. Correlations between $\delta^{13}C_R$ and environmental variables have provided evidence that a large proportion of carbon fixed in photosynthesis cycles rapidly through forested ecosystems (Bowling et al. 2002; Ekblad and Högberg 2001; Lai et al. 2005; Ometto et al. 2002). Ekblad and Högberg (2001) observed a correlation between $\delta^{13}C$ of soil-respired CO_2 and atmospheric humidity that lagged by 1–4 days, which they interpreted as an indication of the influence of recent photosynthesis on root respiration. These results were supported by Bowling et al. (2002), who observed a correlation between whole ecosystem $\delta^{13}C_R$ and time-lagged atmospheric vapor pressure deficit (VPD) in several ecosystems in Oregon, USA. VPD strongly influences stomatal conductance, photosynthesis, and the ratio of stomatal conductance to photosynthesis, and therefore $\delta^{13}C$ of assimilate through its influence on C_i/C_a, the ratio of leaf intercellular to ambient CO_2 concentration (see Box 4.1). Scartazza et al. (2004) and Fessenden and Ehleringer (2003) showed that $\delta^{13}C_R$ is also influenced by soil moisture, presumably through the influence of drought on stomatal closure. Although changes in the proportion of above- and belowground respiration and influences of declining soil moisture on the isotopic composition of soil respiration are alternative explanations, Scartazza et al. (2004) show that soil moisture-driven variations in $\delta^{13}C_R$ were related to $\delta^{13}C$ of phloem sugar. Notably, the relationship between $\delta^{13}C_R$ and soil moisture showed a similar slope in two disparate coniferous forests in the eastern and western coastal regions of the United States (Fig. 4.1). Integrated over time, these relationships lead to spatial variability in $\delta^{13}C_R$ as a function of water availability (Fig. 4.2).

In addition to providing a greater mechanistic understanding of ecosystem physiology and its influence on carbon cycling, measurements of the isotopic composi-

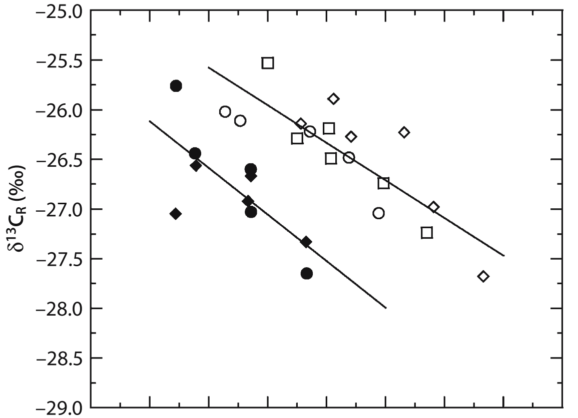

Fig. 4.1. Relationship between the monthly mean carbon isotope composition of ecosystem respiration ($\delta^{13}C_R$) and average soil moisture content during the growing season at two coniferous forests: the Wind River Canopy Crane Facility in Washington, USA (*open symbols*) and Howland Forest in Maine, USA (*closed symbols*). Measurements from different years are indicated by different symbols as *squares* (2001), *circles* (2002) and *diamonds* (2003) (from Lai et al. 2005, reproduced by permission of Blackwell Publishing)

tion of CO_2 can be used to partition ecosystem fluxes into specific component parts (Bowling et al. 1999; Bowling et al. 2001; Lai et al. 2003; Lloyd et al. 1996; Ogée et al. 2003; Yakir and Wang 1996). During daylight hours, Net Ecosystem Exchange (NEE) of CO_2 reflects the balance between photosynthesis (A) and respiration (R):

$$F_{\mathrm{NEE}} = F_{\mathrm{A}} + F_{\mathrm{R}} \tag{4.6}$$

where F represents a flux of CO_2. A similar mass balance can be applied to the isotopes of CO_2:

$$\delta^{13}\mathrm{C}_{\mathrm{NEE}} F_{\mathrm{NEE}} = F_{\delta} = \delta^{13}\mathrm{C}_{\mathrm{A}} F_{\mathrm{A}} + \delta^{13}\mathrm{C}_{\mathrm{R}} F_{\mathrm{R}} \tag{4.7}$$

where F_{δ} represents an "isoflux", analogous to net ecosystem exchange of $^{13}CO_2$ (μmol m^{-2} s^{-1} ‰) (Bowling et al. 2001). Values of $\delta^{13}\mathrm{C}_{\mathrm{NEE}}$, $\delta^{13}\mathrm{C}_{\mathrm{A}}$ and $\delta^{13}\mathrm{C}_{\mathrm{R}}$ denote the carbon isotope ratios associated with NEE, photosynthetic and respiratory fluxes, respectively.

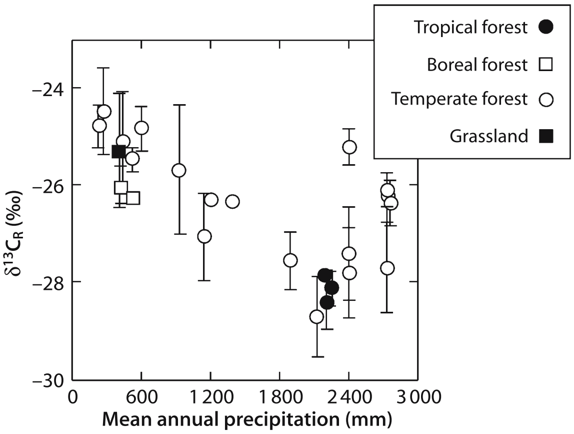

Fig. 4.2. The carbon isotope composition of ecosystem respiration ($\delta^{13}\mathrm{C}_{\mathrm{R}}$) at several sites throughout North and South America in relation to mean annual precipitation. *Error bars* show the standard error of all observations for a given site. A correlation is observed across all sites, with the exception of coniferous forests in the northwestern United States, where rainfall exceeds 2 400 mm yr^{-1} (from Pataki et al. 2003b, reproduced by permission of the American Geophysical Union)

F_{NEE} is routinely measured at numerous sites around the world as part of the FLUXNET suite of networks (http://daac.ornl.gov/FLUXNET). To apply Eq. 4.6 and 4.7 to solving for F_{A} and F_{R}, methods to measure or estimate the isotopic composition of the individual fluxes are required. Equation 4.5 is commonly used to determine $\delta^{13}\mathrm{C}_{\mathrm{R}}$ as discussed earlier. Quantifying $\delta^{13}\mathrm{C}_{\mathrm{NEE}}$ and $\delta^{13}\mathrm{C}_{\mathrm{A}}$, however, is more challenging (Bowling et al. 2003a). Yakir and Wang (1996) used δ^{13}C and δ^{18}O measurements to partition F_{NEE} of agricultural fields. They estimated $\delta^{13}\mathrm{C}_{\mathrm{NEE}}$ and $\delta^{13}\mathrm{C}_{\mathrm{A}}$ by measuring the isotopic composition of plants and soil samples, which integrate over seasonal time scales. However, to partition $\mathrm{F}_{\mathrm{NEE}}$ at half-hourly intervals, capturing diurnal variations in $\delta^{13}\mathrm{C}_{\mathrm{NEE}}$ and $\delta^{13}\mathrm{C}_{\mathrm{A}}$ is necessary (Bowling et al. 2001). Using an aerodynamic approach to estimate canopy conductance and Fick's law of diffusion to estimate C_{i}, Bowling et al. (2001) calculated $\delta^{13}\mathrm{C}_{\mathrm{A}}$ for the whole-canopy:

$$\delta^{13}\mathrm{C}_{\mathrm{A}} = \delta^{13}\mathrm{C}_{\mathrm{a}} - a - (b - a)\frac{C_{\mathrm{i}}}{C_{\mathrm{a}}} \tag{4.8}$$

which combines Eqs. 4.2 and 4.12. An estimate of canopy-scale $\delta^{13}\mathrm{C}_{\mathrm{A}}$ can also be achieved by coupling biochemical photosynthesis models with a stomatal conductance model (Lai et al. 2003). Finally, if another parameter is known such as F_{R}, which can be modeled as a function of temperature, Eqs. 4.6 and 4.7 can be used to solve for $\delta^{13}\mathrm{C}_{\mathrm{A}}$ (Bowling et al. 2003a).

Carbon isotopes are particularly useful for discerning photosynthetic pathways because there is considerable contrast in δ^{13}C ratios between C_3 and C_4 plants (Box 4.1). In the context of ecosystem respiration, measurements of δ^{13}C can be used to partition contributions

Box 4.1. Isotopic discrimination in photosynthesis

Discrimination of ^{13}C in photosynthesis occurs in two steps. First, discrimination occurs during diffusion of CO_2 into the stomatal pores, followed by enzymatic discrimination in carboxylation by RuBP carboxylase (Rubisco). For plants utilizing the C_3 photosynthetic pathway, these effects can be represented as:

$$\Delta^{13}\mathrm{C}_{\mathrm{P}} = a + (b - a) \cdot C_{\mathrm{i}} / C_{\mathrm{a}} \tag{4.12}$$

where $C_{\mathrm{i}}/C_{\mathrm{a}}$ denotes the ratio of intercellular to ambient CO_2 partial pressure, a the fractionation in diffusion, and b the net fractionation of carboxylation (Farquhar et al. 1982). Because a and b are known (4.4 and 27‰, respectively) photosynthetic discrimination of C_3 plants can be predicted with estimates of $C_{\mathrm{i}}/C_{\mathrm{a}}$, which is affected by photosynthetic rates and stomatal conductance. It should be noted that this approach neglects resistance to CO_2 transfer from the sub-stomatal cavity to the mesophyll, which may be significant in some species (Ethier and Livingston 2004).

Photosynthetic discrimination by C_4 plants may also be quantified with estimates of $C_{\mathrm{i}}/C_{\mathrm{a}}$. However, the "leakiness" of the unique C_4 anatomy must also be considered, as it affects the extent to which fractionation of Rubisco influences $\Delta^{13}\mathrm{C}_{\mathrm{P}}$, in addition to the C_4 enzyme PEP carboxylase. This is represented as:

$$\Delta^{13}\mathrm{C}_{\mathrm{P}} = a + (b_4 + b_3\phi - a) \cdot C_{\mathrm{i}} / C_{\mathrm{a}} \tag{4.13}$$

where b_4 denotes the fractionation factor of PEP carboxylase (−5.7‰), b_3 is the fractionation factor of Rubisco (30‰), and ϕ is the leakiness of bundle sheath cells, where C_4 photosynthesis takes place (Farquhar 1983). Rubisco has a small influence on photosynthetic fractionation in most C_4 plants, and the fractionation of PEP carboxylase is also fairly small. Thus, $\Delta^{13}\mathrm{C}_{\mathrm{P}}$ in C_4 plants is significantly lower than in C_3 plants, making these pathways isotopically distinct. Typical values of $\Delta^{13}\mathrm{C}_{\mathrm{P}}$ range from 13 to 25‰ in C_3 plants and 2.5 to 5‰ in C_4 plants (Dawson et al. 2002; Farquhar et al. 1989; Lloyd and Farquhar 1994).

of plants utilizing different photosynthetic pathways in C_3-C_4 mixtures (e.g., grassland and savannas), which are mainly distributed in sub- and tropical regions (Still et al. 2003a; Still et al. 2003b). The fraction of C_3 (λ) contributing to total ecosystem respiration can be estimated by:

$$\delta^{13}C_R = \lambda\delta^{13}C_3 + (1-\lambda)\delta^{13}C_4 \qquad (4.9)$$

where $\delta^{13}C_3$ and $\delta^{13}C_4$ denote the $\delta^{13}C$ ratios of C_3 and C_4 species, respectively. Still et al. (2003b) used this approach to estimate that C_4 species contributed 60 to nearly 100% of the total respiration between May and September in a tallgrass pasture in central Oklahoma, U.S.A. Lai et al. (2003) found a comparable range of C_4 contributions in a tallgrass prairie with similar species composition and climate. The contribution of C_3 vs. C_4 plants is critical to the application of measurements of $^{13}CO_2$ at a global scale, as we will discuss in the next section.

4.3 The Global Carbon Cycle

There is a high degree of short-term interannual variability associated with the rate of increase in atmospheric CO_2 concentration (Fig. 4.3). We know from statistics of energy use that CO_2 emissions from fossil fuel combustion are increasing at a nearly steady rate from year to year (Andres et al. 2000; IPCC 2001). The principal sources of interannual variability are therefore ocean fluxes and terrestrial ecosystem processes. Isotopes of carbon dioxide are useful to distinguish between these components on regional and global scales.

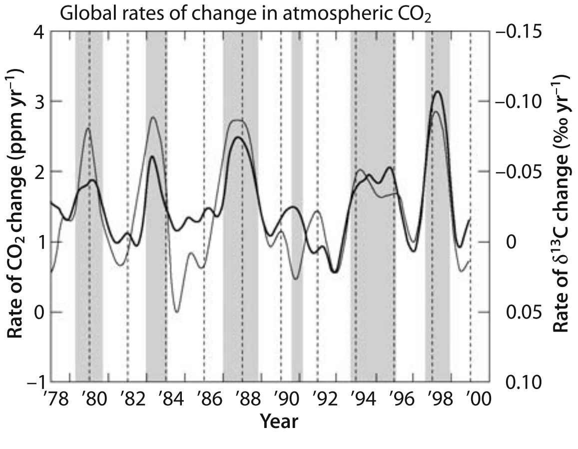

Fig. 4.3. The rate of change in atmospheric CO_2 concentration (*bold line, left axis*) and the rate of change in the carbon isotope composition ($\delta^{13}C$) of atmosphere CO_2 (*right axis*) (from Keeling et al. 2005, used by permission)

We have discussed that photosynthesis of terrestrial plants discriminates against $^{13}CO_2$ (Box 4.1), leaving heavier $^{13}CO_2$ behind in the atmosphere, while the process of respiration returns isotopically light carbon to the atmosphere. In contrast, fractionation of CO_2 dissolution into the ocean is small, on the order of 2‰ (Inoue and Sugimura 1985; Wanninkhof 1985; Zhang et al. 1995). Therefore, gradients of $\delta^{13}C$ of CO_2 in the atmosphere may be used to distinguish between terrestrial and oceanic sinks if the magnitude of photosynthetic discrimination and the isotopic composition of respiration can be estimated well enough on a global scale. Because C_3 and C_4 photosynthesis differ greatly in fractionation of $^{13}CO_2$, this requires robust estimates of the proportion of productivity of C_3 vs. C_4 plants globally. However, the information gained from applying these estimates can be significant. Figure 4.3 shows the rate of change of $\delta^{13}C$ of atmospheric CO_2 in addition to the rate of change of atmospheric CO_2 concentration for the last two decades. The close correlation between the two time-series strongly suggests that terrestrial processes have dominated the short-term interannual variability in the growth rate of atmospheric CO_2. By applying mass balance to atmospheric observations of CO_2 and its isotopic composition, sources and sinks of CO_2 can be inferred:

$$\frac{\partial}{\partial t}C_a = F_{FF} + F_{DEF} + F_{ao} + F_{oa} + F_{ab} + F_{ba} \qquad (4.10)$$

$$\begin{aligned} C_a\frac{\partial}{\partial t}\delta^{13}C_a = &(\delta^{13}C_{FF} - \delta^{13}C_A)F_{FF} \\ &+(\delta^{13}C_{DEF} - \delta^{13}C_A)F_{DEF} \\ &+\varepsilon_{ao}(F_{ao} + F_{oa}) + D_oF_{oa} \\ &+ -\Delta_p(F_{ab} + F_{ba}) + D_bF_{ba} \end{aligned} \qquad (4.11)$$

where the subscripts 'FF' and 'DEF' denote the fossil fuel- and land-use change-derived releases of CO_2 to the atmosphere, subscripts 'AO' and 'OA' denote the one-way ocean-atmosphere fluxes, and subscripts 'AP' and 'BA' denote the one-way biosphere-atmosphere fluxes (Francey et al. 1995; Fung et al. 1997; Tans et al. 1993). Also included in order to solve Eqs. 4.10 and 4.11 for the oceanic and terrestrial fluxes are symbols to denote CO_2 emissions from fossil fuel combustion, $\delta^{13}C_{FF}$; CO_2 emissions from land-use change, $\delta^{13}C_{DEF}$; fractionation factors associated with the net oceanic, ε_{ao}; and terrestrial discrimination, Δ_P; and two "disequilibrium" terms, D_o and D_b. These latter terms express the extent to which older carbon, dissolved in ocean waters or fixed in photosynthesis in the past and later released, has a more enriched $\delta^{13}C$ than current carbon due to the dilution of atmospheric CO_2 by fossil fuel combustion in the last century.

Mass balances expressed in Eqs. 4.10 and 4.11 have been applied in a number of global studies of carbon sources and sinks that utilized atmospheric measurements to infer regions of carbon uptake (Battle et al. 2000; Ciais et al. 1995; Francey et al. 1995; Fung et al. 1997; Tans et al. 1993). A limitation to this approach is that the parameterization of Δ_P, the discrimination associated with net carbon uptake by the terrestrial biosphere, is difficult to validate with measurements. Ecosystem studies commonly measure the isotopic composition of the one-way, nighttime flux, $\delta^{13}C_R$, but estimating the signature of photosynthetic discrimination from direct measurements is difficult at whole ecosystem scales. For lack of data to the contrary, Δ_P has been generally fixed as a constant value in global mass balance studies (Battle et al. 2000; Francey et al. 1995; Tans et al. 1993). However Randerson et al. (2002) demonstrated that if large-scale regional changes in Δ_P covary with changes in gross fluxes, as could occur during climatic anomalies such as the El Niño Southern Oscilliation (ENSO), applying constant values of Δ_P to Eq. 4.11 could introduce significant errors into global mass balance calculations. Modifying the mass balance approach to explicitly consider gross fluxes and their time varying anomalies could improve top-down estimates of carbon sinks from atmospheric measurements (Randerson et al. 2002).

It has been noted that the peaks in atmospheric CO_2 growth rate have generally been associated with the occurrence of ENSO events (Francey et al. 1995; Keeling et al. 2005; Keeling et al. 1995), which brings warm, dry conditions to highly productive tropical regions (Dai et al. 1997; Ropelewski and Halpert 1987). One hypothesis for the underlying correlation between ENSO conditions and terrestrial sources and sinks of carbon has been that drought conditions, and in particular dry atmospheric conditions, in tropical regions have resulted in reduced productivity and subsequently smaller terrestrial sinks in tropical forests during ENSO years. Measurements of $\delta^{13}C$ of atmospheric CO_2 have generally supported this hypothesis (Fig. 4.3), which would also be expected based on the data in Fig. 4.1 and 4.2. However, recent work utilizing carbon monoxide and methane tracers in addition to measurements of CO_2 concentration and $\delta^{13}C$ of CO_2 suggests that an increased occurrence of biomass burning and wildfire during ENSO years, also associated with drought, may also be an important mechanism (Van der Werf et al. 2004).

The oxygen isotopic composition of CO_2 also has great potential to distinguish between components of the carbon cycle, namely, between assimilation and respiration of the terrestrial biosphere. The oxygen isotopic signature of assimilation and respiration are generally very different – more so than the carbon isotope signatures in ecosystems that contain only C_3 plants. However, oxygen isotopes have been applied less frequently in global carbon studies, largely because of the complexity of modeling oxygen fractionation effects at the global scale.

CO_2 and water in the liquid phase equilibrate isotopically so that the isotopic composition of CO_2 is strongly influenced by the isotopic composition of water where water is abundant, as in plants and soils (Amundson et al. 1998; Farquhar and Lloyd 1993; Farquhar et al. 1993; Hesterberg and Siegenthaler 1991). Assimilation and respiration have different isotopic signatures because leaf water is enriched in oxygen-18 relative to soil water due to the evaporative effects of transpiration. Approximately two-thirds of the CO_2 that diffuses into leaves is not fixed by photosynthesis, but this CO_2 does equilibrate with leaf water and diffuses back into the atmosphere with an isotopically enriched signature that is distinct from that of respired CO_2 which has equilibrated with soil water (Farquhar and Lloyd 1993; Flanagan et al. 1997; Francey and Tans 1987). Quantifying these processes in global models requires hydrologic models that predict the isotopic composition of regional precipitation, as well as ecological models and models of atmospheric transport.

Despite this complexity, there has been recent progress in quantifying the oxygen isotopic composition of CO_2 on a global basis for carbon cycle applications. Ciais et al. (1997a) combined a global biospheric model with global climate model simulations to estimate monthly global surface fluxes of ^{18}O in CO_2 from the terrestrial biosphere. Integrated with an atmospheric tracer transport model, this approach yielded results that agreed well with atmospheric observations, and led to the conclusion that the temporal and spatial patterns of $\delta^{18}O$ of CO_2 in the atmosphere were largely attributable to terrestrial ecosystem processes (Ciais et al. 1997b; Peylin et al. 1999). Cuntz et al. (2003a,b) expanded global simulations of ^{18}O fluxes with a well-integrated suite of model components that provided estimates on the diurnal time-scale. These advances will likely provide a basis for utilizing observations of $\delta^{18}O$ of atmospheric CO_2 to constrain carbon sources and sinks and distinguish between assimilation and respiration components of terrestrial fluxes.

Further research is needed on an interesting aspect of the atmospheric CO_2 record, which showed a decline in $\delta^{18}O$ of CO_2 of about 0.5‰ in the mid-1990s (Gillon and Yakir 2001; Ishizawa et al. 2002). Gillon and Yakir (2001) found variations in the activity of the enzyme of carbonic anhydrase, which catalyzes oxygen isotope exchange between CO_2 and water, suggesting that full equilibration is not reached in many species, particularly C_4 grasses. The authors concluded that large-scale conversions of forested ecosystems to pastures dominated by C_4 plants during the 1990s could have led to a global decline in $\delta^{18}O$ of atmospheric CO_2 of 0.02‰ yr^{-1}. Ishizawa et al. (2002) pointed out that such conversions can only partially explain the observed decline in $\delta^{18}O$ of CO_2, and that an additional mechanism could be an increase in both photosynthesis and respiration of the terrestrial biosphere. Advances in global modeling of $\delta^{18}O$ of CO_2 and additional observations of mechanisms of ecosystem fractionation and the isotopic composition of atmospheric CO_2 will likely lead to further interpretation and application of variations in $\delta^{13}C$ and $\delta^{18}O$ of CO_2 for understanding the role of the terrestrial biosphere in the carbon cycle.

4.4 Future Directions

Research on the application of stable isotopes in ecosystem and global carbon cycles was synthesized and coordinated by the Biosphere-Atmosphere Stable Isotope Network (BASIN) of GCTE beginning with an initial workshop in 1997. The BASIN network (http://basinisotopes.org) is carrying forward with additional coordination and synthesis of traditional aspects of data collection, such as the isotopic composition of ecosystem respiration, as well as other applications of stable isotopes in understanding the role of terrestrial ecosystems in biogeochemistry. Data are increasingly available on the isotopic composition of other gases present in the atmosphere in lower concentrations than CO_2, and therefore more difficult to measure. Stable isotopes of methane (Snover and Quay 2000), N_2O (Perez et al. 2000; Perez et al. 2001), and hydrogen (Rahn et al. 2002), for example, are providing additional information on the role of ecosystem physiology in land-atmosphere interactions. Also promising are new studies on the isotopic composition of non-methane hydrocarbons such as isoprene (Affek and Yakir 2003; Goldstein and Shaw 2003), and the highly abundant atmospheric components, water vapor (Moreira et al. 1997; Yepez et al. 2003) and diatomic oxygen (Angert et al. 2003; Stern et al. 2001), which are strongly influenced by terrestrial processes.

Monitoring of a wider variety of ecosystem types will also provide a broader information base for understanding the influence of the land surface on the atmosphere and scaling from ecosystems to regional and global scales. Data from tropical ecosystems, semi-arid systems, and human-dominated ecosystems have been sparsely represented in the BASIN network, but new datasets in these areas are increasingly available (Ometto et al. 2002; Pataki et al. 2003a; Yepez et al. 2003). New technologies also promise to increase spatial and temporal coverage of the isotopic composition of the atmosphere. Automated samplers for collecting atmospheric samples have recently been deployed in a number of ecosystems and have demonstrated the dynamic influence of ecosystems processes on the atmosphere and the utility of long-term monitoring (Lai et al. 2005; Lai et al. 2003; Schauer et al. 2003). These monitoring programs will be greatly extended by the application of optical measurements of rare isotopes with instruments such as Tunable Diode Lasers (TDL) that measure $^{13}CO_2$ concentrations in real time. TDL and similar technologies will increase analytical capabilities severalfold in terms of sample number, allowing large numbers of samples to be collected over short time-periods in a number of locations throughout plant canopies (Bowling et al. 2003b).

Results from atmospheric monitoring programs in ecosystems are being incorporated into a growing number of models of isotopic fractionation and its influence on the atmosphere (Baldocchi and Bowling 2003; Riley et al. 2003; Suits et al. 2005). These linkages have been largely indirect, that is, as isotopic measurements improved our basic understanding of fractionation and its physical and physiological basis, new theoretical and empirical relationships have been incorporated into ecosystem-atmosphere models. However, direct linkages between isotopic data-streams and ecological models are emerging as data assimilation or "data-model fusion" techniques are becoming common in ecological and biogeochemical applications. Similar to approaches already common in global scale studies of the carbon cycle, these quantitative methods optimize the solution for a given set of equations, e.g., a mass balance of ecosystem carbon sources and sinks, using available datasets as constraints. This method has been used to model ecosystems fluxes (Raupach 2001; Styles et al. 2002), estimate the mean residence time of carbon pools (Barrett 2002; Luo et al. 2003), and partition fluxes into their component parts (Luo et al. 2004). The increasing temporal and spatial coverage of isotopic measurements in various ecosystems will likely be directly incorporated into improved estimates of ecosystem-scale physiological and biogeochemical parameters with these methods.

Measurements of the isotopic composition of trace gases in the atmosphere and within and above terrestrial ecosystems have provided new insights into ecosystem functioning and the role of the terrestrial biosphere in the carbon cycle. These insights have included partitioning carbon cycle components such as terrestrial and oceanic carbon sinks, photosynthetic and respiratory components of NEE, and C_3 and C_4 contributions to ecosystem respiration. Improvements in both measurement techniques and ecosystem- to global-scale models are rapidly resulting in refined estimates of these aspects of the carbon cycle and the underlying mechanisms for their spatiotemporal variations. This is a rapidly evolving area of research, and one in which the GCTE core project made an important and lasting contribution through its support of the BASIN network.

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In Memoriam

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Chapter 5

Effects of Urban Land-Use Change on Biogeochemical Cycles

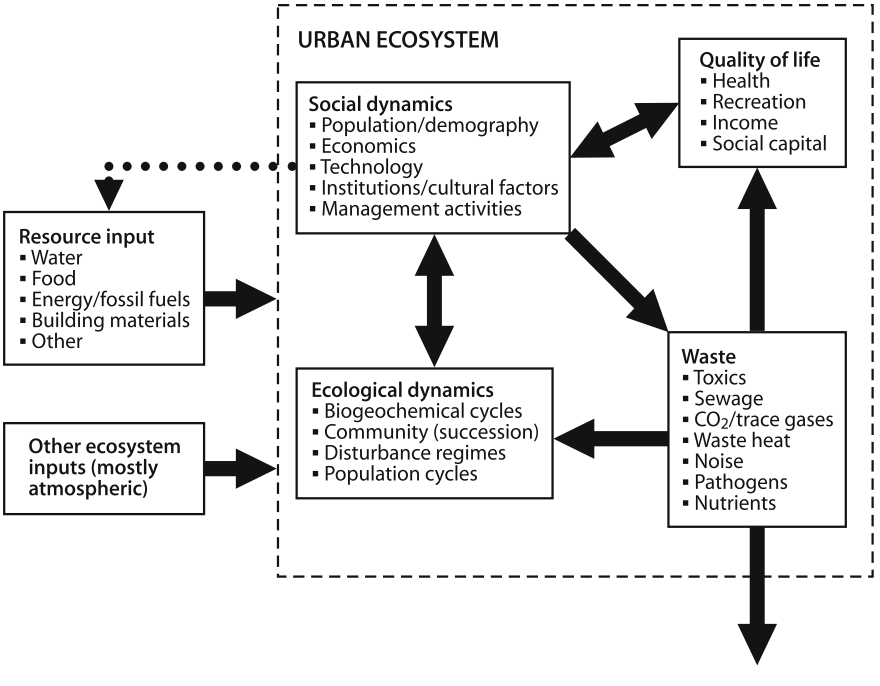
Richard V. Pouyat · Diane E. Pataki · Kenneth T. Belt · Peter M. Groffman · John Hom · Lawrence E. Band

5.1 Introduction

Urban land-use change, the conversion of agricultural and natural ecosystems to human settlements, has become an important component of global change. Virtually all of the projected increase in the world's population is expected to occur in cities so that by the year 2007 more than half of the global population is expected to live in urban areas (United Nations 2004). Yet, urban settlements and surrounding areas are complex ecological systems that have only recently been studied from a rigorous ecological perspective (Pickett et al. 2001). Clearly, urban areas represent ecosystems with modified biogeochemical cycles such that fluxes and pools of matter, energy, and organisms differ greatly from the previous ecosystem (Collins et al. 2000). Our knowledge of the magnitude and extent of these biogeochemical changes at local, regional, and global scales is a major area of uncertainty in our understanding of global change.

In the ecological sciences, the ecosystem approach has been used successfully in studying the effects of disturbance and exogenous inputs of nutrients and pollutants on biogeochemical cycles (Likens 1992). To study biogeochemical cycles in urban areas, Grimm et al. (2003) recommended the ecosystem approach where: (1) urban ecosystems are viewed as spatially homogenous, i.e., "well-mixed reactors," or (2) urban ecosystems are considered a heterogeneous assemblage of parts or "patches." Indeed, cities have been viewed as well-mixed reactors in answering questions about how they affect biogeochemical cycles at regional and global scales (Fig. 5.1). In so doing, mass balances have been constructed for entire cities to assess their "ecological footprint," that is, the amount of land resources acquired from other ecosystems needed to sustain the urban population (Rees 2003). Moreover, the mass balance approach allows investigations into the movement of nutrients and pollutants across ecosystem boundaries and the cycling of these materials within the system itself. For example, Baker et al. (2001) constructed a nitrogen balance for the Phoenix metropolitan area and found that inputs (human and

Fig. 5.1.
Conceptual diagram of an urban ecosystem showing interrelationships between human and biophysical components. *Dashed line* indicates ecosystem boundary if city considered a "well-mixed reactor" such that inputs and outputs into and out of the ecosystem can be measured. Model includes feedback loop from the human social component of the system to resource acquisition, i.e., demand for resources dependent on population density, quality of life issues, and the ability of ecosystem to assimilate waste



natural) to the urban ecosystem were an order of magnitude higher than inputs to the surrounding desert areas. Furthermore, human hydrologic modifications within the urban area promoted the accumulation of N within the ecosystem.

Urban ecosystems maintain a high state of resiliency due to the socioeconomic influence of their inhabitants. This enables them to continually obtain resources from other areas. However, this dependence disconnects urban populations (and their social systems) from locally occurring ecological constraints (Luck et al. 2001). As a result, the ecological impact of cities can extend to regional and global scales without negative feedbacks directly affecting the system itself (Rees 2003). Moreover, urban areas can affect adjacent non-urban ecosystems through the production and transport of waste products and by altering regional weather patterns (e.g., Cerveny and Balling 1998; Shepherd and Burian 2003; Gregg et al. 2003).

An alternative to the well-mixed reactor approach is to delineate and recognize the parts or patches of urban ecosystems (Collins et al. 2000; Pickett et al. 2001). With this approach, ecosystems and the patches that comprise them are treated as well-mixed reactors at some scales and heterogeneous systems at others (Grimm et al. 2003). In this way input-output budgets can be developed not only for entire cities but also for individual functional parts of the urban ecosystem. This allows investigations of the effects of urban development on biogeochemical processes of a patch of lawn or remnant forest, which themselves may have cycling and fluxes of resources that interact with neighboring patches. Pouyat et al. (in press) suggested that researchers should exploit the heterogeneity of urban landscapes using the diverse array of patches as surrogates for field manipulations, or "natural experiments."

In this chapter we address the question: what is the net effect of urban land-use change on biogeochemical cycles at local and metropolitan area scales? Our use of the term *urban* is inclusive of landscapes having >2 500 persons km^{-2} or densities at which human populations cannot be supported by local agricultural production (Ellis 2004). We use the phrase *urban land-use change* to describe coarse scale conversion of natural or agricultural ecosystems to urban land uses, as well as fine scale or local changes in land use that may occur in post-urban development. We will focus on the local scale because it is the most relevant one in making mechanistic assessments of urban biogeochemical processes. Our discussion relies on data available in the literature (mostly from temperate systems of North America) and from current research at the Long Term Ecological Research (LTER) site in Baltimore, MD USA (Baltimore Ecosystem Study). We devote most of our discussion to carbon (C) and nitrogen (N) pools and fluxes, both of which are important at multiple scales (Vitousek et al. 1997; Schlesinger and Andrews 2000) and may be indicators of urban stress and disturbance (Carreiro et al. in press). While heavy metals and organic compounds are important constituents in urban environments, their effects on plants, animals, and human health are beyond the scope of this chapter. Nor do we discuss the far-reaching effects of natural resource importation by cities, i.e., the aforementioned urban ecological footprints. The ability of urban inhabitants to exploit land resources at great distances has important anthropogenic impact on biogeochemical cycles at regional and global scales. But we believe that these impacts should be weighed against the effect of alternative settlement patterns on a per-capita basis – a comparison that requires extensive discussion. Excellent discussions of urban ecological footprints are included in Folke et al. (1997) and Rees (2003).

5.2 Urban Land-Use Change

In developed nations during the last half century, urban growth has occurred in a dispersed pattern relative to older and more densely populated cities that developed before and during the Industrial Revolution. Between 1980 and 2000 alone, land devoted to urban uses grew by more than 34% in the United States (USDA Natural Resource Conservation Service 2001). By contrast, the population grew by only 24% during the same period (USDC Census Bureau 2001). This dispersed growth pattern, or suburbanization, has occurred at the expense of agricultural and forested land (Imhoff et al. 1997). A recent analysis based on satellite imagery suggests that the land area covered by impervious surfaces (such as pavement and buildings) is larger than the surface area covered by herbaceous wetlands in the conterminous United States, or roughly the size of Ohio USA (Elvidge et al. 2004).

Although biogeochemical effects of agricultural land conversions and their recovery after abandonment have been relatively well studied, conversions to urban land uses have received little attention (Pouyat et al. 2002). We know that agricultural uses lead to drastic changes in biogeochemical cycling (Matson et al. 1997). However, once these lands are abandoned, many of the biogeochemical functions of the preagricultural ecosystem are recovered. For example, forest regrowth on agriculturally abandoned land has resulted in a gradual recovery of above- and below-ground C pools in the eastern and central United States (Houghton et al. 1999; Caspersen et al. 2000; Post and Kwon 2000). In fact, what are now considered "pristine" forest habitats at one time were some of the most densely populated regions of the world, for example, the Central American Mayan forests (Turner et al. 2003) and the Amazon River Basin (Heckenberger et al. 2003).

Converting agriculture, forest, and grasslands to urban and suburban land uses entails a complex array of land and ecosystem alterations. Dense human inhabi-

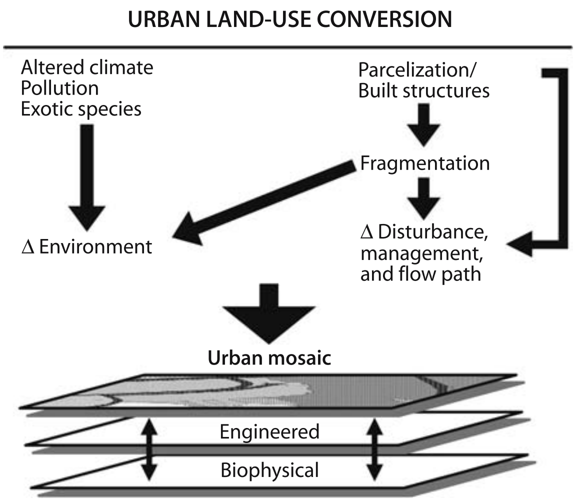


Fig. 5.2. Conceptual diagram of the effect of urban land-use conversions on native ecosystems. As landscapes are urbanized, natural habitats are increasingly fragmented as parcels of land ownership become smaller. During this process humans introduce novel disturbance and management regimes and flow paths to the landscape (*arrows on right*). Concurrently there is a change in the environmental conditions in which the ecosystem functions (*arrow on left*). See text for detailed explanation (modified from Pouyat et al. 2003)

tation along with urban land-use change necessitates the construction of various built structures, e.g., roads, buildings, civil infrastructure, as well as the introduction of human activities. The spatial pattern of these human features and activities are largely the result of "parcelization," or the subdivision of land by property boundaries, as landscapes are developed for human settlement. Parcelization typically leads to habitat loss and fragmentation as landscapes are continually subdivided into ever smaller patches, each with an individual land owner. Overlaid on the patch mosaic are various environmental factors that typically are associated with urban areas. The result is a patchwork or landscape mosaic of remnant ecosystems, managed parcels, and a built environment that overlay the preexisting ecosystem's biophysical features (Fig. 5.2).

5.3 Urban Environmental Factors

A complex of environmental factors altered by urbanization potentially affects biogeochemical cycling: atmospheric, soil, and water pollution; CO_2 emissions; micro- and meso-climates; and introductions of exotic plant and animal species (Pouyat et al. 1995). In some metropolitan areas, the net effect of such factors is analogous to predictions of global environmental change (Carreiro and Tripler 2005), e.g., increased temperatures and rising atmospheric concentrations of CO_2 (Ziska et al. 2004). In the following sections we discuss environmental factors that could affect biogeochemical cycles in urban and suburban landscapes.

5.3.1 Climate and Atmospheric Composition

Urban environments are characterized by localized increases in temperature known as the "heat island" effect (Oke 1990). Urban heat islands occur when vegetation cover is replaced by built structures. This reduces evapotransporation rates while the introduction of building materials increases the absorption and storage of solar energy that later is released as sensible heat (Oke 1990). The combined effect of these changes is to increase minimum (and to a lesser degree maximum) temperatures such that the difference between rural and urban temperatures typically is greatest several hours after sunset. This difference has been as much as 3 to 5 °C (Brazel et al. 2000). While cities embedded within desert ecosystems have warmer temperatures during the night, they typically have lower temperatures during the day, i.e., the "oasis effect" (Brazel et al. 2000).

How higher urban temperatures affect plant growth depends partly on the interactive effect of other environmental factors that may enhance plant growth such as N deposition and concentrations of atmospheric CO_2, the latter of which can reach 520 ppm in urban areas (Idso et al. 2002; Körner and Klopatek 2002; Pataki et al. 2003), or nearly double the preindustrial level of 280 ppm. Still other urban environmental factors may negatively affect plant growth such as tropospheric ozone (Chappelka and Samuelson 1998; Skärby and Ro-Poulsen 1998; Gregg et al. 2003).

The interactive effect of these multiple atmospheric and climate factors on plant productivity is a major uncertainty in global change research due to the difficulty of implementing controlled, factorial experiments in most ecosystems (Norby and Luo 2004). Hence, ecological studies in urban ecosystems have been proposed as a means of improving our understanding of multiple effects of global change (Pouyat et al. 1995; Grimm et al. 2000; Carreiro and Tripler 2005). Although this work is at an early stage, some results have been reported. Ziska et al. (2004) found plant productivity increases of 60 to 115% along an urban-rural gradient in Maryland, USA that corresponded to a 21% increase in CO_2 and a 3.3 °C temperature increase at the urban end of the gradient. Gregg et al. (2003) found that the growth of cottonwood seedlings was highest in the urban portion of an urban-rural gradient in the New York City area because of high ozone concentrations in rural areas downwind of urban pollution. Outside of the Los Angeles area, a large body of research in the San Bernardino Mountains Gradient Study has shown that foliar injury and chlorotic mottling is common at polluted sites due to ozone exposure, concurrent with decreased root biomass and increased aboveground biomass due to high N deposition (Arbaugh et al. 2003; Grulke et al. 1998; Grulke and Balduman 1999).

Additional work is necessary to determine whether these trends are robust in a large number of urban ecosystems.

Differences in air temperature also have been noted for soil temperatures. Mean annual temperatures in highly disturbed soils (0–10 cm depth) on a playground in New York's Central Park were more than 3 °C warmer than in soils in an adjacent wooded area (Mount et al. 1999). In comparing soil heat flux of several urban surfaces, Montague and Kjelgren (2004) found that heat fluxes were greatest beneath asphalt and concrete and least under pine bark mulch. For woodland soils in the New York City metropolitan area, surface temperatures (2 cm depth) differed by as much as 3 °C between urban and rural forest patches (Pouyat et al. 2003). Assuming that these soil temperatures are representative of those in urban areas, the difference between highly disturbed soils and natural forested soils in a metropolitan region can be as high as 6 °C. This difference in temperature can have significant effects on microbial activity and N availability in soil (Carreiro et al. in press).

Higher air temperatures and heat loading by impervious surfaces in urban areas also can affect the temperature of streams. First- and second-order streams in urban areas may have less shade than their rural counterparts and receive considerable runoff from impervious surfaces, which typically store a great amount of heat energy from solar radiation. In headwater streams, the major effect of urban-heat loading occurs early in the storm event as the first flush of runoff reaches the stream. The amount of temperature change is related to the percentage of impervious area in the watershed. For example, stream-temperature monitoring in the Baltimore Ecosystem Study showed that storm events in headwater streams resulted in a rapid increase in temperature. The increase was related directly to the housing density and proportion of impervious cover in the watershed (Fig. 5.3a). Similarly, in a study of headwater streams in Wisconsin and Minnesota USA, the percentage of impervious area in the watershed had a positive, linear relationship with water temperature during dry weather flows (Wang et al. 2003). Stream invertebrates and leaf breakdown processes are highly sensitive to elevated stream temperatures (Wang and Kanehl 2003; Webster and Benfield 1986).

Besides temperature, soil-moisture regimes can be modified by urban environments. Disturbed soils in urban areas typically have limited infiltration capacities due to hydrophobic surfaces, crust formation, and soil compaction (Craul 1992; Pouyat and Effland 1999). Compounding slow infiltration rate is the potential of impervious surfaces to drain concentrated flow into pervious areas. This can prevent water infiltration even during small storm events. Soil-moisture levels also can be reduced in urban areas due to higher air temperatures, which generate higher evaporative and transpirative demand on soil water resources. In contrast to factors that reduce soil moisture levels, soils in urban areas often are irrigated and have abrupt textural and structural interfaces that can restrict drainage resulting in higher soil-moisture content (Craul 1992). Moreover, below-ground infrastructures such as pressurized potable water distribution systems can leak water into adjacent soils by as much as 20 to 30% (Law et al. in press).

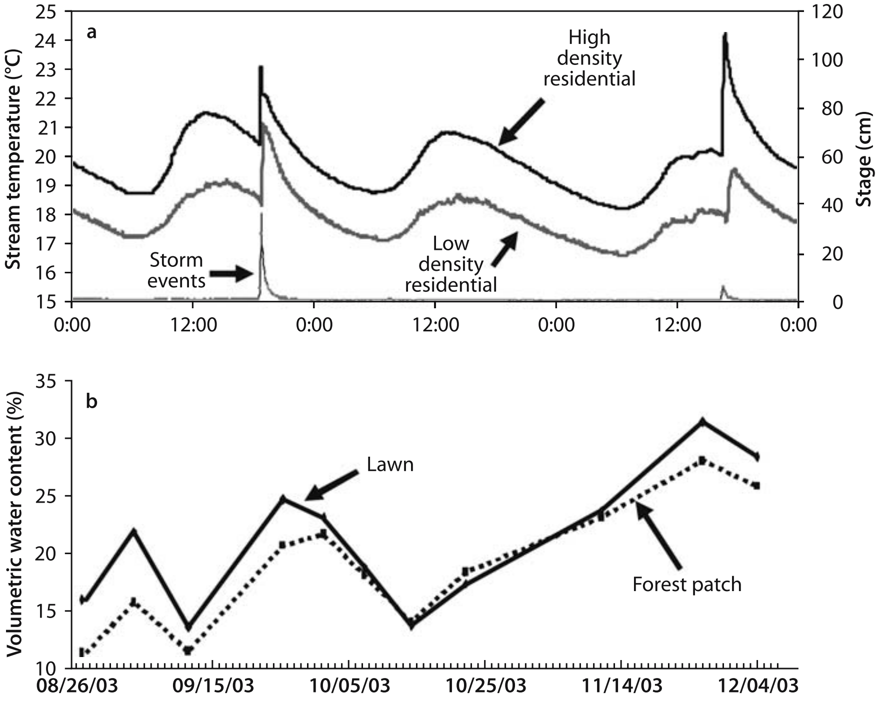


Fig. 5.3.
a Stream temperatures, May 25 to 27, 2004, for high density residential and lower density residential small headwater catchments. Stage at one of watersheds (*right axis legend*) shows two storm events (0.63 and 0.15 inches of rain). **b** Soil moisture (% by volume) of soils sampled at weekly intervals (depth of 0 to 10 cm) at Cub Hill eddy flux tower site of Baltimore Ecosystem Study. In forest patch, measurements taken along three transects perpendicular to slope ($n = 30$). Lawn measurements taken in two parcels along 30-m transects ($n = 24$)

Currently, we lack long-term continuous data with which to make comprehensive comparisons of soil moisture between urban and rural forest patches or between urban forest soils and disturbed soils. In the Baltimore Ecosystem Study, synoptic measurements of soil moisture (0–5 cm depth) in a medium-density residential area and adjacent deciduous woodland indicate that differences in soil moisture occur between land-use and cover types in urban landscapes. Residential lawns within a 150 m radius of the forest patch showed that un-irrigated turf soils had higher moisture levels than forest soils during the summer. There were no differences between the two patch types after leaf drop (end of October) (Fig. 5.3b). Presumably, differences in the summer were due to higher transpiration rates of the broad-leaved trees. In late fall and early winter, the moisture level in turf soil increased more rapidly than in forest soil, possibly reflecting concentrated runoff from roof gutters or snow melt (Fig. 5.3b). How these differences affect C and N cycling is being studied.

5.3.2 Atmospheric and Soil Pollution

Urban environments usually have higher concentrations and depositional fluxes of atmospheric chemicals than rural environments (Gatz 1991). Most urban atmospheric pollutants originate from the combustion of fossil fuels and industrial emissions. These include nitrogen oxides, sulfur oxides, heavy metals, and various organic chemicals. The pollutants are emitted locally into a restricted geographic area, particularly relative to the area from which the resources were derived, resulting in high atmospheric concentrations (Wong et al. 2004). High pollutant concentrations in the atmosphere combined with numerous temperature inversions increase the depositional rates of chemicals into urban areas (Seinfeld 1989). Since the capacity of ecosystems to assimilate atmospheric chemicals is correlated with the amount of leaf area of plants and soil biological activity, highly altered urban ecosystems have greatly diminished capacities to assimilate chemicals, especially when inputs are high.

Not surprisingly, studies of forest ecosystems along urban-rural gradients suggest that urban forest remnants receive relatively high amounts of heavy metals, organic compounds, N, and sulfur (S) in wet and dry atmospheric deposition (Pouyat and McDonnell 1991; Lovett et al. 2000; Wong et al. 2004). Lovett et al. (2000) quantified atmospheric N inputs over two growing seasons in oak forest stands along an urban-rural gradient in the New York City metropolitan area. They found that N entering urban forests in throughfall was 50 to 100% greater than the N flux into rural and suburban forests. These inputs fell off in the suburban stands 45 km from the city (New York's Central Park), which Lovett et al. suggested was due to the reaction of acidic anions with larger alkaline dust particles (Ca^{2+} and Mg^{2+}) of 2 µm or less in diameter that precipitated closer to the city. They hypothesized these particles (urban dust) originated from construction and demolition activity within the city. Similar results were found for the city of Louisville, KY USA and the San Bernardino Mountains in the Los Angeles metropolitan area where both N and base cation deposition rates into urban forest patches have been found to be higher than in rural forest patches (Bytnerowicz et al. 1999; Carreiro et al. in press; Fenn and Bytnerowicz 1993).

Evidence for a similar depositional pattern was found for heavy metals along the New York City transect. Pouyat and McDonnell (1991) found two to threefold increase in contents of lead (Pb), copper (Cu), and nickel (Ni) in urban than in suburban and rural forest soils. A similar pattern but with greater differences was found by Inman and Parker (1978) in the Chicago, IL USA, metropolitan area, where levels of heavy metals were more than five times higher in urban than in rural forest patches. Other urban-rural gradient studies have shown the same pattern though for smaller cities differences between urban and rural stands were narrower (Carreiro et al. in press; Pavao-Zuckerman and Coleman in press). Finally, Wong et al. (2004) found a large gradient of Polycyclic Aromatic Hydrocarbons (PAH) concentrations in forest soils in the Toronto (Canada) metropolitan area, with concentrations decreasing with distance from the urban center to surrounding rural areas by a factor of at least 60.

How these pollutants affect biogeochemical fluxes is uncertain, but preliminary results suggest that the effects are variable and depend on various urban environmental factors (Carreiro et al. in press). For example, Inman and Parker (1978) found slower leaf litter decay rates in urban stands that were highly contaminated with Cu ($75.7\ \mathrm{mg\ kg^{-1}}$) and Pb ($399.9\ \mathrm{mg\ kg^{-1}}$) compared to unpolluted rural stands. Apparently, the heavy metal contamination negatively affected the activity of decomposers in these urban stands. By contrast, where heavy metal contamination of soil was moderate to low relative to other atmospherically deposited pollutants such as N, rates of decomposition and soil N-transformation increased in forest patches near or within major metropolitan areas in southern California (Fenn and Dunn 1989; Fenn 1991), Ohio (Kuperman 1999) and southeastern New York (Carreiro et al. in press).

5.3.3 Introductions of Exotic Species

The expansion of urban areas has resulted in some of the greatest local extinction rates observed in the world (McKinney 2002). Cities also have become epicenters of many of introductions of nonnative species (Steinberg et al. 1997; McKinney 2002), some of which have become important pathogens or insect pests, e.g., Dutch elm disease and the Asian long-horned beetle. Local extinctions of native species and the invasions by urban-adapted nonnative species have resulted in a pattern where the species richness of nonnative species increases from outlying rural areas to urban centers while native species decrease (Blair 2001; Hope et al. 2003).

While native plant and animal species richness may be depressed, plant species richness apparently is greater in urban than in rural environments. Urban plant communities tend to have higher species richness and diversity than natural forests because of planting choices of multiple land owners (Nowak 2000). For instance, Nowak et al. (2002) found 81 and 57 tree species with Shannon-Weiner diversity index values of 3.6 and 3.4 in Baltimore MD and Brooklyn NY, USA, respectively. These values are higher than those found for eastern deciduous forests (1.9 to 3.1) of the United States (Barbour et al. 1980). In Phoenix, USA, overall species richness was greater in the urban area than in the surrounding desert. Within the urban area, species diversity was positively correlated to median family income, such that the highest biodiversity was associated with the wealthiest neighborhoods, a phenomenon termed the "luxury effect" (Hope et al. 2003).

Invasive species can play a disproportionate role in controlling C and N cycles in terrestrial ecosystems (Bohlen et al. 2004; Ehrenfeld 2003). Therefore, the relationship between invasive species abundances and urban land-use change has important implications for biogeochemical cycling of C and N (Pouyat et al. in press). For example, in the northeastern and mid-Atlantic United States where native earthworm species are rare or absent, urban areas are important foci of nonnative earthworm introductions, especially Asian species from the genus *Amynthas*, which are expanding toward outlying forested areas (Steinberg et al. 1997; Groffman and Bohlen 1999; Szlavecz et al. 2006). These invasions into forests have resulted in highly altered C and N cycling processes (Bohlen et al. 2004; Carreiro et al. in press). Other examples of species invasions in urban areas that have altered C and N cycles include shrub (*Berberis thunbergii*), tree (*Rhamnus cathartica*), and grass (*Microstegium vimineum*) species (Ehrenfeld et al. 2001; Heneghan et al. 2002; Kourtev et al. 2002).

5.4 Disturbance and Management Effects

For most urban landscapes, human-caused disturbance is more pronounced during rather than after the land-development process. Urban development of land typically includes the clearing of existing vegetation, massive movements of soil, and the building of structures. The extent and magnitude of these initial disturbances is dependent on infrastructure requirements (e.g., storm water retention ponds), topography, and other site limiting factors. As an example, a topographic change analysis of 30 development projects in Baltimore County USA showed that the total volumetric change of soil per development was positively correlated with mean slope of the site ($r = 0.54$, $p = 0.002$) (McGuire 2004). In addition, these development projects resulted in massive soil disturbances with the potential to have large effects on soil organic C. Using data from this study, we estimated that the amount of soil organic C that was disturbed during a development project covering 2 600 m^2 was roughly 2.7×10^4 kg. This assumes that the original soil had a soil organic C density of a deciduous forest (10.3 kg m^{-2}) to a depth of 3 m, i.e., the average depth of the soil disturbance. How much soil organic C actually is lost during the development process is unknown and depends partly on the ultimate fate of the surface soil layers (topsoil).

The previous development scenario typically predates residential, institutional, and commercial land uses, for which turfgrass is the resultant plant-cover type. Nowak et al. (1996) found that residential, institutional, and commercial land uses made up on the average 39.0, 5.7, and 13.6% (total 58.3%) of the land cover in the major U.S. metropolitan areas, respectively. The total estimated lawn area for the conterminous USA is 16.38 ±3.58 million ha (Milesi et al. 2005). Management of this vast area of turfgrass typically includes adding pesticides and supplements of water and nutrients as well as being regularly clipped during the growing season. In the following sections we discuss how these lawn and horticultural management practices may affect biogeochemical cycles.

5.4.1 Lawn and Horticultural Management

To manage turfgrasses in lawns, homeowners and institutional land mangers in the USA apply about 16 million kg of pesticides each year (Aspelin 1997) as well as fertilizers at rates similar to or exceeding those of cropland systems (Talbot 1990). In addition, lawns typically are clipped on a regular basis during the growing season. This management scenario may or may not result in increases in plant productivity. In comparing results from studies of mowed lawns in Wisconsin, California, and Maryland, Falk (1980) estimated that the range for net primary productivity in temperate climates was about 1.0 to 1.7 kg ha yr^{-1}, most of which is below ground. Although above-ground productivity increased with N fertilization and irrigation, total productivity (above and below ground) did not differ. Other studies have shown somewhat lower productivity rates for lawns (0.6 to 0.7 kg ha yr^{-1}) (Blanco-Montero et al. 1995; Jo and McPherson 1995). Still others have reported direct relationships between management and productivity (Heckman 2000; Kopp and Guillard 2002; Golubiewski 2006). As a comparison, net primary production in temperate grasslands ranges from 0.1 to 1.5 kg ha yr^{-1} (Leith 1975).

While total turfgrass productivity may or may not increase with management inputs, soil organic C sequestration appears positively related to supplemental inputs of fertilizer and water. In comparing surface soils of 15 golf courses, Qian and Follett (2002) found that total C sequestration rates ranged from 0.9 to 1.0 t ha^{-1} yr^{-1}. This is similar to rates obtained for the recovery of perennial grasslands following cultivation (1.1 t ha^{-1} yr^{-1}) (Gebhart et al. 1994), but much higher than unmanaged grasslands (0.33 t ha^{-1} yr^{-1}) (Post and Kwon 2000). Similarly, Higby and Bell (1999) found that soil organic matter was higher in fertilized golf course fairways than in adjacent unfertilized areas. Using long-term simulations of the CENTURY model for lawn ecosystems, Qian et al. (2003) showed that N fertilization coupled with a management regime in which grass clippings were left on site increased soil organic C accumulations by up to 59% in comparison to sites that were not fertilized and clippings were removed. How much C is sequestered in soils under turfgrass depends on the differential effects of management practices on above- and below-ground productivity and the rate of decomposition in the surface soil (Qian and Follett 2002).

While lawn care management practices input chemicals at rates comparable to cropland systems, they are potentially less disruptive of biogeochemical cycles. Cropland systems have a greater magnitude and frequency of soil disturbances and generally remove a greater proportion of the standing crop (Asner et al. 1997; Pouyat et al. 2003). As a result, cropland systems lose substantial amounts of soil organic C and N (Matson et al. 1997). The net effect of an initial soil disturbance and subsequent lawn care management on C and N dynamics is less certain. In natural ecosystems, C sequestration increases with N additions until N is no longer limiting (Asner et al. 1997), i.e., a condition of N saturation (Aber et al. 1989). Nitrogen limitation is determined by biological demand and the ability of soil to accumulate N, which, in turn, is attributed partly to site history, climate, soil fertility, and vegetation type (Aber et al. 1998). In cultivated ecosystems, N additions over the long term can increase C storage, but due to annual disturbances of soil and the removal of plant biomass, these gains are less than those for grassland and forested ecosystems. On the other hand, turfgrass ecosystems can accumulate soil organic C at rates similar to those for grasslands and some forests due to the absence of annual soil disturbances (Qian and Follett 2002; Pouyat et al. 2003).

Carbon sequestration is an important regulator of the net effect of ecosystems on atmospheric carbon dioxide levels, which influence the atmospheric “greenhouse effect.” This effect is also influenced by other soil-atmosphere gas exchanges, especially nitrous oxide and methane that are influenced by urban land-use change. Kaye et al. (2004) found that lawns in Colorado had reduced methane uptake and increased nitrous oxide fluxes relative to native shortgrass steppe, with fluxes similar to irrigated corn. Goldman et al. (1995) found reduced methane uptake in forests in urban areas. In both cases, these changes were linked to nitrogen enrichment associated with urban land-use.

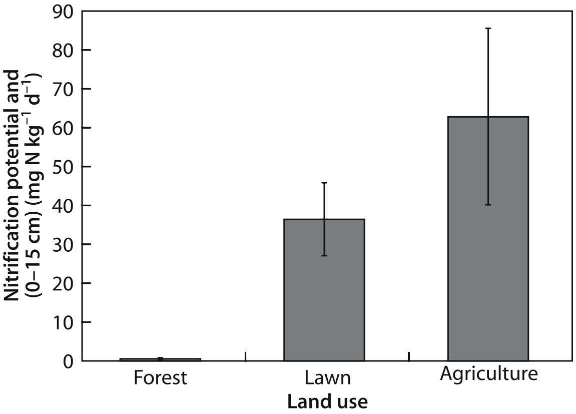


Fig. 5.4. Mean (±S.E.) potential net nitrification rates (mg NO_3^- kg d^{-1}) of 0–15 cm mineral soil samples after 14-d incubation period of 0.04 ha plots in the Baltimore LTER study. *Bars* represent comparison of forest, lawn, and agriculture land-use types ($n = 14, 10,$ and 10, respectively) (data from C. Williams, unpubl.)

The potential of turfgrass ecosystems to sequester soil organic C and thus maintain or increase microbial demand for N suggests a high capacity of these systems to retain N. Preliminary data from comparisons of lawn, forest, and cultivated patch types in the Baltimore Ecosystem Study suggest that lawns fall between temperate forests and cultivated land in C sequestration, N cycling, and N retention (Fig. 5.4). Currently, we are investigating the interactive effects of high N inputs, C pool dynamics, biomass removal, and altered hydrologic pathways in lawn ecosystems.

5.4.2 Management Effort

Perhaps the most distinctive characteristic of urban landscapes is the number and diversity of potential land managers on a per area basis. Parcels of land generally tend to become smaller from rural to suburban and urban residential areas, with a slight increase at the urban core (Pouyat et al. in press). This pattern potentially results in greater variation in management practices in high-density residential areas than in larger rural parcels because of the greater number of potential land managers (Collins et al. 2000). Parcel size also may affect the amount of effort of individual land owners. For example, in comparing fertilizer application rates in two small residential watersheds in Baltimore County, MD USA, Law et al. (2004) found that the application rate per unit of lawn area was higher for the watershed with smaller lot sizes, suggesting that homeowner input is inversely related to lot size. They also found that soil bulk density, an indicator of soil compaction, was positively related to the average annual application rate of fertilizer. The relationship between human impact and lot size also was evident at a coarser scale. In Baltimore, mean bulk densities of surface soils (0–5 cm) in high- and medium-density residential land-uses were 1.30 and 1.17 Mg m^{-3}, respectively. Bulk density was inversely related ($r = 0.52$, $P < 0.001$) to soil organic matter (Pouyat et al. 2002).

In addition to parcel size, management effort varies with socioeconomic factors in residential neighborhoods. In a survey conducted in the Columbus, OH USA, metropolitan area, Robbins et al. (2001) found that residents with houses valued at more than $250 000 were much more likely to apply chemicals on their lawns than owners of houses valued at less than $80 000. However, Law et al. (2004) and Osmond and Platt (2000) found that households with intermediate value applied the most lawn fertilizer. Whatever the relationships between socioeconomic factors and management effort, decisions involving horticultural management in much of the urban landscape are largely independent of government regulations (Robbins et al. 2001).

Management effort also should be related to the magnitude of the natural constraints on the system. For example, irrigation rates for lawns in dry land areas should be higher than for lawns in more temperate climates. The net result of these relationships is that while natural constraints on biological systems in urban landscapes are important, human desires and efforts to overcome these constraints result in vegetation structure and soil characteristics that are remarkably similar across urban settlements on a global scale (McDonnell et al. in press). Therefore, urban landscapes might be similar in vegetation structure and soil characteristics at coarse scales (regional and global) but highly variable at finer scales (Pouyat et al. 2003).

5.5 Effects of Built Environment

To fully grasp the effects of urban land-use change on biogeochemical cycles, we need to understand the ways the built environment affects energy and material flows in urban ecosystems. Our conceptual framework of urban land-use change (Fig. 5.5) incorporates the importance of built structures and the effect of impervious surfaces on ecosystem processing by differentiating between natural and engineered templates, either of which may constrain ecosystem processes. For example, both soil drainage and irrigation infrastructure can partially constrain distributions of plant species and trace gas fluxes, as well as the movement of nutrients and contaminants in urban ecosystems. Perhaps more interestingly, the natural and engineered templates may intersect; the proportion and "connectivity" of each determining the importance of each template in constraining biogeochemical processes. For example, hydrologists use the concept of "effective imperviousness" to more accurately model runoff volumes, that is, the connectivity between the natural and engineered templates. Effective impervious areas (EIA) drain immediately to storm-drain pipes and are equal to the total impervious area (TIA) minus the impervious surfaces draining to pervious areas where infiltration is possible (Sutherland 1995).

If measurements of EIA and TIA were made at the scale of a small watershed (<100 ha) for a given metropolitan area we suggest they would form a continuum of watersheds ranging from totally pervious cover to those with an almost entirely engineered template. Thus, the continuum would represent an array of small watersheds varying in area and connectivity of the engineered and natural templates, at least for hydrologic flow paths. Measurements of connectivity between engineered and natural templates also can be made for other flow paths (e.g., organic-matter transport or atmospheric deposition onto built and biological surfaces) and for other ecosystem delineations at various scales.

These relationships are important in determining the degree to which the engineered system mediates flows of energy and material. A totally engineered system has pathways that entirely separate or disconnect material flows from natural elements of the ecosystem, though over time, all human built structures fail to function to some degree, resulting in exchanges between engineered and natural templates. This disconnect "short circuits" the biological system, which diminishes the system's overall ability to buffer changes in water, nutrient, and contaminant inputs. As a result, the system's capacity to retain or process these materials is altered. For totally engineered systems, atmospherically derived contaminant and nutrient inputs can accumulate on impervious surfaces and be washed off repeatedly by small rainfall events into the engineered system. Thus, there is little chance of being accumulated in soil or biologically processed in the terrestrial system. In addition, gaseous exchanges between the atmosphere and the soil-plant continuum will be diminished, again short circuiting the ability of the biological system to assimilate C or gas-phase contaminants. We propose that the point in the continuum at which the constraints of the engineered and natural templates shift in importance from one to the other may serve as a useful delineation between urban and non-urban-dominated ecosystems.

At some point, all engineered pathways flow to natural systems, for example, sewage treatment outflows, power plant emissions, storm water runoff, and effluent from septic systems. All of these systems have important effects on ecosystems receiving their flows. In most cases, flows from engineered pathways concentrate materials collected from a larger area. The functional size of the area is dependent on the extent and connectivity of the infrastructure. For example, septic systems collect waste from a single detached house and release these flows into a relatively small volume of soil, while sewage treatment

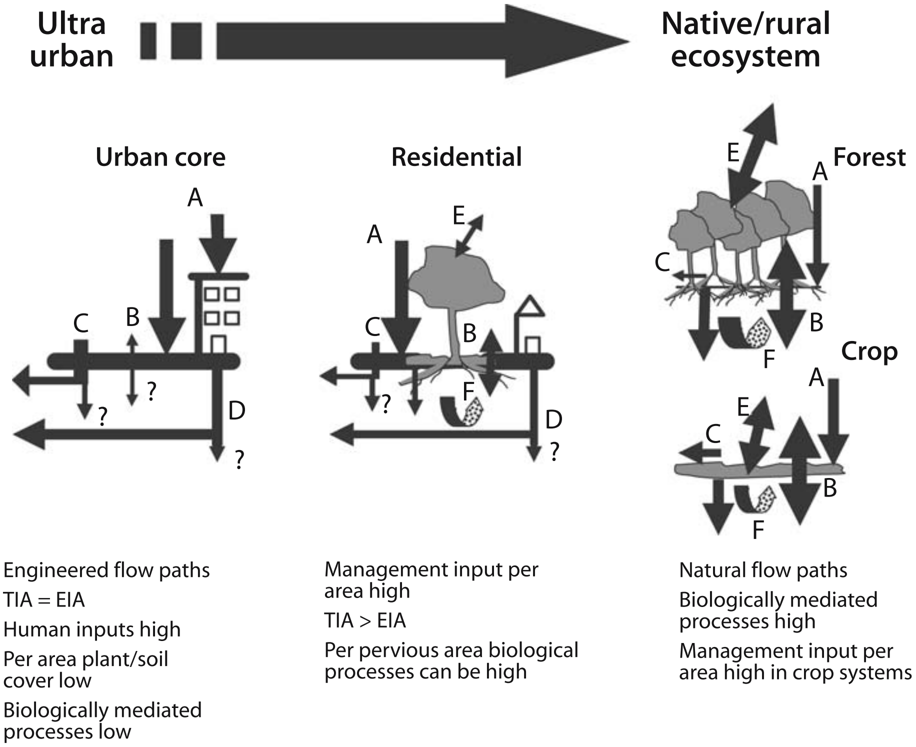


Fig. 5.5. Conceptual framework where anthropogenic and biophysical ecosystem characteristics form a continuum from highly urban (almost entirely human-made) to native or rural ecosystem types (those with the least human modification). Agricultural ecosystems also are depicted. The framework incorporates the importance of built structures and the effect of impervious surfaces on ecosystem processing. At the urban core, engineered flow paths (*C* and *D*) disconnect material inputs and flows (*A*) from natural processing that occurs in native/rural ecosystems. In these areas, the connectivity between the engineered and biophysical templates is low (*B*). In residential areas, the connectivity between engineered and biophysical templates can be relatively high depending on the spatial relationship of impervious and pervious surfaces. Management and environmental inputs in residential areas can be high (*A* and *E*) on a per-unit pervious area. However, depending on site history, soil type, and the concentration of flows these areas can have surprisingly high cycling rates (*F*) for processing or storing these inputs (adopted from Kay et al. 2006)

plants receive waste flows from tens and hundreds of thousands of residences and release flows to surface waters with varying abilities to assimilate the waste. As mentioned previously, the waste flows in both cases are byproducts of resources originating outside the urban ecosystems – often from great distances. Compounding the concentration of flow is the ability of built surfaces to accumulate various atmospherically derived contaminants through the development of organic films that increase the capture efficiency of impervious surfaces (Law and Diamond 1998). These films ultimately increase the movement of contaminants from the atmosphere to surface waters following wash-off (Diamond et al. 2000).

A clear example of the effects of concentrated flows is the impact of impervious cover on stormwater flows and the resulting impact on urban-stream ecosystems. Schueler (1994) and Morse et al. (2003) concluded from reviewing data in the literature that as little as 6% impervious cover in a watershed can result in measurable responses in stream-channel morphology and invertebrate populations. Moreover, changes in soil-drainage patterns associated with urban development and altered stream morphology can have marked effects on soil organic C and N processing, particularly in riparian soils (e.g., Groffman et al. 2002). An important question in urban hydrology is whether responses in stream ecology and riparian function differ between catchments with the same total impervious area but with different measures of effective impervious areas (Walsh 2004).

The tendency of the built environment and human activity to concentrate flow paths and chemical inputs can result in the development of "hot spots" in the landscape. Hotspots are areas or patches that show disproportionately high reaction rates relative to the surrounding area or matrix (McClain et al. 2003). The concept of hotspots developed from studies of N processing in soil cores (Parkin 1987) and riparian zones that showed that anoxic microsites with high C content were zones of elevated denitrification rates. Generally, hotspots are sites where reactants for specific biogeochemical reactions coincide in an environment conducive for the reaction to take place (McClain et al. 2003). Human activities and the introduction of built structures provide such conditions in urban landscapes at various scales. Examples include septic systems, golf greens, stormwater retention basins, and compost piles.

The importance of hotspots in the biogeochemistry of urban ecosystems is largely unknown. In urban fringe areas, there is concern about nitrate contamination of ground water from septic systems, which when functioning properly can be thought of as purposely engineered hot spots for processing human waste (Band et al. 2004). Hotspots in urban landscapes also can be sinks for contaminants, nutrients, or C. For example, the conversion of what was predominately prairie grassland into an urban landscape resulted in the development of C sequestration hotspots in the Boulder, CO USA, metropolitan area (Golubiewski 2003). These hotspots were composed of relatively small parcels with highly managed turfgrass and woody vegetation whose productivity rates and C storage were much higher than in the native grasslands they replaced. Similarly, detention basins designed to capture urban stormwater and protect streams may be hotspots of denitrification, replacing functions that occurred in riparian areas before urbanization (Groffman and Crawford 2003).

5.6 Assessing Biogeochemical Effects – the Importance of Scale

A critical task in using the ecosystem approach is the ability to make practical and meaningful delineations of ecosystem boundaries (Likens 1992). In nonhuman-dominated ecosystems, this task is challenging since many environmental factors vary as a continuum on the landscape. Ecologists and biogeochemists have addressed this challenge by using discontinuities of biophysical processes in the landscape as ecosystem boundaries, e.g., a watershed. Determining boundaries for urban ecosystems is an even greater challenge as there are no generally accepted ecological definitions of "urban" (Mcintyre et al. 2000). Nor do we know how urban environmental factors vary spatially (Pouyat et al. in press). This is especially problematic in viewing cities as well-mixed reactors because urban areas often are expanding in area, forming roughly concentric circles of development (McDonnell and Pickett 1990). For landscapes where development patterns are less dispersed, e.g., desert ecosystems, the boundary of urban expansion is more apparent (e.g., Baker et al. 2001).

To address the difficulty in delineating urban ecosystem boundaries for investigations of biogeochemical cycles, we propose a two-pronged approach: (1) conduct investigations for parts or patches of the urban landscape that have more readily recognizable boundaries, and (2) assess the interrelationship of these patches at multiple scales: one at the scale of individual parcels (<km) each with a distinctive landscape context, site history, land manager, and natural and engineered template, and the other at coarser scales, e.g., watershed or well-defined area of the landscape (e.g., Ellis 2004), to assess the interrelationships among parcels and investigate the net change in biogeochemical cycles due to urban-land transformations. At coarse scales, we suggest comparisons on both a per-unit pervious cover and per-unit total area basis. The latter includes built surfaces and considers urban landscapes as a whole. To distinguish between the two approaches, in the first case, productivity on a pervious-area basis can be greater than the native ecosystem replaced (or nonurbanized areas at the rural end of the continuum); in the second case, a city generally would have lower overall productivity than the native ecosystem it replaced. When human use of fossil fuels are included in these calculations, cities would be considered heterotrophic (primary productivity < total ecosystem respiration) rather than natural ecosystems, which are autotrophic (Grimm et al. 2003).

These relationships suggest a paradox of urban ecosystems: the engineered template reduces the ability of an ecosystem to assimilate or process energy and materials on a per-unit ecosystem basis such that when compared to natural systems urban ecosystems exhibit less biological activity. At the same time, the engineered template and human activity concentrate energy and matter into smaller areas (volumes) such that fluxes and biological activity will be higher on a per-unit pervious area basis than in the native ecosystem replaced. The latter characteristic is significant since the ability of biological systems to assimilate energy and material is determined at the scale at which organisms are using the resource. This can occur at very fine scales, e.g., hotspots. Thus, assessments at coarse scales that fail to distinguish between the built and pervious component of urban ecosystems will miss the scale at which biological processes are being constrained.

A comparison of N budgets of residential watersheds in the Baltimore Ecosystem Study illustrates the importance of scale. Law et al. (2004) calculated N input from fertilizer into a low- and medium-density residential watershed at three spatial aggregations: by the area of the watershed, subdivision, and residential lawns. For the more sparsely populated watershed, application rates were 9.5, 27.8, and 37.1 kg N ha^{-1} yr^{-1} on a watershed, subdivision, and residential lawn area, respectively. For the more densely populated watershed, rates were 12.5, 26.7, and 83.5 kg N ha^{-1} yr^{-1}. Therefore, the greatest distinction between the two watersheds is on a lawn-area basis, or the scale at which added N will be processed by the soil community and management decisions will be made by individual land owners. In addition, the watershed with lower housing densities had an aggregated septic load that was significantly lower than N fertilizer inputs and roughly equal to atmospheric deposition inputs (Band et al. 2004). However, this septic load was concentrated in 1 to 2% of the watershed area (leach fields), resulting in a loading rate that was an order of magnitude higher than N loading per unit of watershed area. Indeed, stream sampling in the Baltimore Ecosystem Study revealed that nitrate concentrations were higher in watersheds at the suburban fringe that are septic-serviced than in central city streams or sanitary sewer-serviced suburbs with similar lawn fertilization rates (Band et al. 2004; Groffman et al. 2004).

As another example, Nowak (2000) estimated the amount of C sequestered by trees in Baltimore to be 0.71 t C $ha^{-1} yr^{-1}$. His estimate was for the entire land area of the city. Estimates for pervious areas in Baltimore are not available, though Jo and McPherson (1995) measured carbon budgets on a per-pervious-area basis for two residential neighborhoods in Chicago, IL USA. They found that C sequestered by woody vegetation was as high as 3.29 t C $ha^{-1} yr^{-1}$. Assuming that C budgets of residential areas are similar across urban ecosystems, comparison of these rates to gross sequestration rates for a 25 yr old loblolly plantation (2.6 t C $ha^{-1} yr^{-1}$) and a naturally regenerating spruce-fir forest (1.0 t C $ha^{-1} yr^{-1}$) (Birdsey 1996) suggests the urban values are somewhat low when the entire landscape is considered (thus the net change from converting from a natural ecosystem to an urban ecosystem), but high when only pervious surfaces are considered. This suggests that on average, urban trees have higher growth rates than trees growing in nonirrigated and nonfertilized stands under rural environmental conditions. This finding is consistent with measurements of the productivity of urban trees (McPherson 2000), urban-rural comparisons of containerized plants (Gregg et al. 2003), and eddy flux tower measurements above a residential area (Hom et al. 2003).

On the basis of these comparisons, we propose that the net effect of urban land-use change on biogeochemical cycles depends on the overall constraints of the native ecosystem replaced. For example, converting a temperate deciduous forest ecosystem to an urban landscape results in a decrease (per land area) in plant productivity, but potentially higher rates on a pervious area basis. By contrast, converting a desert ecosystem to an urban landscape should result in both a land-area and per-pervious-area increase in primary productivity. Differences in the direction of the ecosystem response are the result of the relatively severe limitations in soil-water availability in desert vs. temperate environments. Thus, the technical ability and desire of humans to manage for specific types of plant communities irrespective of natural limiting factors have resulted in a convergence of urban vegetation structure and ecosystem function on a global basis (Pouyat et al. 2003).

5.7 Summary and Conclusions

Urban areas represent ecosystems with modified biogeochemical cycles such that fluxes and pools of matter, energy, and organisms differ greatly from the previous unaltered ecosystem. The conversion of agriculture, forest, and grasslands to urban and suburban land uses entails a complex array of land and ecosystem alterations. These include the construction of various built structures, e.g., roads, buildings, and civil infrastructure, as well as the introduction of horticultural management practices. In addition to land altering activities, a complex of urban environmental factors can potentially affect biogeochemical cycling including atmospheric and soil pollution, CO_2 emissions, micro- and meso-climates, and introductions of exotic plant and animal species. In some metropolitan areas, the net effect of such factors is analogous to predictions of global environmental change, which we feel represents an opportunity to study ecosystem responses to such factors at a scale not practical in controlled field experiments.

To fully understand the effects of urban land-use change on biogeochemical cycles, the effect of the built environment must be considered. A conceptual framework of urban land-use change was presented that incorporates the importance of built structures and the effect of impervious surfaces on ecosystem processing. This framework differentiates between natural and engineered systems, either of which may constrain biogeochemical processes. A totally engineered system has pathways that entirely separate or disconnect material flows from natural elements of the ecosystem, though all human built structures fail to function to some degree, resulting in exchanges between engineered and natural templates. This disconnect "short circuits" the biological system, which diminishes the system's overall ability to buffer changes in water, nutrient, and contaminant inputs.

To assess the overall impact of urban land-use change on biogeochemical cycles, we propose comparisons at: (1) individual parcels each with a distinctive set of characteristics, and (2) coarser scales to assess the interrelationships among parcels and investigate the net change in biogeochemical cycles due to urban land transformations. At coarse scales, we suggest comparisons on both per-unit pervious cover and per-unit land area (ecosystem) basis. The latter includes built surfaces and considers urban landscapes as a whole. Preliminary analyses of the available data suggest that process rates on a pervious-area basis can be greater than those of the native ecosystem replaced, while on an ecosystem basis urban areas tend to have lower overall process rates than to the native ecosystem replaced. The former comparison suggests the continued importance of biological processes in urban areas, which we believe results from human efforts to overcome environmental constraints on biological processes and the tendency for horticultural management activities and urban infrastructure to concentrate flows of energy and matter into the remaining biologically active areas in the urban landscape.

We conclude that global and regional comparisons of urban ecosystems on an ecosystem and pervious-area basis will provide an analysis of the net effect of urban land conversion on biogeochemical cycles, e.g., soil C pools and fluxes, as well as insight into the mechanisms causing those changes. We hypothesize that the net effect of urban land-use conversion will depend partly on the characteristics of the native or rural ecosystem replaced. For arid regions, the net overall effect of urbanization may be higher productivity rates and thus the potential to actually increase C sequestration; in more humid environments, the net effect will be a reduction in C sequestration rates. Therefore, we suggest that cross-system comparisons on regional and global scales will be necessary to determine the net effect of urbanization on biogeochemical cycles.

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Chapter 6

Saturation of the Terrestrial Carbon Sink

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6.1 Introduction

There is strong evidence that the terrestrial biosphere has acted as a net carbon (C) sink over the last two and half decades. Its strength is highly variable year-to-year ranging from 0.3 to 5.0 Pg C yr^{-1}; an amount of significant magnitude compared to the emission of about 7 Pg C yr^{-1} from fossil fuel burning (Prentice et al. 2001; Schimel et al. 2001; Sabine et al. 2004). Uncertainties associated with C emissions from land-use change are large. On average, the terrestrial C sink is responsible for removing from the atmosphere approximately one third of the CO_2 emitted from fossil fuel combustion, thereby slowing the build-up of atmospheric CO_2. The ocean sink is of similar magnitude (Sabine et al. 2004). Given the international efforts to stabilize atmospheric CO_2 concentration and climate (i.e., Kyoto Protocol, C trading markets), the terrestrial C sink can be viewed as a subsidy to our global economy worth trillions of dollars. Because many aspects of the terrestrial C sink are amenable to purposeful management, its basis and dynamics need to be well understood.

There is a sparse understanding of the multiple processes responsible for the terrestrial C sink, the relative importance of each of them, and their future dynamics. Such information is needed to predict the future strength and distribution of biospheric terrestrial sinks, and therefore critical for the design of future pathways of decarbonization.

Terrestrial biospheric models and fully carbon-coupled General Circulation Models (GCMs) are progressively incorporating more C processes thought to drive significant carbon-climate feedbacks. However, being limited by poor understanding and the slow process of building ever more complex models, they still represent a partial set of processes. This limits the ability to produce robust projections of the biosphere's role in the future atmospheric CO_2 growth and its impacts on climate change.

In this paper we demonstrate that the underlying ecology of terrestrial biospheric CO_2 sinks suggests that, despite having the potential for increased C sink owing to atmospheric and climate change over the next decades, most of the biological sinks will eventually level-off and subsequently declined to zero (hereafter referred as "sink saturation") whereby no further C will be removed from the atmosphere.

Coupled with this sink decline, global warming and deforestation have the potential to destabilize large biospheric C pools (hereafter referred as "vulnerable C pools") which would add CO_2 to the atmosphere. This C source component will further diminish the net gains of C sinks and could even diminish the sink strength beyond zero, thereby moving from being a C sink to a source during this century. Such an eventuality would put further pressure on society to select higher targets of CO_2 emission reductions from fossil fuel burning.

In this paper, we first introduce briefly the current understanding of the global distribution of C sources and sinks. Second, we discuss processes thought to be responsible for the current terrestrial C sink and their likely future dynamics highlighting their potential contribution to saturation of the terrestrial C sink. Third, we discuss the dynamics of the future terrestrial C balance based on results from stand-alone and fully coupled carbon-climate models, and their accuracy in representing various physiological and ecological sink/source processes. Recommendations for future research are made at the end of the chapter.

6.2 Location of the Current Terrestrial Carbon Sinks

The dual constraint of the measured global atmospheric CO_2 concentration growth rate and the relatively weak north-south CO_2 concentration gradient indicate a net sink of about 2 Pg C yr^{-1} in the northern extratropics (Tans et al. 1990). These observations are corroborated by additional information from $\delta^{13}C$ and O_2/N_2, as well as increasingly sophisticated inverse modeling with augmented flask data (Rayner et al. 1999; Kaminiski et al. 1999; Gurney et al. 2002).

Despite the robustness of the global and latitudinal average estimates, inverse modeling calculations are poorly constrained at the continental scale, particularly with regard to the longitudinal partition of the sink. Model intercomparisons suggest that the Northern Hemisphere terrestrial sink is relatively evenly distributed across North America, Europe and Asia, with boreal North America being C neutral (Gurney et al. 2002; Yuen et al. 2005). Large uncertainties still remain for northern Africa, tropical America, temperate Asia and boreal Asia. Interpretations of global distributions of atmospheric O_2/N_2 ratio (Keeling et al. 1996) and inverse analyses (Rayner et al. 1999; Gurney et al. 2002) conclude that tropical ecosystems are not a strong net sink, and most likely they are C neutral. Given that tropical forests are well documented as current large CO_2 emitters via deforestation, this implies that there must be a strong balancing tropical sink of equivalent magnitude to that of emissions from tropical deforestation. During the 1980s–1990s this was estimated to be 0.6 to 2.2 Pg C yr^{-1} (DeFries et al. 2002; Archard et al. 2002; Houghton 2003).

Atmospheric data provides limited information about the processes driving terrestrial sinks. Such information requires the addition of ground-based observations, experiments, and modeling (Canadell et al. 2000; Global Carbon Project 2003). Processes responsible for the sinks in the tropical, mid-, and high-latitudes need to be equally understood since the saturation of any one can have large impacts on the growth rate of atmospheric CO_2.

6.3 Dynamics of Processes that Contribute to Carbon Sink Saturation

A decrease in the long term terrestrial net CO_2 sink can arise from a decrease in the C uptake component or increase in the emission component (see Box 6.1). Key sink processes are CO_2 fertilization of photosynthesis, N fertilization of net primary production, woody vegetation thickening and encroachment, forest regrowth in abandoned cropland, and afforestation/resforestation. Key C emission processes are soil respiration in response to warming, permafrost thawing and subsequent decomposition of organic matter, fires, deforestation, and peatland drainage. Sink saturation occurs when the increase in efflux becomes equal to the increase in uptake for a given period of time producing no increase in net uptake.

Box 6.1. Description of GPP, NPP, NEP and NBP

Plants take up carbon dioxide via photosynthesis. The sum of photosynthesis over a year is termed Gross Primary Productivity (GPP). The actual C fixed into plants, the Net Primary Productivity (NPP) of an ecosystem or growth of an individual plant, is the balance between GPP and the C lost through plant respiration (i.e., the construction and maintenance cost). It is not until C losses by microbial respiration (heterotrophic respiration, Rh) in litter and soil, and by herbivory are accounted for that we obtain the net C balance of an ecosystem. This net balance is termed Net Ecosystem Productivity (NEP). However, when considering long periods of time and large regions (or the whole terrestrial biosphere for that matter) we need to include other processes that contribute to loss of C such as, fires, harvest, erosion, and export of C in river flow. The ecosystem C balance measured over the full disturbance/recovery cycle is often termed the Net Biome Productivity (NBP) which for a system in equilibrium is zero. Continuous enrichment of the resource base on which the biome depends by CO_2 enrichment or N-deposition could lead to a positive NBP. Continuous global warming might lead to a positive NBP initially followed by a negative NBP later.

When assessing whether and when C sinks might saturate in the future, there are two types of dynamics to be considered: *(i)* Saturation of C uptake processes which refers to the diminishing sensitivity of a sink process to an external forcing or stimulus (e.g., CO_2 fertilization effect on photosynthesis as atmospheric CO_2 increases); and *(ii)* increasing C emission driven by external forcing (e.g., warming effects on heterotrophic respiration).

We refer to C pool saturation when the annual emission itself becomes equal to the annual uptake which involves two types of processes: *(i)* the "fast response" C uptake (e.g., net photosynthesis) is matched by the "fast response" C emission (e.g., heterotrophic respiration), or *(ii)* long timescale, "slow response" processes cause pools to reach maximum size (e.g., tree death rate matches new tree growth rate or, for soil, the capacity for organic matter stabilization by clay surfaces is exhausted).

6.4 Processes Contributing to Terrestrial Carbon Sink Saturation

Our current understanding of the global net C sinks requires invoking three types of processes (Table 6.1): *(i)* processes driven by changes in atmospheric composition (e.g., CO_2 fertilization on photosynthesis, nitrogen (N) deposition fertilization, pollution damage); *(ii)* processes driven by climate change (e.g., temperature and precipitation effects on gross primary production and heterotrophic respiration); and *(iii)* processes driven by land-use change or land management (e.g., deforestation, forest regrowth, woody encroachment, forest thickening due to fire suppression, afforestation and reforestation, changes in soil C pools under cultivation and grazing). The relative strengths of each of these processes contributing to the current sink and its spatial distribution remain largely to be evaluated (Houghton 2002; Smith 2005).

6.4.1 Processes Driven by Atmospheric Composition Change

6.4.1.1 *CO_2 Fertilization Effect*

Short term responses of leaf net photosynthetic rate to CO_2 concentration saturate at around 800–1 000 ppm. The response shows a compensation point (zero net rate) of about 50 ppm for C_3 species, followed by a near-linear increase up to around present ambient atmospheric CO_2

Table 6.1.
Sink and source processes driving the anthropogenic perturbation of the net C exchange between land and atmosphere

Processes	Sink, source
Processes driven by atmospheric composition change	
CO_2 fertilization of photosynthesis	Sink
Nitrogen deposition fertilization on net primary production	Sink
Air pollution effects on net primary production	Reduced sink
Processes driven by climate change	
Temperature and precipitation effects on net primary production	Sink/reduced sink
Temperature and precipitation effects on heterotrophic respiration	Source
Permafrost thawing	Source
Shifts in natural disturbances (wildfires and insect attacks)	Source/sink
Shifts in vegetation types	Sink/source
Processes driven by land-use change and land management	
Afforestation and reforestation	Sink
Forest regrowth in abandoned cropland	Sink
Vegetation thickening and encroachment	Sink
Shifts in fire regimes and other disturbances	Source/reduced source
Soil erosion and C burial	Source/sink
Crop management	Source/sink
Deforestation	Source
Peatland drainage	Source

concentration which is determined by the abundance of the CO_2-fixing enzyme RuBP carboxlyase (Rubisco) (Farquhar et al. 1980; Farquhar and Sharkey 1982). That is, when the activity of this enzyme is limiting, overall photosynthetic rate rises proportionally with CO_2 concentration. At higher concentrations, the photosynthetic rate becomes limited by the regeneration capacity of the CO_2 acceptor molecule, ribulose-1,5-biphosphate (RuBP), resulting in a curvilinear response to increasing CO_2 concentration (Fig. 6.1a). From this leaf-level saturation response, we can infer that in the absence of any other limiting factor (e.g., light, nutrients, water) net primary productivity will not increase with increasing CO_2 beyond 800–1 000 ppm (Fig. 6.1b). When other limiting factors co-occur with CO_2, the response and saturation point is different. In the short term, water limitation increases the saturation point with respect to atmospheric CO_2 concentration because water stress reduces stomatal conductance thereby decreasing the CO_2 concentration inside of the leaf. Nutrient limitations, however, can significantly decrease the saturating concentration.

Plants growing in a CO_2 richer atmosphere with sub-optimal resources acclimate to the greater C availability by lowering photosynthetic capacity below that expected for a given CO_2 concentration (Long et al. 2004). This down regulation of C fixation appears to express an optimization of the deployment of limited C and nutrient resources, particularly N (Xu et al. 1994; Wolfe et al. 1998).

Herbaceous species growing in sub-optimal conditions with multiple levels of atmospheric CO_2 (including sub-ambient CO_2 concentrations) showed that the biomass of C_3 plants is linearly related to CO_2 at CO_2 concentrations corresponding to pre-industrial (280 ppm) to present (380 ppm) (Fig. 6.1c; Polley et al. 1992; Polley et al. 1993; Polley et al. 1994; Dippery et al. 1995). At future CO_2 concentrations greater than 450–550 ppm most species enter the saturating responses zone. Woody species have similar responses with a consistent linear increase in plant biomass from pre-industrial to ambient concentrations, and often a saturating growth response in the same range as for herbaceous species (450–550 ppm) (Fig. 6.1d). Hättenschwiler and Körner (2000) found the same behavior for six European temperate tree species growing in the low light regime of a forest understory.

It is well established that N limitation prevents the full expression of the CO_2 fertilization effect on plant growth, and that a progressive N limitation is likely to be the principal factor driving the above saturation curves (Luo et al. 2004; Reich et al. 2006; Groenigen et al. 2006). That is, N becomes increasingly limiting (at least in the period up to a few years typical of elevated CO_2 experiments) as both N and C are immobilized in new plant and soil organic matter fractions. Other nutrients, particularly phosphorus, also limit plant growth responses to increasing atmospheric CO_2 (Barrett and Gifford 1995; Dukes et al. 2005; Edwards et al. 2005).

There are systems that already show saturation at present CO_2 concentrations due to nutrient or other environmental constraints (Körner et al. 2007, Chap. 3 of this volume). This is the case for: *(i)* a mature temperate trees

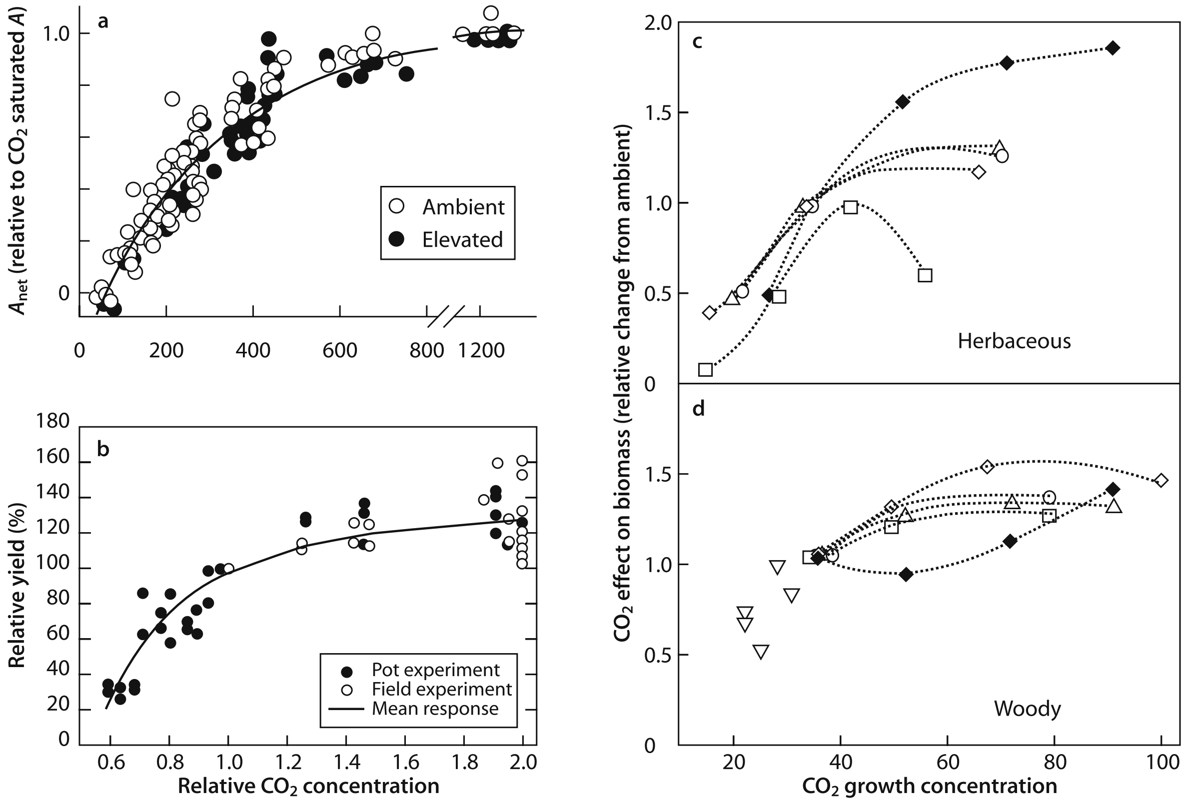

Fig. 6.1. Plant responses with saturation dynamics to increasing levels of atmospheric CO_2. **a** Typical A/C_i curve: Leaf net C assimilation at increasing leaf internal CO_2 concentrations (CO_2 concentration at the site of carboxylation in the chloroplasts). **b** Wheat responses to increasing CO_2 levels (data from field experiments (*open symbols*) and pot/glasshouse experiments (*solid symbols*, Olesen and Bindi 2002). **c** Data for the herbaceous species *Abutilon theophrasti* (Dippery et al. 1995), *Homogyne alpina* (Hättenschwiler and Körner 1996), *Arabidopsis thaliana* (Ward and Strain 1997), and *Glycine max* (*closed symbols*, Rogers et al. 1983; *open symbols*, Allen et al. 1991). **d** Data for the woody species *Quercus alba* (Norby and O'Neill 1989), *Liriodendron tulipifera* (Norby and O'Neill 1991), *Pinus taeda* (Rogers et al. 1983), and *Liquidambar styraciflua* (*closed symbols*, Rogers et al. 1983; *open symbols*, Tolley and Strain 1984). For *Prosopis glandulosa*, data were available for subambient concentrations only, and the *dashed line* is a linear regression ($R^2 = 0.55$, $P = 0.09$, Polley et al. 1994)

in Switzerland (100 years, 30–40 m tall) which after three years of CO_2 fumigation showed no growth response (Körner et al. 2005); *(ii)* trees growing nearby natural CO_2 springs (Tognetti et al. 2000); *(iii)* 30 yr old *Pinus* spp. growing at the high elevation tree-line in the Swiss Alps (Handa et al. 2005); and *(iv)* grassland in California after 5 years of elevated CO_2 exposure (Dukes et al. 2005). A number of other studies showed no responses to increased atmospheric CO_2 (Mooney et al. 1999; Luo et al. 2006).

Eleven Free-Air CO_2 Enrichment (FACE) experiments encompassing bogs, grasslands, desert, and young temperate tree stands report an average increased NPP of 12% at 550 ppm when compared to ambient CO_2 (Nowak et al. 2004). Four FACE studies on forest stands showed a 23% median increased NPP, an expectedly high response for stands made up of young trees and saplings (Norby et al. 2005). A meta-analysis of over a hundred studies shows about ⅔ of the experiments responding positively to increased CO_2 (Luo et al. 2006). This analysis also shows that ecosystems under elevated CO_2 can accumulate N, supporting the hypothesis that terrestrial ecosystems have certain capacity to gradually acquire additional N required to continue accumulating C under increasing CO_2 concentrations (Gifford 1992, 1994; but see Reich et al. 2006; Groenigen et al. 2006).

Just as increased leaf-level photosynthesis does not necessarily translate into whole plant growth, increased NPP does not necessarily translate into increased Net Ecosystem Productivity (NEP) (i.e., net C sequestration). Ecosystem-level net C fixation is constrained by water, temperature, light, nutrients, and a host of biotic interactions between individuals and species that involve CO_2 emissions from ecosystems. There are few elevated CO_2 experiments that have been able to measure annual net C exchange owing to intrinsic methodological difficulties. Over a three-year period, NEP of a nutrient-limited tundra ecosystem exposed to a step increase in CO_2 in Alaska exhibited a pulse-increase producing a temporary C sink (Oechel 1994). The positive NEP declined over time and completely disappeared after three years. More recently a Mojave Desert shrubland that was still accumulating C (i.e., positive NEP) exposed to 8 years of elevated CO_2 using FACE technology showed in its 8th year a decreased annual net C uptake at elevated CO_2 compared to ambient levels (Jasoni et al. 2005). These examples illustrate that a variety of responses of NEP to CO_2 can occur in different ecosystems.

In summary, ecosystem responses to large step increases of CO_2 concentration can show a strong saturation behavior driven by resource limitation. Plant growth is most stimulated under pre-industrial to present atmospheric CO_2 concentrations with some systems showing saturation at present CO_2 concentrations. For a large portion of systems studied, CO_2 exposure to higher CO_2 concentrations does stimulate plant growth. In these cases, increasing CO_2 concentrations results in a saturation response at around 500–600 ppm, a much lower level than that expected based on solely leaf-level physiological grounds. It is unclear to what extent over decades of gradual annually increasing CO_2 concentration the acquisition of atmospheric N by symbiotic and free-living N fixation (and by increased N capture from N deposition and N-cycle turnover) will be enhanced by elevated CO_2 concentration.

The CO_2 fertilization effect on C accumulation is not solely the result of photosynthesis fertilization, but also of increased water use efficiency by plant canopies owing to increased photosynthesis at lower stomatal conductances (Morison et al. 1985; see review by Mooney et al. 1999). The result can be a slower rate of depletion of soil moisture, so that higher rates of photosynthesis may be maintained for longer fractions of soil wetting/drying cycles under high CO_2, particularly in arid and semiarid ecosystems. This effect has been consistently reported for water-limited systems such as deserts (Pataki et al. 2000), Mediterranean grassland (Field et al. 1996) and savanna ecosystems (Owensby et al. 1997). The implication is that "well-watered" ecosystems, including the most productive forest regions of the tropics and boreal zone (likely to play the largest role in C sequestration), take the least advantage from the beneficial effects of reduced stomatal conductance. Therefore, they may be the first systems to approach an upper limit for the physiological effects of increasing CO_2.

6.4.1.2 *Fertilization by Nitrogen Deposition*

Given that N often limits plant growth in terrestrial ecosystems, particularly temperate regions (Vitousek and Howarth 1991), it has long been speculated that increased plant growth from N deposition is likely to be an important C sink process. Much of this reactive atmospheric N results from N fertilizer use in agriculture and the combustion of fossil fuel in industrial activities. The first process produces reactive N, predominantly as NH_3 (and NO_3); the second produces NO_x ($NO + NO_2$), which eventually deposit on vegetation and soils as dry and wet deposition (Galloway and Cowling 2002). However, it is known from fertilization trials and long term N deposition studies that there is an upper limit to which additions of N into the system will results in increased NPP. Past this threshold, pollutants associated with N deposition have a negative effect on ecosystems particularly tropospheric ozone (Aber et al. 1998; see Sect. 6.4.1.3).

Early modeling studies showed that N deposition could have a significant impact on enhancing C sequestration in forests, due to their high C/N ratio, particularly at mid-latitude forests in the Northern Hemisphere, where N deposition is highest and N-limitation is common (Holland et al. 1997; Townsend et al. 1996). These models suggested that N deposition could result in increased C sequestration at a rate of 0.1 to 2.3 Pg C yr^{-1}. At its upper plausible limit, N fertilization could account for the entire net terrestrial C sink. Subsequent field experimentation suggests 0.25 Pg C yr^{-1} as the upper realistic limit of C stimulation by N deposition (Nadelhoffer et al. 1999). More recent analyses using the Biome-BGC model and new N deposition data reinforce this lower end value with an additional C uptake due to N deposition of 0.19 Pg C yr^{-1} and 0.26 Pg C yr^{-1} for the decades of 1980s and 1990s respectively (Galina Churkina, in preparation). That analysis attributed 8 Pg C of the terrestrial sink during the period 1950–2000 to fertilization by N deposition in Northern Hemisphere forests.

Global analyses of N deposition impacts continue to be poorly constrained by lack of high quality spatially-explicit datasets of N deposition (but see Holland et al. 2005 for the US and Europe) and an incomplete knowledge of the various pathways by which deposited N is incorporated into ecosystem components, including N absorption directly by plant canopies.

Taking into account future projections of increased N deposition over the next 100 years, largely in tropical Americas, Southern Africa, and China-India (Galloway and Cowling 2002; Fig. 6.2), it is unlikely that N deposition will create any major additional C sinks. Field experiments using N additions in phosphorus-limited

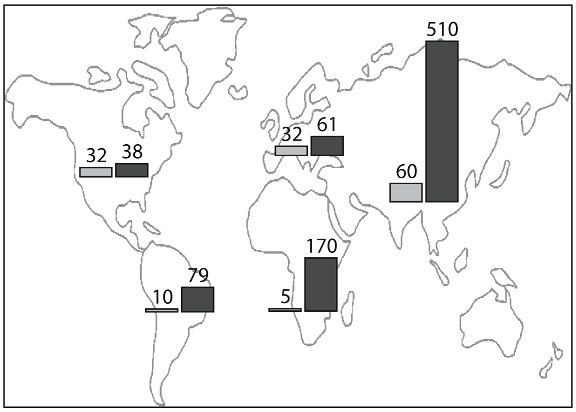

Fig. 6.2. Current and future projections of reactive nitrogen N creation rates in different regions of the world (Galloway and Cowling 2002). *Left bar* indicates the reactive N in 1996 (Tg N yr^{-1}), *right bar* indicates maximum reactive N at the time of projected peak population in 2100

tropical forest show higher emissions of nitrogen oxides than in N-limited forests, both after single pulse and chronic N additions (Hall and Matson 1999). In fact, anthropogenic N inputs may reduce productivity due to the indirect effects on acidity and the availability of phosphorus and cations (Matson et al. 1999). In China and India, most of the N deposition increases in will occur on agricultural lands with little or no sink potential. Therefore the fertilization effect of N deposition on C uptake at present is probably close to the saturation level if it has not already been reached.

There are, however, two related processes by which N may be able to stimulate further C uptake. First, N-deposition concurrent with increasing atmospheric CO_2 concentration may be acting synergistically to progressively increase the standing C pool in terrestrial ecosystems by partially reducing the limitation that its availability imposes on C uptake (Gifford et al. 1996). Second, increased soil respiration in a warmer world, provided water is not limiting, will release additional soil N which can stimulate C uptake to some degree (see Sect. 6.4.2.2).

6.4.1.3 *Air Pollution*

Air pollution, particularly tropospheric ozone (O_3) background concentrations, has increased since the beginning of the industrial revolution. Tropospheric O_3 is formed in photochemical reactions between carbon monoxide, methane (CH_4) and other hydrocarbons, and NO_x. All precursors are largely the result of fossil fuel combustion (Felzer et al. 2004 and references within). Unlike other more localized pollutants, tropospheric ozone is a major regional issue with hot spots in Eastern US, Eastern Europe and China, and with teleconnections to other regions making tropospheric O_3 a global pollutant (Sanz and Millán 1999; Derwent et al. 2004).

Plants exposed to tropospheric O_3 reduce C uptake because O_3 damage cellular tissue which in turn reduces photosynthesis and stomatal conductance. Historical analyses of the possible negative effects of O_3 damage on terrestrial carbon sequestration show a reduced sink between 0.1 and 0.3 Pg C yr^{-1} for the period 1950–1995 (Felzer et al. 2005). The suppression of the sink although small is very significant over the 45-year cumulative period, and the relative change was several times larger for hot spot regions such as US, Europe and China.

Physiologically stressed vegetation is often more susceptible to insect and fungal attacks. Karnosky et al. (2002) showed that aspen (*Populus tremuloides*) developed 3–4-fold increases in levels of rust infection (*Melampsora medusae*) following long exposures to O_3. This further exacerbated the reduction in C update.

Background O_3 concentrations and peak levels are predicted to stay high or increase in the future (Fowler et al. 1999).

6.4.2 Processes Driven by Climate Change

6.4.2.1 *Precipitation and Temperature Effects on Net Primary Production*

Increased length of the growing season, increased precipitation, increased temperature, and decreased cloud cover are factors thought to be responsible for an estimated 6% increased terrestrial NPP (3.4 Pg C) over the last two decades of the 20th century (Nemani et al. 2003); this suggests a possible increase in C sequestration. IPCC (2001) reported that the net sink in the Northern Hemisphere increased from 0.2 Pg C yr^{-1} during the decade of the 1980s to 1.4 Pg C yr^{-1} during the 1990s with associated large uncertainties.

These are the processes and trends, along with CO_2 fertilization, that support model projections suggesting a likely increase in the terrestrial C sink over the next half a century. The same model projections suggest that soil respiration will surpass levels of C uptake later in this century, and that the tropical sink will be ultimately destabilized due to drought (Cao and Woodward 1998; Cramer et al. 2001; Cox et al. 2000; Fung et al. 2005; Friedlingstein et al. 2006). This is projected to lead to an overall decline of the net terrestrial sink which becomes a source by the end of the century in some of the model projections. A key model assumption here is that soil respiration will be as highly temperature dependent in the long term as is found in short term experiments (months to a few years).

Interestingly, new observations are already showing a dampening of regional C sinks strength due to increased climate variability (particularly due to hotter droughts), and thus challenging the expectation of C sink enhancement over the next few decades. An analysis of the entire Northern Hemisphere shows that since 1994 the well known acceleration of C uptake during early spring was offset by decreased uptake during summer, most likely due to drier summers in mid and high latitudes (Angert et al. 2005). The heatwave in 2003 alone reduced the gross primary productivity of European ecosystems by 30% resulting in a net CO_2 source to the atmosphere of 0.5 Pg C yr^{-1} (Ciais et al. 2005), equivalent to about 4 years of C accumulation in these systems lost in a single extreme event of just a few weeks duration.

In the tropics, drought can enhance NEP in the short term because it suppresses heterotrophic respiration (Saleska et al. 2003). However, over the longer term, drought and associated fire (Werf et al. 2004) are likely to diminish the Net Biome Productivity (NBP) in regions that experience an increasingly dry environment.

Thus, increases in intra- and inter-annual variability (frequency and/or intensity) as predicted by some climate models under higher greenhouse gas (GHGs) concentrations (Giorgi et al. 2004; Meehl and Tebaldi 2004) could depress the net C sink of the Northern Hemisphere and even push it to become a CO_2 source. If the increase in climate variability (e.g., frequency of extreme events) that has occurred in the past decade were to persist as part of climate change, the net terrestrial C sink could soon be declining, well before model predictions that show a possible sink saturation between the middle and end of this century (Cox et al. 2000; Cramer et al. 2001; Friedlingstein et al. 2006).

6.4.2.2 *Temperature and Water Effects on Heterotrophic Respiration*

The sensitivity of soil C pools to global warming is the single biggest uncertainty in the C cycle to determine future growth rates of atmospheric CO_2. Terrestrial ecosystem models and coupled C cycle GCMs suggest large positive feedbacks to climate due to an assumed high sensitivity of soil heterotrophic respiration to warming (Cramer et al. 2001; Cox et al. 2000; Friedlingstein et al. 2006). This assumption is supported by some short term soil warming field experiments and laboratory soil incubations which consistently show an increase in soil respiration when exposed to elevated temperatures. A meta-analysis of thirty-two field studies showed a 20% increase in soil respiration when soils were experimentally heated 0.5 °C to 5 °C for periods ranging from 2 to 9 years (Rustad et al. 2001; Fig. 6.3). Studies with laboratory soil incubations at various temperatures have also shown that temperature sensitivity is usually high at low temperatures (Q_{10} as high as 8 close to 0 °C) and low at higher temperatures (Q_{10} at around 2 for temperatures above 20 °C) (Kirschbaum 1995).

Other studies show either no correlation between respiration fluxes and temperature or enhanced soil respiration that disappears after some time (Giardina and Ryan 2000; Valentini et al. 2000; Jarvis and Linder 2000; Luo et al. 2001). The latter experiments suggest that once the more labile C fraction has been respired, the remaining more recalcitrant and stable pools are not sensitive to temperature.

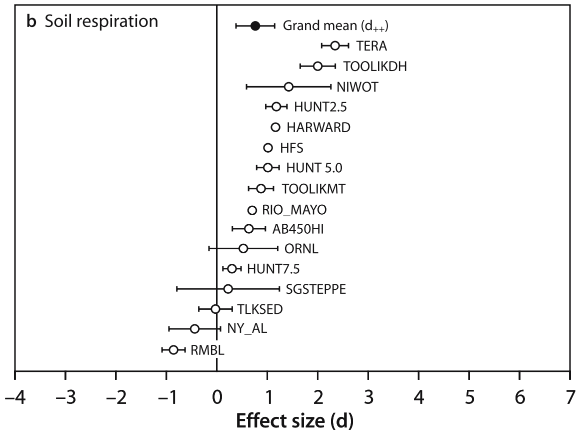

Fig. 6.3. Effects of field experimental warming on soil respiration in 16 studies (Rustad et al. 2001). Mean effect sizes and 95% confidence interval for individual experiments. Soils exposed to elevated temperatures of 0.3 to 6.0 °C for periods of 2 to 9 years

More recently, modeling and experimental studies have shed light on this apparent paradox by showing that more recalcitrant pools of Soil Organic Carbon (SOC) do not show lower sensitivity to temperature than labile pools (Knorr et al. 2005; Fang et al. 2005; Fierer et al. 2005). In fact the studies show that slow turnover pools, the largest and therefore dominant component, are equally (Fang et al. 2005) or more (Knorr et al. 2005) sensitive to warming than fast pools.

It is important to note that concurrent with organic C mineralisation to CO_2 during heterotrophic respiration, there is N mineralisation to ammonium and nitrate that could feedback onto productivity. The meta-analysis of soil warming experiments found that associated with an average 20% increase of heterotrophic respiration with warming there was an average 46% increase in net mineralisation of soil N (Rustad et al. 2001). Given the C cycle is tightly coupled with the N cycle (Gifford 1994) some of this increased production of mineral N can be taken up by plants and converted to biomass; this would compensate to some extent for soil C lost under warmer conditions.

Thus it is not well established as to the extent global warming will decrease soil C pools. Certainly the N-cycle feedback can reduce the magnitude of the net long term decline in soil C due to increased temperature. In some ecosystems the compensation can be significant whereas in ecosystems with largest soil C pools (e.g., tundra and taiga with frozen soils and peatlands which are highly sensitive to temperature) the compensation will be smaller. A more detail analysis of C emissions from frozen soils and peatlands are described in Sect. 6.4.2.3 and 6.4.3.7.

6.4.2.3 *Permafrost Thawing*

Frozen soils hold over 400 Pg C which have been accumulated over thousands of years (Sabine et al. 2004). Approximately 54% of frozen soils occur in Eurasia, largely in Russia, and 46% in North America, largely in Canada (Tarnocai et al. 2003). An additional 500 Pg C exist in frozen loess that have been accumulated in glacial times in the north plains of Siberia (Zimov et al. 2006). With the rapid warming of the northern latitudes well above the global averages (IPCC 2001), C in frozen ground can be exposed to warmer aerobic conditions which would result in increased decomposition of organic matter and thus C emissions. In fact, widespread observations exist of permafrost thawing leading to the development of thermokarst and lake expansion, followed by lake drainage as the permanent permafrost further degrades (Camill 2005; Smith et al. 2005).

Preliminary estimates show that permafrost area could shrink by up to 25% with a mean global warming of 2 °C (Anisimov et al. 1999). More recent estimates using a fully coupled GCM show that of the 10 million km^2 of present-day permafrost as little as 1 million km^2 near surface permafrost will remain by the end of this century (Lawrence et al. 2005). Melting permafrost will increase CO_2 and CH_4 emissions, and it is estimated for the Canadian permafrost alone that up to 48 Pg C could be sensitive to oxidation under a 4 °C warming scenario (Tarnocai 1999).

In addition to C exchange between land and atmosphere, lateral transport of DOC from thawing permafrost is another process by which C is lost from peatlands. Frozen permafrost watersheds in Western Siberia release little DOC to the rivers while permafrost-free watersheds show considerably higher amounts that are proportional to the extent of the peatland area (Frey and Smith 2005). For Western Siberia, climate models predict a doubling of the area above a mean average temperature of −2 °C (which coincides with permafrost distribution) and an associated 700% increase in DOC concentrations in streams. Part of the DOC reaching the Arctic Ocean will oxidize and return to the atmosphere.

A preliminary global estimate suggests that up to 5 Pg C could be released from permafrost over the next 20 years and up to 100 Pg C in the next 100 years if it is assumed that 25% of the C locked in frozen soils could be oxidized (Gruber et al. 2004; Raupach and Canadell 2006). This amount could increase to as much as 200 Pg C if we include the loess frozen sediments which have been recently reported. Whether this C is released initially as CO_2 or as CH_4 depends on the local hydrological conditions. Although studies suggest an increased gross C uptake by the newly established vegetation (Payette et al. 2004), long term warming and fertilization studies show increased losses of C from deep soil layers (Mack et al. 2004). These losses were sufficient to counteract increased plant biomass C, thereby contributing a net C flux to the atmosphere.

There are compensating feedbacks to consider. The northwards movement of the permafrost boundary is accompanied by northward movement of the vegetation that fixes C and thus compensating to some extent the loss of soil C (see Sect. 6.4.2.4). However, thawing will expose deep deposits of C to aerobic conditions and the losses of the integrated soil profile (including deep soil layers) will offset the possible C gains from increased productivity.

6.4.2.4 *Shifts in Vegetation Types*

The distribution of the world's vegetation has changed throughout glacial and interglacial periods largely forced by climate and to lesser extent atmospheric CO_2. Consequently it is expected that the distribution of vegetation will change commensurately to the extent of future climate change with associated changes in the size of carbon pools and fluxes (VEMAP members 1995).

Vegetation shifts will change significantly regional C balances, but two of the most important ones at the global scale are: *(i)* woody encroachment in high latitudes due to warmer temperatures (e.g., boreal summer green trees moving into herbaceous systems) (see Sect. 6.4.3.3 for other types of woody encroachment), and *(ii)* the more controversial die-back of Amazonia and subsequent savannization driven by increased water stress (Cox et al. 2004; Schaphoff et al. 2006). In the first case, warmer temperatures are already allowing for longer growing seasons and a substantial increase of C pools in vegetation which will likely result in an additional C sink (but see Schaphoff et al. 2006 who argue otherwise due to the concomitant increased soil respiration; see Sect. 6.4.2.1). In the second case, savannization of Amazonia would result in substantial emissions to the atmosphere which is the largest contributor to a positive carbon-climate feedback projected to increase global warming by 0.1–1.5 °C by the end of this century (Friedlingstein et al. 2006).

Some of these vegetation shifts may have transient dynamics with abrupt releases of C emissions, often associated with disturbances (e.g., fire), several times bigger than the slower increased of C pools in biomass and soils in other regions of the biosphere (Smith and Shugart 1993).

6.4.3 Processes Driven by Land-Use Change and Land Management

6.4.3.1 *Afforestation and Reforestation*

Globally, the upper "biological" boundary of C sequestration by land management could be estimated as the amount of C lost historically from land-use change, about 180–200 Pg C (DeFries et al. 1999). This could decrease atmospheric CO_2 concentration at the end of this century by 40 ppm to 70 ppm (House et al. 2002). Taking account of expanding demands for food, fiber, energy and urbanization, the potential of forest C sequestration is reduced to an achievable capacity of only 10 to 50 Pg C (Cannell 2003) or 5% to 25% of the upper boundary for C sequestration estimated based only on biophysical considerations.

In addition, there is a whole fabric of interlinked environmental and socio-economic constraints and opportunities which will ultimately determine the achievable capacity to sequester C such as costs of land for sequestration and for maintaining C stores, environmental requirements for other resources, environmental constraints, social factors, economical feasibility, institutional factors, and demographics (Raupach et al. 2004).

Thus, despite a significant potential for creating C sinks through afforestation and reforestation, the ultimate impact on atmospheric CO_2 growth will be relatively modest and limited in time because globally there will be a balance between intensification (and reduced requirements of land) and an expanding population largely in less developing world with a large demand for new land to meet food and energy requirements. However, a larger potential exist for future enhancement of the C sink if there is greater adoption of biofuels, which could provide the incentive for the establishment of additional plantations.

6.4.3.2 *Forest Regrowth on Abandoned Cropland*

Forest regrowth on abandoned agricultural land has been identified as one of the most significant process to explain the net C sink in the Northern Hemisphere (USA: Houghton et al. 2000; Pacala et al. 2001; Europe: Janssens et al. 2005). The western movement of agricultural lands from the forests of the east to the prairies of the midwest has been the main driver of land abandonment and subsequent regrowth in eastern North America since the beginning of the last century, while agricultural intensification was the principal driver in Europe (Kauppi et al. 1992; see in Ramankutty and Foley 1999; Goldewijk 2001).

This agricultural shift has resulted in a substantial expansion of relatively young forests with fast growth rates in abandoned cropland, and therefore, with high C sink capacity. Forest cover in Europe and North America has increased over this period and is considered to be an important, if not the dominant, component of their current C sink. Caspersen et al. (2000) showed that for Eastern USA, where the largest amount of cropland abandonment has taken place, that regrowth explains 98% of the sink that is driven by the dynamics of forest demographics (i.e., age structure). Only 2% of forest growth was attributable to increased CO_2 and N deposition.

Stand NEP declines with stand age as measured in a variety of forests in the temperate and boreal regions of Europe, Siberia, and North America (Law et al. 2003; Desai et al. 2005; Fig. 6.4). As forests reach maturity (maximum C pool size) they cease to be sinks (Bond-Lamberty et al. 2004) and even later may become C sources (Goulden et al. 1998; Schulze et al. 1999; Carey et al. 2001).

From a regional and global perspective, persistence of the C sink due to regrowth can only be sustained by continuous expansion of new forests, something that is unlikely to happen in the light of increasing pressures on existing land for multiple uses (urbanization, industrialization, recreation in the industrial world) including fossil fuel substitution with energy crops. In fact, crop abandonment has largely ceased in North America and Europe, while in other parts of the world conversion to cropland is still the primary means by which to meet the food demands of an increasing human population. Forest management can maintain a sustained C sink over the years but at a much lower strength because wood extraction generally returns C to the atmosphere. Old growth forest may not be important globally for the removal of C from the atmosphere, but they hold large C pools that cannot be matched by other land uses (Knohl et al. 2003; Field and Kaduk 2004).

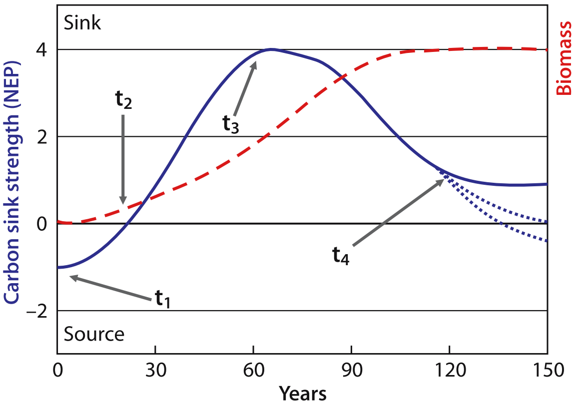

Fig. 6.4. Diagrammatic representation of C sink strength (i.e., net primary productivity, kg C yr^{-1}) and biomass (kg C) accumulation over time of an hypothetical forest stand. t_1: initial state (e.g., after clear cut); t_2: flip point from C source to sink; t_3: maximum net C uptake; t_4: slow down of the C sink, potentially becoming neutral or even flipping from C sink to source. *Dotted lines* indicate alternative trajectories at maturity

6.4.3.3 *Vegetation Thickening and Encroachment*

Vegetation thickening in forests and woodland, and woody encroachment in savannas and grasslands increase the amount of C stored on land. Many processes are responsible, but fire suppression as a means to control wildfire damage and fuel reduction by grazing may be the most important. Other factors may be also important (for a review see Gifford and Howden 2001).

Managed fire exclusion during the twentieth century has resulted in an increase of biomass in forest and woodlands in many regions (Mouillot and Field 2005; Luger and Moll 1993; Houghton et al. 2000), and the potential exists for further accumulation. For instance, for the USA, forest and woodland biomass in 1990 was 75% of what it was in 1700 and 63% of what it would be in the absence of disturbance; that is, if all forests had the biomass estimated for undisturbed forests lacking wildfire. In the unrealistic scenario of excluding fire from all areas currently lacking trees, the estimated upper limit of C sequestration by woody encroachment would be about 2 Pg C yr^{-1} (Scholes and Hall 1996), although it would not be sustainable for too long.

Woody thickening and encroachment is an important C sink process estimated to account for a substantial proportion of the sink in various parts of the world although it is recognized as the single least well constrained of all sink estimates. For Australia, the introduction of livestock grazing and fire suppression has shifted the dominance from natural open woodlands to tree-grass dominated systems with an estimated 0.035 Pg C yr^{-1} sink in northeastern Australia alone, equivalent to 25% of the total national net emissions (Burrows et al. 2002). Forest thickening and woody encroachment in the US accounts for 0.12–0.13 Pg C yr^{-1} or 22–40% of the apparent total US terrestrial sink (Pacala et al. 2001).

The suppression of wildfire has allowed C accumulation, a process which is not sustainable in the long term as the accumulated C can eventually return to the atmosphere when fire occurs (see Sect. 6.4.3.4). Forests under routine control-burn management will hold less C than the maximum possible, but over the long term they may hold more than forests experiencing occasional catastrophic fires. The fact that the burned area in the extra tropics has increased in a number of regions (Boreal North America and Europe: Mouillot and Field 2005; Fig. 6.5) may indicate that fire exclusion has already reached, or exceeded, a maximum C storage, unless attempts to prevent fire are intensified. Furthermore, this increase in wildfires is also enhanced by the interactions with a changing climate.

In savannas, woody thickening also tends to saturate. As the global terms of trade for ruminant products continues its long term decline, the extent of woody encroachment onto grazed tropical grasslands may continue for decades. However, C accumulation does not always occur. Little or no net C accumulation was found in wet grasslands invaded by *Prosopis*, *Larrea*, and *Juniperus* (Jackson et al. 2002) and drier grasslands invaded by *Juniperus virginiana* (Smith and Johnson 2003). Thus the C sink estimates attributed to woody encroachment may not be great.

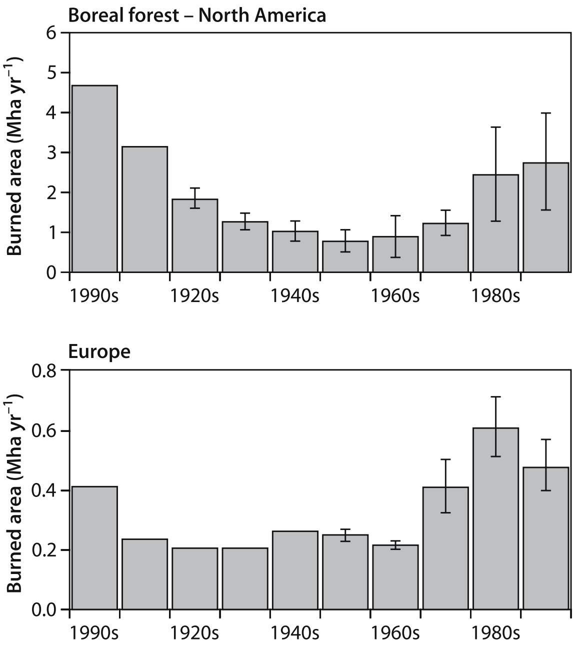

Fig. 6.5. Temporal trend of burned areas (in Mha yr^{-1}) for the 20th century for Europe and Boreal forest in North America (Mouillot and Field 2005)

6.4.3.4 *Shifts in Fire Regimes and Other Disturbances*

Disturbances to vegetation can have dramatic effects on short-term C dynamics, although they are neutral in the long term C cycle. That is, the often quick C release during a disturbance event (e.g., wildfire) will be balanced by C uptake of regrowing vegetation during the following decades (fire as a tool to clear land is considered in Sect. 6.4.3.7 on Deforestation). However, changing climate, atmospheric CO_2 concentrations, and land use and management can alter the frequency and intensity of disturbance regimes and the net contribution to the atmospheric CO_2 growth. It is during the transient dynamics in moving from one fire regime to another that a C imbalance is created: a sink when reducing the frequency of disturbances frequency and a source when increasing the frequency of disturbances.

The annual gross C flux to the atmosphere from global savanna and forest fires (excluding biomass burning for fuel and land clearing) is estimated to be in the range of 1.7 to 4.1 Pg C (Mack et al. 1996). Thus, the potential for fire to alter the terrestrial C sink is significant. One of the most striking examples of fire sensitivity to climate (e.g., drought) was the fires in tropical regions during El Niño in 1997–1998. Fire emissions contributed 2.1 ±0.8 Pg C or the equivalent of 66% of the CO_2 growth rate anomaly during that period (Werf et al. 2004). Although most of the fires ignited by human activities, the area burned and intensity were largely the result of drought.

Despite the sensitivity of fire frequency and intensity to climate change and variability, the long term trends over the past century were driven primarily by the implementation of fire suppression policies in temperate regions and increased use of fire to clear forest in tropical regions.

Fire frequency in the boreal forests of Canada and Russia decreased during most of the last century but has increased during the last two decades as a result of changes in management practices perhaps reinforced by strong climate warming (Dixon and Krankina 1993; Kasischke and Stocks 2000). As a result, modeled C emissions from fires in Canada have consistently increased over the last 40 years, and changed the net C balance of the Canadian forest from being a sink to a small source (Fig. 6.6; Kurtz and Apps 1999).

Future fire activity will continue to be dominated to some extent by fire suppression policies and the use of fire for forest clearing (see Sect. 6.4.3.3). However, greenhouse induced climate change, especially if accompanied by increased climate variability and particularly drought events, will affect overall fire extent and intensity. Models predict increased fire activity with a warmer climate for North America, Russia and Europe (Stocks et al. 1998; Flannigan et al. 1998; Flannigan et al. 2000).

In the tropics, El Niño-drought events have an overriding effect on fire intensity, and therefore are likely to determine the future strength of the terrestrial C sink in that part of the world to a large extent (along with deforestation). Future dynamics of El Niño/La Niña cycles are still uncertain but one view is that there will be more frequent or more severe El Niño-like conditions in a warmer climate (Timmermann et al. 1999).

In addition, the interactive nature between management practices (e.g., fire suppression in temperate forests, deforestation) and climate change largely determine the future fire frequencies. One example concerns how the unnaturally high biomass accumulation in forests due to fire exclusion may respond to warming and increased drought frequency in some parts of the world. Grissino-Mayer and Swetnam (2000) have suggested that excessive biomass accumulation in the southwest of the USA is responsible for an increase in the areas burned in recent years. A second example is the evidence that increased landscape fragmentation in tropical regions as a result of higher pressure for multiple land uses favors the rapid spread of fire (Nepstad et al. 1999; Laurance 2000).

There are other sources of disturbances linked to climate change that are important for the net carbon balance. One of the most notable examples is insect damage linked to warmer conditions in boreal forests which has been as extensive as fire during some years (Kurz and Apps 1999; Carroll et al. 2004). Shifts in the regimes of hurricanes, tornadoes, and windstorms are also linked to global warming although their effects on the future net carbon balance are more difficult to be determined.

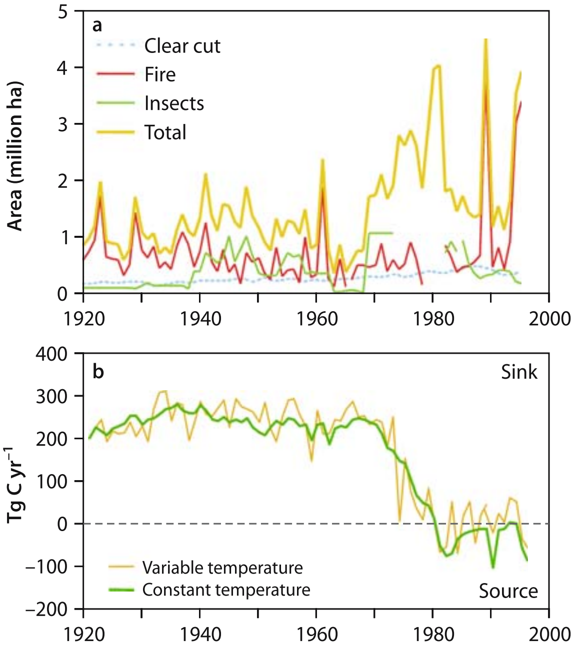

Fig. 6.6. Disturbances and its effects on the net carbon balance of Canada's forests (1920–1995): **a** Area in Mha yr^{-1} disturbed by fire and insect damage, and **b** net ecosystem C fluxes (after Kurz and Apps 1999)

6.4.3.5 *Soil erosion and Carbon Burial*

Changes in land cover and use are estimated to contribute 10–100 times the natural background levels of soil erosion, stimulating the increase of sediment load into the world's rivers by 2.3 Pg yr^{-1} since pre-agricultural times (Syvitski et al. 2005). Of the total C sediment in rivers, about 0.4 Pg C yr^{-1} is total organic C and 0.4 Pg C yr^{-1} is dissolved inorganic C (Richey 2004). Part of this C is intercepted by dams (estimated to be 1–3% of total river sediment (Syvitski et al. 2005)) and wetlands and the rest reaches the coastal zones. For both pathways only a fraction of that C is stored in long term pools and the rest is mineralized releasing CO_2 back to the atmosphere. Recent estimates on the CO_2 outgassing of rivers shows that a large portion of riverine C is mineralized during transport and quickly returned to the atmosphere as CO_2 (Richey et al. 2002). Although this C redistribution may have important effects on regional C balances, the fact that C previously stored in soils may end up under different sequestration characteristics (e.g., anaerobic conditions at the bottom of dams or in ocean sediments) may not necessarily result in a net global greenhouse gas sink. This is only the case if the C residence time in sediments is so much longer than that in the upper soil horizons from which soil was eroded; this would also need to overcompensate for the outgassing during river transport and mineralization at the final destination (C in sediments may be emitted as CH_4 under anaerobic conditions). Therefore, claims for net C sinks due to sediment burial as big as 1 Pg C yr^{-1} globally (Smith et al. 2001; Stallard 1998) are unlikely to be true and require further investigation. Likewise, little is know on the future of this C sink.

6.4.3.6 *Crop Management*

Cultivation has resulted in a loss of 55 Pg C from soils worldwide (Cole et al. 1996), and improved management practices can restore some of this soil C. For example, the introduction of conservation tillage in the USA has increased soil organic matter pools by about 1.4 Pg over the past 30 years (Donigian et al. 1994), with the potential to store a further 5 Pg over the next 50 years (Kern and Johnson 1993; Lal et al. 1998). If best management practices could be implemented at the global scale, agricultural soils could mitigate up to ⅓ of the current annual atmospheric CO_2 increased. However, this would be effective for only 20–50 years (Smith 2004) because soils, as with many other biological C sinks, have an upper limit above which no additional C can be stored. This upper limit could change to a lower level from that of pre-agriculture (e.g., if major soil erosion has occurred) or to a higher level if future climate change increased productivity (e.g., at higher atmospheric CO_2 concentrations).

Over the next 50–100 years, if one includes all available management practices, the potential exists for agricultural management to sequester 0.075 to 0.208 Pg C yr^{-1} in USA arable land (Lal et al. 1998 Metting et al. 1999). In the USA, full adoption of best management practices would likely restore SOC to about 75–90% of its pre-cultivation total (Donigian et al. 1994). Similarly in Europe, it is estimated that 0.113 Pg C yr^{-1} could be offset over the next 100 years (including C offsets from bioenergy crops planted on surplus arable land) (Smith et al. 2000). Changes in management practices in Europe and the USA combined may restore ⅓ to ½ of SOC lost through agriculture globally.

In addition to the limited effectiveness of this process given the ultimate saturation of the pool, the biophysical potentials described above are probably unachievable when socio-economic and other environmental constraints are taking into account. Recent estimates for soil C sequestration potential suggest a global technical potential of about 1.9 Pg C yr^{-1}, whereas the realistically achievable potential is estimated to be 0.2–0.4 Pg C yr^{-1}, with the level of implementation of mitigation measures determined by the market price of CO_2 equivalents (Smith et al. 2006). For Europe, using projections in actual management trends suggest negligible actual sequestration between 1990 and 2000, and negligible sequestration expected by 2010 due to lack of policy incentives to encourage C sequestration (Smith et al. 2005).

6.4.3.7 *Deforestation*

Land-cover shifts from one type to another are responsible for large C fluxes in and out of the terrestrial biosphere. Human activities have altered land cover for thousands of years but the intensity and magnitude have accelerated during the last centuries. Historically, between 3 253 and 3 470 × 10^6 ha have been converted from natural vegetation, approximately 10% of the total land surface. This has reduced global NPP by about 5% and released 182–199 Pg C to the atmosphere (DeFries et al. 1999). Overall, changes in land use and cover since 1850 are responsible for 33% of the increased concentrations of CO_2 observed in the atmosphere (Houghton 1998), 68% of which was due to cropland establishment (Houghton 1999). Some of these values have been challenged on the basis of lower deforestation rate obtained using remote sensing measurements (Archard et al. 2002; Defries et al. 2002) but the overall values are likely to remain high (Fearnside and Laurance 2004). Recent high resolution remote sensing analyses in the Brazilian Amazon show that unaccounted selective logging increased previously reported deforestation areas by 60% to 120% (Asner et al. 2005).

Future conversion of forest and grasslands to pastures and croplands will without doubt increase atmospheric CO_2 concentration. With increasing population, increased consumption, and apparent shifts in diets, either land must become more productive or agricultural area must be expanded. In the most developed world the former is being achieved through technological intensification, but major expansion of agricultural land must occur in many parts of the world, particularly in subtropical and tropical countries where the technology or capital for intensification may not be available. Using the UN intermediate population estimates about ⅓ of the Earth's land cover will change in the next hundred years (Alcamo et al. 1996a,b), with the largest changes expected within the next few decades (Walker et al. 1999).

In a compilation of dozens of scenarios of C emissions from anthropogenic land-use change, the IPCC-SRES (2000) predicts that the largest emissions will result from deforestation in tropical Africa, Asia and Latin America. Deforestation in all these three major regions is expected to decrease towards the end of this century to a small fraction of the levels in 1990. It is worth noting that the declines in Asia and Africa are driven by the depletion of their forests, while Latin America shows the highest uncertainty given the extent of forest resources. Carbon emissions from tropical deforestation may release between 85–130 Pg C by 2100 (Houghton 2005).

In addition to the primary effect of increased C emissions resulting from deforestation, there is a secondary (or amplifier) effect on increasing atmospheric CO_2 due to the reduced sink capacity owing to the shorter residence time of C pools in the newly established pastures or croplands (Gitz and Ciais 2004). Using the IPCC-SRES A2 future scenario, the amplifier effect is responsible for an extra 61 ppm of atmospheric CO_2 by the end of the century, after subtracting the additional C uptake by the oceans and remaining vegetation. The magnitude of this effect, which is not accounted for in climate model projections (IPCC 2001), is of a similar magnitude to the carbon-climate feedbacks reported recently (Jones et al. 2005; Friedlingstein et al. 2006).

It is difficult to know whether the current size of the deforestation source will remain steady for a number of decades before declining or whether it will accelerate C emissions due to the implementation of new land-use practices (Carvalho et al. 2001) followed by a step decline. The role of deforestation in terrestrial sink saturation is, therefore, complex but large given the size of this emission term in the global C budget.

6.4.3.8 *Peatland Drainage*

Water-logged peatlands are subject to CO_2 emissions from drying out and from fire. A drop of the water table brought about by land use and/or climate change, can expose large quantities of C to decomposition that otherwise are locked under anaerobic conditions. Interestingly, recent observations suggest that increased atmospheric CO_2 concentrations alone could also lead to a loss of peatland C through larger fluxes of Dissolved Organic Carbon, DOC (Freeman et al. 2004).

High-latitude peatlands have been a net C sink since early in the Holocene (Smith et al. 2005 for Russia's West Siberian lowland peatlands) but there has been a recent slowdown or cessation in net C accumulation (Botch et al. 1995; Peteet et al. 1998; Turunen et al. 2001; Turetsky et al. 2002; Friborg et al. 2003). There exists a balance in wetlands between increased CO_2 emissions when water tables fall or temperature goes up, and CH_4 emissions when water tables rise. In cold regions, changes in precipitation and temperature will largely determine the net balance between CO_2 and CH_4 emissions. Friborg et al. (2003) illustrates this complexity by showing that a Siberian wetland, despite being a net C sink, was an important source of radiative forcing owing to emissions of CH_4 (which has a warming potential 21 times larger than that of CO_2 over 100 years).

Lowland tropical peatlands, accounting for about 10% of global peatland extent, contain up to 70 Pg C in deposits as deep as 20 m (Page et al. 2002; Page et al. 2004 and references therein). Indonesia, Malaysia, Brunei and Thailand hold the largest tropical peatlands in the world which have been an overall net C sink since late Pleistocene (Page et al. 2004). However, over the last decade a combination of intense draining for agriculture and increasing climate variability in the form of more intense droughts (associated or not to El Niño events) have destabilized this millennia-long C sink (Page et al. 2004; Aldhous 2004; Murdiyarso and Lebel 2007, Chap. 21 of this volume).

During El Niño 1997–1998 events in Indonesia, burning of peat and vegetation resulted in an estimated loss of C between 0.81 and 2.57 Pg in 1997 equivalent to 13% to 40% of the mean annual global C emissions from fossil fuels (Page et al. 2002).

With large tracts of drained swamp forests and new peatland conversion projects to agriculture, tropical peatlands will continue contributing to increased C emissions over the coming decades. With some projections of decreased precipitation over the tropics during the dry season (Wenhong Li, in preparation) and the possibility of El Niño-like events becoming more intense or frequent under a warmer climate, C emissions from peatlands have increased and will continue to diminish the strength of the terrestrial net C sink.

Together, high latitude and tropical peatlands account for over 450 Pg C (Sabine et al. 2004). A preliminary estimate suggests that up to 100 Pg C of CO_2 equivalents could be released to the atmosphere from wetlands and peatlands over the next 100 years (Gruber et al. 2004).

6.5 Integration and Model Predictions

So far it has been difficult to integrate the above disparate knowledge under a common framework that allows the various processes and top-down measurements to constrain one another, and informs estimates of the relatively contribution and spatial distribution of the multiple processes driving the net terrestrial C sink. Suggestive of how little constrained the results are is that, added together, the sink estimates from each individual sink process described in Sect. 6.4 amount to a larger terrestrial net C sink than can be accounted for in the global C budget or the observed growth of atmospheric CO_2. This creates a paradoxical problem of an apparent missing large C source.

The limited understanding of some of the processes and pools has also prevented models from representing the necessary dynamics and underlying processes. The result is that there is no single model that includes all phenomena described above. Global climate models used to predict the effect of increasing GHGs on future climate (GCMs), and specifically the ones with coupled C cycle models (i.e., in the C4MIP family of models; Friedlingstein et al. 2006) deal just with simplified versions of photosynthesis and respiration.

Nevertheless, there have been important global and regional analyses. McGuire et al. (2001) attempted a global analysis to partition the historical global C sink from 1920 to 1992 including climate and atmospheric CO_2 change, land conversion to crops and crop abandonment, and forest harvests. They reported that from 1920 to 1957 terrestrial ecosystems were responsible for a net release of 8.8 Pg C, largely due to cropland establishment. During the period 1958 to 1992 the terrestrial biosphere stored 14.3 Pg C largely due to the physiological effects of rapidly rising atmospheric CO_2, although cropland establishment continued to release C. This is one of the best global mechanistic analyses to date but it only accounted for a portion of the sink processes believed to be important.

A sectoral approach has been used by some nations to attribute national sinks and sources to specific activities of their economy and ecosystems. Such studies do not provide information on the ultimate causes of the various sink processes but partition the individual fluxes contributing to a regional C sink. For the conterminous USA (1980–1989) eight atmosphere-land fluxes contributing to the overall C sink were reported (Pacala et al. 2001): (1) forest tree growth, (2) other forest components such as nonliving organic matter, (3) agricultural soils, (4) non-forest systems including woody encroachment, (5) wood products both in use and in landfills, (6) sediments of reservoirs and rivers, (7) atmospheric C fixed by U.S. ecosystems and then exported by rivers, or (8) exported commercially (food and fiber). The analysis showed that only 30% of the sink was the result of sectors susceptible to the influences of CO_2 fertilization (i.e., (1), (3), and (4)), which was until recent years thought to be the primary driver of the entire terrestrial sink. A similar analysis has been also presented for Europe (Janssens et al. 2003, 2005).

Several attempts have been made to assess the future terrestrial C sink using different types of model: *(i)* physiological and biogeochemical models without dynamic vegetation (do not allow for carbon-climate feedbacks), *(ii)* Dynamic Global Vegetation Models (DGVMs) (do not allow for carbon-climate feedbacks) (Fig. 6.7a), and *(iii)* the C4MIP GCM family (provide coupled carbon-climate projections and allow for carbon-climate feedbacks, but most of them do not have yet dynamic vegetation) (Fig. 6.7b).

Despite the large differences in complexity of the various models, all projections show varying degrees of increased NPP and heterotrophic respiration during the next century due to increasing atmospheric CO_2 concentration (i.e., CO_2 fertilization effects) and associated climate changes. This results in increased global NEP during the next few decades and a subsequent decline of the terrestrial C sink strength. The models under categories *(i)* and *(ii)* that emphasised N limitation without increased N fixation showed the fastest saturation and subsequent decline of NEP. The timing and magnitude of the downturn depends critically on the sensitivity of soil respiration to warming and how the response of biological N fixation is represented (Gifford et al. 1996; Cao and Woodward 1998; Kicklighter et al. 1999; Cramer et al. 2001; Fig. 6.7a).

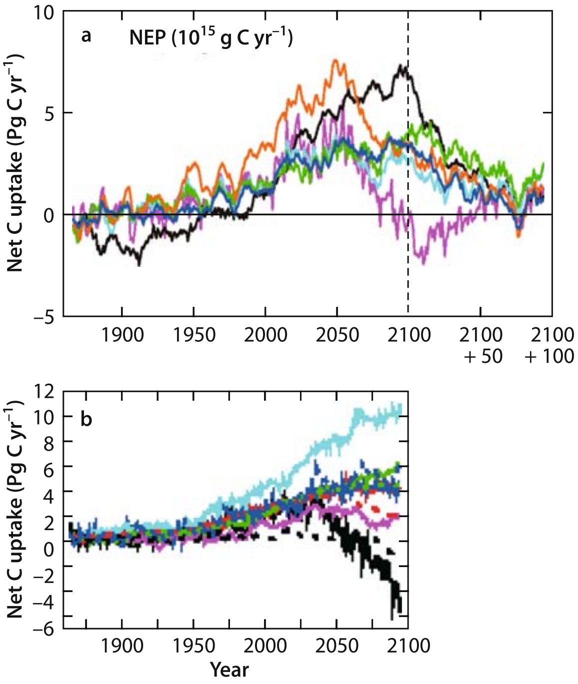

Fig. 6.7. Terrestrial net C uptake from 1850 to 2100 with atmospheric CO_2 and climate change: **a** six dynamic global vegetation models (Cramer et al. 2001); and **b** ten global circulation models with coupled carbon cycle model (Friedlingstein et al. 2006)

More recently GCMs that have been further developed to take into account carbon-climate feedbacks after Cox et al. (2000) showed that the feedback resulted in an additional 200 ppm in the atmosphere by the end of this century (model type iii). There are now 11 GCMs with such capacity and they were recently evaluated for the magnitude of the carbon-climate feedback (Friedlingstein et al. 2006). By the end of the century, the C feedback is modeled to account for an additional CO_2 of 20 to 200 ppm with 8 of the models falling between 50 and 100 ppm (Fig. 6.7b). This could lead to an additional 0.1 to 1.5 °C in surface warming.

A few of the models in categories *(i)* and *(ii)* account for additional processes such as N limitation and fire; models in category *(iii)* are driven exclusively by simple representations of photosynthesis and soil respiration as the overall controls of C exchange between the terrestrial biosphere and the atmosphere. The exclusion of some of the sink processes and vulnerable C pools (Fig. 6.8) tend to overestimate the CO_2 fertilization effect and underestimate biospheric C emissions, thus underestimating what we think is a larger magnitude of carbon-climate feedbacks than currently estimated. The omission of four of these processes/pools will illustrate this point:

The legacy of land-use change. We discussed in Sect. 6.4.3.2 and 6.4.3.3 that there is strong evidence that a significant component of the current northern hemisphere net terrestrial C sink may be the result of past land practices, particularly from forest regrowth in abandoned cropland and vegetation thickening due to fire exclusion. If that is the case and given the saturation nature of these processes, we should expect a rather quick sink decline within a few decades as forests mature and its sink strength diminishes accordingly (Fig. 6.9). Our current estimates of the future strength of the terrestrial sink (IPCC 2001; Friedlingstein et al. 2006) falsely attribute any C sink that is due to vegetation recovery from past disturbances to the CO_2 fertilization effect with the consequent overestimation of the sensitivity of CO_2 for future sinks.

Nitrogen limitation. Hungate et al. (2003) calculated the amount of N required to accumulate between 260 and 890 Pg C over the 21st century as predicted by terrestrial ecosystem models used in the IPCC Third Assessment (IPCC 2001). Despite accounting for large increases in atmospheric N deposition and biological fixation, and decreased C/N ratios, Hungate et al. were only able to account for 1.2 to 6.1 Pg of N by the end of the 21st century, not sufficient to meet the models demands in all but two simulations for the high end N production (6.1 Pg N),

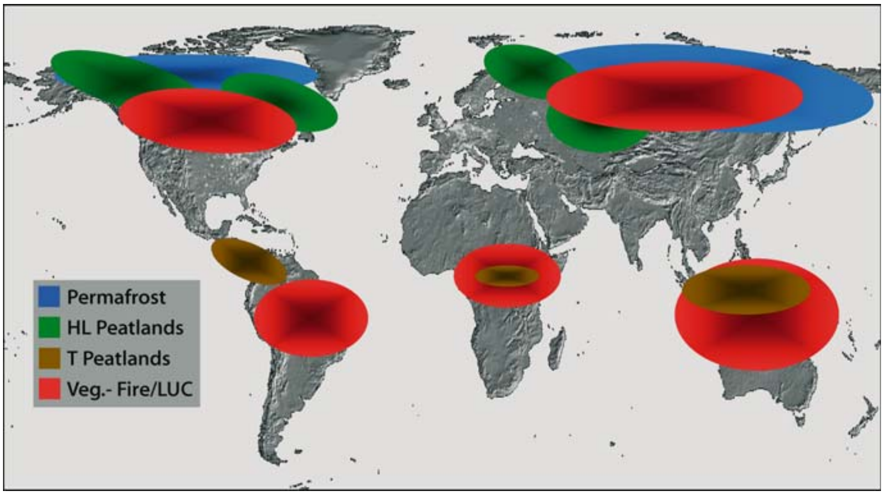

Fig. 6.8. C pools vulnerable to global warming and land-use change. They include: *(i)* frozen ground, *(ii)* tropical and high-latitude peatlands, and *(iii)* vegetation susceptible to land use and fire

and in all simulations for the low end (1.2 Pg C). Therefore, failure to account for what is a well established constraint on terrestrial NPP (P is also important in the tropics) will result in a gross overestimation of the CO_2 fertilization effect.

Carbon oxidation by fire. Currently there are no coupled carbon-climate models that distinguish soil respiration emissions from fire emissions. Very warm years such as El Niño in 1997–1998 were used to test the sensitivity of soil respiration to temperature which was then used to forecast the soil C sensitivity to future warming (Cox et al. 2000) without accounting for the fact that those same years had high fire emissions. The unintended consequence of this false attribution is to overestimate C emissions from soil respiration. The total C emissions are not necessarily overestimated but omitting fire as a process results in a more smooth dynamics of changes in the sink capacity over time while changes brought about by high fire activity can result in major vegetation shifts which would diminish the strength of the terrestrial sink more abruptly.

Carbon in frozen ground. Soil C databases used in global modeling are still incomplete. Particularly C stored in frozen ground, both in soils and sediments, is poorly known and often estimated only for to the first 30 cm of the soil profile. Sect. 6.4.2.3 reported new findings on the depth and an extension of frozen carbon, particularly with the finding of 500 Pg C in loess sediments in Siberia not previously accounted for (Fig. 6.8). An underestimation of the size of C pools will lead to the underestimation of the potential carbon-climate feedback and therefore overestimation of the potential terrestrial C sink.

6.6 Summary and Conclusions

The current measured net C sink in the Northern Hemisphere and the inferred biosphere sink over the tropics

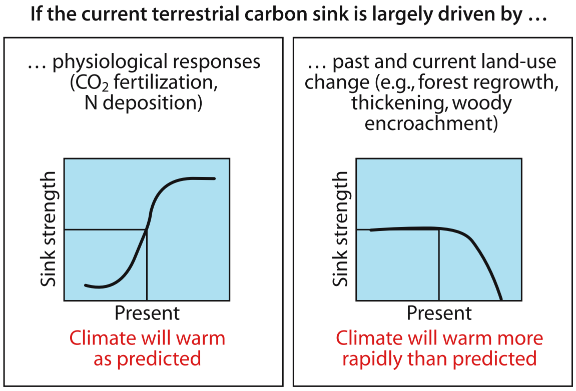

Fig. 6.9. Two alternative scenarios on future dynamics of the terrestrial net biospheric C sink

are not permanent features of the terrestrial biosphere but the result of an imbalance driven by past and present human activities. The sink strength shows high interannual variability and there is evidence that the sink cannot be sustained indefinitely. It is conceivable that by the end of this century or earlier the terrestrial sink may significantly decrease or disappear. Uncertainties in partitioning the historical and current C sinks into various possible processes limits our capacity to predict the future sink strength. Plausible processes that can explain the current sink are land-use change, including forest regrowth on abandoned croplands and fire exclusion, and responses of ecosystem C storage to the related increases in atmospheric CO_2, N deposition and climate change, among others acting individually or synergistically/antagonistically. Some of the sink processes have response curves that saturate at higher forcing levels expected to be reached during the next few decades to a century, while others produce inherently temporary sinks that disappear over time. The saturation of the sink will occur sooner if the prevalent sink processes are related to legacies of past land-use change, and slower, if the prevailing processes are driven by physiological effects of atmospheric CO_2 and N fertilization which are expected to continue in the future (Fig. 6.9). High C-density regions on land such as permafrost and peatlands are vulnerable to global warming and land-use change, and are likely to add large amounts of C into the atmosphere over the coming decades (Fig. 6.8). With the present level of our understanding, it is certain that the terrestrial biosphere sink cannot be maintained indefinitely.

Future Research:

- Integrated analyses of key C sink processes for regional and global C budgets using a multiple constraints approach (bottom-up and top-down measurements and models).
- Resolution of the extent and effect of woody encroachment and forest thickening.
- Integration of the legacy effects of past land-use change (e.g., forest age structure) in biogeochemical models.
- Persistence of new sinks created by afforestation and reforestation.
- Temperature and soil water effects on heterotrophic respiration integrated with feedback constraints, and associated temperature sensitivity of soil organic matter pools.
- Accurate assessment of the extension and pool size of vulnerable C pools to climate and land-use change (e.g., C in frozen ground, peatlands, forest biomass).
- Increase sophistication of C models in coupled carbon-climate GCMs (i.e., Earth System Models) with the inclusion of key terrestrial C-cycle and land surface processes (e.g., vegetation shifts, anthropogenic and wild-fires, forest-age structure, nutrient feedbacks) and vulnerable C pools (e.g., C in frozen soils and sediments, C in cold and tropical peatlands).

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Part B

Changing Biodiversity and Ecosystem Functioning

Chapter 7

Functional Diversity – at the Crossroads between Ecosystem Functioning and Environmental Filters

Sandra Díaz · Sandra Lavorel · F. Stuart Chapin III · Paula A. Tecco · Diego E. Gurvich · Karl Grigulis

7.1 Introduction

Functional diversity, i.e., the *kind*, *range*, and *relative abundance* of functional traits present in a given community, is one of the major factors influencing ecosystem functioning (Chapin et al. 2000b; Díaz and Cabido 2001; Loreau et al. 2001; Hooper et al. 2005). Through its effects on ecosystem functioning, plant functional diversity (hereafter FD) is both affected by and affects all the major global change drivers identified by the international scientific community (Fig. 7.1, path 1). Changes in climate, atmospheric composition, land-use and disturbance regime, and biotic exchanges (deliberate or accidental introduction of organisms to an ecosystem) all have non-random effects on FD, i.e., they select for or against species bearing certain traits. For example, the more drought- and/or frost-sensitive species are eliminated first under an increased frequency of climatic extreme events (Díaz et al. 1999). Slow-growing species are eliminated when ecosystems experience nitrogen loading (Thompson 1994). Non-resprouting species are strongly reduced by increased fire return intervals (Russell-Smith et al. 2002; Johnson and Cochrane 2003). At the same time, through its effect on ecosystem processes, FD influences climate, carbon exchange with the atmosphere,

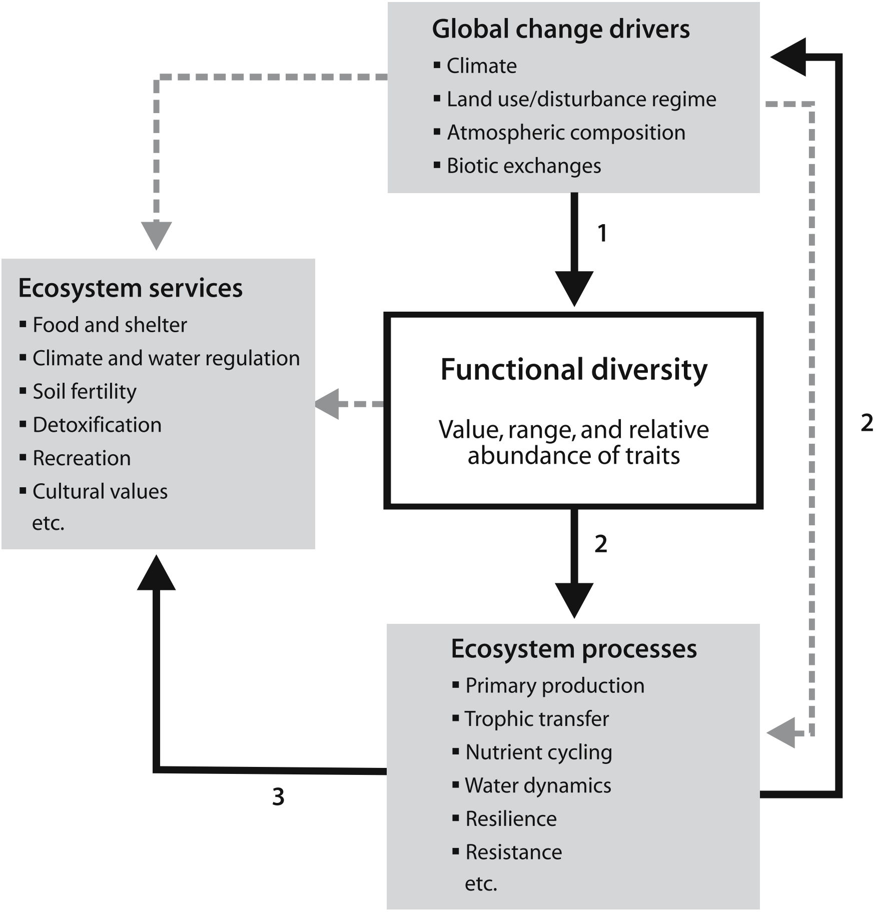

Fig. 7.1. Functional diversity is both a response variable modified by, and a factor modifying global change drivers. *Solid arrows* indicate relationships addressed in this chapter. See text for description of numbered links

disturbance regime, and the susceptibility to, and consequences of biotic exchanges (Fig. 7.1, path 2). In this chapter we focus on the processes of mutual influence and feedbacks between global change drivers and FD, and discuss the empirical evidence supporting the effect of different components of FD.

7.2 Environmental Filters Affect FD

FD at any site is the result of the action of environmental filters on the regional species pool. Environmental filters are non-random factors that narrow the range of functional traits in a local community. Filtering operates primarily at the level of ecological sorting (i.e., changing the proportions of different genotypes represented in the established community, but not altering the genotypes themselves), but can lead to stabilizing or directional natural selection over evolutionary time. Climate, disturbance regime, some aspects of atmospheric composition, and biotic interactions are major environmental filters (Keddy 1992; Woodward and Diament 1991; Díaz et al. 1998, 1999), and strongly determine which traits and functions can survive at any particular site. It has been suggested that, at a given site, species richness is limited by the regional species pool, whereas functional diversity is limited by local conditions that determine the availability of niches (Schmid et al. 2002).

The four major global change drivers can be interpreted as environmental filters: they filter out organisms bearing certain sets of traits and allow the establishment, persistence and spread of others (see Lavorel et al. 2007, Chap. 13 of this volume, for more examples of environmental filtering of plant functional traits). Therefore, the dramatic biodiversity loss now experienced at the global scale has two aspects: random extinction as a result of the reduction of inhabitable area (i.e., as expected on the basis of island biogeography theory; MacArthur and Wilson 1967), and non-random global or local extinction as a result of the filtering effect of global change drivers. The latter leads to a biota that not only is taxonomically poorer, but also represents a *biased* subset of the range of traits initially available. Recent assessments have shown strong asymmetries in the extinction risk of species with certain traits (McKinney and Lockwood 1999), or belonging to different habitats (Brook et al. 2003) or biomes (Thomas et al. 2004). Fragmentation because of land use, as well as increasing the random probability of extinction, differentially increases the local extinction risk of certain species, by altering water, wind, nutrient dynamics and flammability (Cochrane et al. 1999). Biotic homogenization, i.e., the replacement of local biotas with widespread non-indigenous species due to habitat modification and transportation of exotic species, is also a process where 'winners' and 'losers' bear different traits (McKinney and Lockwood 1999; see also Vilà et al. 2007, Chap. 8 of this volume). Non-random extinctions and functional shifts in vegetation cover as a consequence of the filtering effects of global change drivers are at least as alarming as global extinctions due to reduction in habitat area. This is because their potential effects on ecosystem processes and services (Fig. 7.1, paths 1, 3), and feedbacks to global environmental drivers (Fig. 7.1, path 2) can be dramatic well before species disappear from the face of the Earth.

7.3 FD effects on Global Change Drivers

Although the evidence of effects of FD on global change drivers and ecosystem services mediated by altered ecosystem functioning is accumulating fast, it is not equally strong for the different components of FD. Theory suggests that the kind, relative abundance, and range of traits present in a community should affect ecosystem processes and thus ecosystem services and global change drivers. However, at present there is much more empirical support for the role of the traits of the dominants (*kind* and *abundance* of traits) than for that of the *range* of traits present. On the other hand, although many (and sometimes dramatic) examples suggest that indirect interactions are crucially important in triggering some ecosystem-level feedbacks, there is still no integrated theoretical framework explicitly linking FD with these feedbacks, or predicting the consequences of indirect interactions in systems with different degrees of FD. In this section, we summarize some basic theoretical issues and the empirical evidence related to each of these components.

7.3.1 The Traits of the Dominants

Despite some remaining controversy on precisely which mechanisms explain diversity effects on ecosystem functioning (see Hooper et al. 2005 for an updated review), most researchers now recognize that FD is more relevant to local-scale ecosystem functioning than taxonomic diversity (Grime 1998, 2002; Chapin et al. 2000b; Díaz and Cabido 2001; Loreau et al. 2001; Tilman 2001; Naeem and Wright 2003; Petchey 2004; Petchey et al. 2004; Hooper et al. 2005). The fact that species show different attributes, and thus their contributions to ecosystem processes are not equal or interchangeable, is at the heart of the mechanisms proposed to explain how biodiversity should affect ecosystem processes. However, most studies of the effects of diversity on local-scale ecosystem functioning have considered only species richness, or have taken a very coarse approach to FD. For example, they consider a small number of life forms or taxonomic groups (e.g., grasses, legumes, composites), all of them with similar abundances (see Box 7.1 for a discussion of links between species richness and FD, and issues involved in FD measurement).

Box 7.1. Measuring FD

Despite the widely recognized importance of FD in determining ecosystem processes, species richness (number of species present in a given community) continues to be the most used and manipulated measurement of diversity (Díaz and Cabido 2001; Petchey 2004). This is partly because of practical reasons. First, it is much easier to count species than to weigh them by their abundance. However, this means in practice ignoring the fact that the effect of a species in an ecosystem is largely a function of its biomass (see Sect. 7.3.1). Giving the same 'weight' to extremely abundant and extremely rare species, as happens in species richness, can substantially obscure links between diversity and ecosystem processes. Second, the objective quantification of FD is far from straightforward. The most common measurement of FD is functional type richness, but the results strongly depend of the grouping into functional types (Díaz and Cabido 2001; Petchey 2004), which may or may not reflect true functional differences among species and in any case makes comparisons among different studies extremely difficult. The most promising methods of quantifying FD thus appear to be those based trait distances between species (Díaz and Cabido 2001; Naeem and Wright 2003; Petchey 2004). These require the measurement (or literature compilation) of the attributes of many species, which is time- and resource-consuming. Also, there is so far no ideal FD index, since none of the available metrics can simultaneously account for functional distances between species independently from species richness and at the same time deal with multidimensional- attribute spaces (see Mason et al. 2005, Petchey et al. 2004 and Moulliot et al. 2005 for thorough comparison of indices). Moreover, even an index with all the desirable properties (e.g., those enumerated by Mason et al. 2005) would be of little use if it is not based on functionally important traits (see Table 7.1 and Lavorel et al. 2007, Chap. 13 of this volume, for examples of 'relevant' traits for different ecosystem processes).

Beyond practical considerations, the use of species richness as a surrogate for FD is based on assumptions, which are unrealistic for most natural ecosystems (Díaz and Cabido 2001; Naeem and Wright 2003). FD is often assumed to vary in direct proportion to species diversity (Lawton et al. 1998; Tilman 1999; Naeem 2002). Species richness should be an adequate surrogate for functional richness only if there is a linear increase in niche space occupation as species richness increases. Theoretically, this can happen only when there is random (Fig. 7.2a) or uniform (Fig. 7.2b) occupation of niche space (Díaz and Cabido 2001), and when all species are equally different (addition of any species to a community and the contribution of each species to functional diversity is independent of species richness (Naeem and Wright 2003). However, these cases are uncommon in nature, as compared to aggregate occupation of niche space (Holling et al. 1996). This is because in nature random assemblage and extinction are much less common than non-random ones (Zobel 1997; Díaz and Cabido 2001; see also Sect. 7.2). When aggregate occupation of niche space is related to strong convergence of different species into contrasting functional types [e.g., annual graminoids, succulents and dwarf shrubs in deserts, Fig. 7.2c], species richness overestimates functional richness. When aggregate occupation of niche space is due to strong differentiation in niche space among different genotypes or phenotypes within a single species (e.g., herbivore-tolerant and herbivore-intolerant grass genotypes in prairie-dog dominated landscapes, Jaramillo and Detling 1988; intraspecific differentiation of the tree *Metrosideros polymorpha* in the Hawaiian islands, Cordell et al. 1998), species richness underestimates functional richness. These mismatches between taxonomic and functional richness can have important practical consequences. Only in cases in which extinction is happening at random should we expect a linear decrease in functional richness (and presumably in associated ecosystem functioning) with species richness loss. In other cases, the consequences of extinctions will likely be non-linear. For example, in the case illustrated in Fig. 7.2d, an assessment of species number loss could grossly underestimate functional richness loss. Biodiversity assessments based only on species richness and checklists will tend to overlook processes of functional extinction, that is, the extinction of local genotypes or phenotypes without immediate risk of global (Estes et al. 1989; Luck et al. 2003), Functional extinction often leads to ecosystems that retain the same richness and taxonomic composition of species, but cannot sustain necessary functions for their long-term persistence (e.g., the 'half-empty forest' of Redford and Feinsinger 2001).

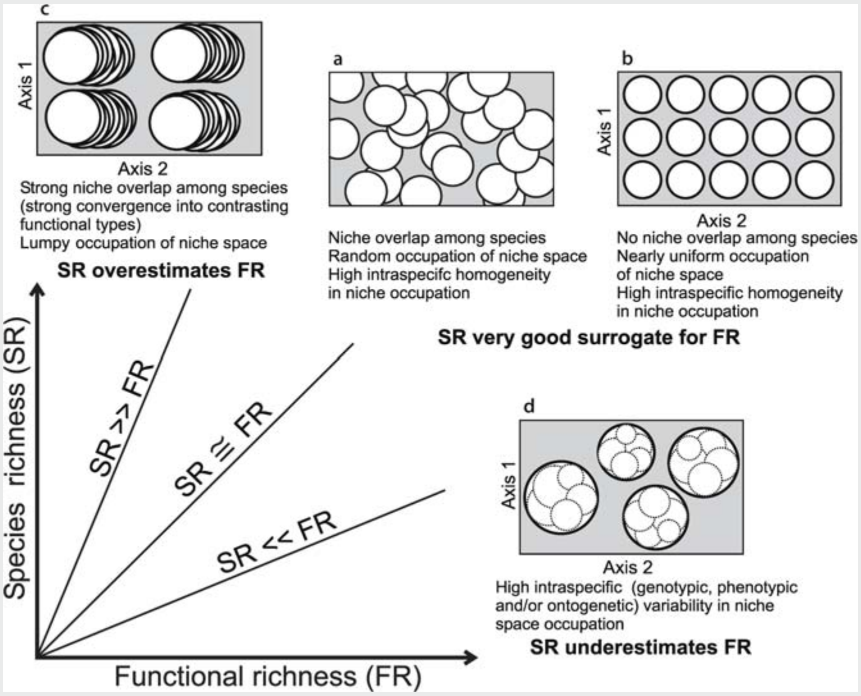

Fig. 7.2. Extreme cases of links between plant species richness and functional richness. *Axes 1* and *2* in the *shaded rectangles* represent different resource or disturbance axes. *Solid-line circles* represent the fundamental niches of different species; *dashed-line circles* represent the niche of different genotypes, phenotypes or ontogenetic stages within a single species (reprinted from Díaz and Cabido 2001, with permission from Elsevier)

In an analysis of synthetic-community and field experiments involving plants, Díaz and Cabido (2001) found that rates and magnitudes of ecosystem processes, such as plant and soil biomass production, decomposition, mineralization or various aspects of stability, were more consistently associated with functional composition (presence of certain *kinds* of plant functional traits; e.g., species with nitrogen-fixing symbionts, or with particularly fast growth rate, or evergreen leaves) and functional richness (number of different plant functional types) than with species richness. Functional composition was associated with ecosystem processes more often than was functional richness, even though most of these experiments kept the relative abundance among species unnaturally even (but see Petchey's 2004 considerations on the assignment of species to functional groups). This can hardly come as a surprise. The fact that the morpho-functional traits of the dominant plant species strongly determine ecosystem properties has been recognized since the earliest days of ecology, and has often been referred to as the 'mass-ratio' hypothesis (Grime 1998). Locally abundant plant traits determine the rate and magnitude (Grime 1977; Hobbie 1992; Chapin et al. 1993; Aerts 1995; Aerts and Chapin 2000; Herbert et al. 1999; Lavorel and Garnier 2002; Díaz et al. 2004; Garnier et al. 2004), and stability (Lepš et al. 1982; McGillivray et al. 1995; Grime et al. 2000) of major ecosystem processes. The existence of recurrent suites of plant traits (e.g., 'acquisitive' vs. 'conservative' syndromes) with predictable controlling effects on ecosystem processes such as primary production, trophic transfer, carbon storage, or nutrient cycling has been proposed (Grime 1977; Chapin 1980; Chapin et al. 1993), and empirically supported at the local (e.g., Chapin et al. 1996; Grime et al. 1997; Garnier et al. 2004) and trans-regional levels (e.g., Díaz et al. 2004).

By affecting ecosystem processes, the traits of the dominant plant species (i.e., *kind* and *relative abundance* of traits) have considerable impact on ecosystem services and therefore human well-being (Fig. 7.1, path 3; Table 7.1). On the other hand, global change drivers affect, and to a certain degree are affected by, locally dominant plant traits (Fig. 7.1, paths 1 and 2). The FD approach thus offers the interesting perspective of tracing some causal relationships and mutual feedbacks between global change drivers, locally dominant plant traits, ecosystem properties, and ecosystem services.

Table 7.1. Causal connections between some individual plant traits, ecosystem processes, and ecosystem services. *ES* = ecosystem service. ES classification follows MEA (2003)

Individual traits	Ecosystem processes	Ecosystem services
Leaf nutrient concentration Leaf toughness Specific leaf area Leaf turnover rate	Net primary productivity Relative productivity rate Consumption by herbivores ungulates (trophic transfer) Decomposition and net mineralization	Soil formation and fertility Food and fiber production Carbon sequestration Resistance of production of goods and services over time Cultural and aesthetic ES (e.g. autumn colours, traditional ungulate-dependent landscapes)
Canopy size Leaf phenology Leaf distribution over stems Growth form Canopy architecture	Evapotranspiration, heat exchange Albedo, roughness	Climate regulation
Shoot height Wood density Lifespan Leaf nutrient concentration	Accumulation of standing biomass	Carbon sequestration Climate regulation (indirectly by carbon sequestration)
Tissue water content Canopy architecture Leaf nutrient and resine content Texture and architecture of litter	Vegetation flammability Fuel load (undecomposed litter) Soil insulation from air temperature and moisture	Nutrient cycling Soil formation, fertility and stability Climate regulation Carbon sequestration Resilience of ES over time
Seed shape and mass	Persistence in the soil seed bank Seed transport by animals	Resilience of production of goods and services over time Maintenance of food-provisioning and cultural ES mediated by animals
Root depth Root architecture	Evapotranspiration Soil exploration by root systems	Climate regulation Water runoff Soil stability

7.3.1.1 *FD and Climate*

FD both responds to and affects the climate system. Local FD is strongly determined by the climatic filter (Fig. 7.1, path 1; Lavorel et al. 2007, Chap. 13 of this volume). In addition, FD affects climate regulation, which is one of the most essential services that natural ecosystems provide to humans (MAE 2003; Fig. 7.1, path 3). FD affects climate indirectly, through changes in the carbon sequestration capacity of the biota (i.e., the more carbon biological systems can sequester, the less will be contributed to the greenhouse effect in the atmosphere), and also directly, through changes in the biophysical properties of the land surface. Not surprisingly, these effects are most pronounced where the ecological changes occur over large areas. For example, in northeast Siberia, widespread fires and other disturbances lead to a replacement of mosses and evergreens, which have a long season (but low rates) of photosynthetic activity, with deciduous plants that have a shorter season (and higher rates) of photosynthesis. Mosses also insulate the soil, so the depth of soil thaw is shallower and soil respiration is less, particularly in late summer and early winter. The net effect of disturbance-induced changes in FD is therefore to increase the magnitude of both summer carbon gain and winter carbon loss. In this way recent increases in disturbance contribute to the increased seasonal amplitude of atmospheric carbon dioxide concentration at high latitudes (Zimov et al. 1999). The feedback from increased carbon dioxide to climate occurs at the global scale because of the rapid mixing of the atmosphere.

FD also interacts with the climate system through changes in water and energy exchange (Foley et al. 2003). Complex canopies often absorb more energy (have a lower albedo) because canopy complexity increases the probability that other surfaces will absorb reflected radiation before it is lost to space. For this reason there is a decrease in albedo from conifer forests to deciduous forests to grasslands. Particularly in open-canopied ecosystems, which account for 70% of the ice-free terrestrial surface (Graetz 1991), species in the ecosystem will likely influence stand-level albedo, with their importance depending on abundance, height, and structural properties. In addition, diversity often contributes to the structural complexity of leaf arrangement in canopies and therefore the efficiency with which incoming radiation is trapped. For example, the increase in shrub density in arctic tundra in response to regional warming (Sturm et al. 2001) has reduced regional albedo and increased regional heating (Chapin et al. 2000a). Structural diversity of the canopy also increases the efficiency with which heat and moisture are transferred to the atmosphere. Even a low density of trees (e.g., <100 ha^{-1}) in a savanna or woodland substantially increases turbulent exchange with the atmosphere (Thompson et al. 2004).

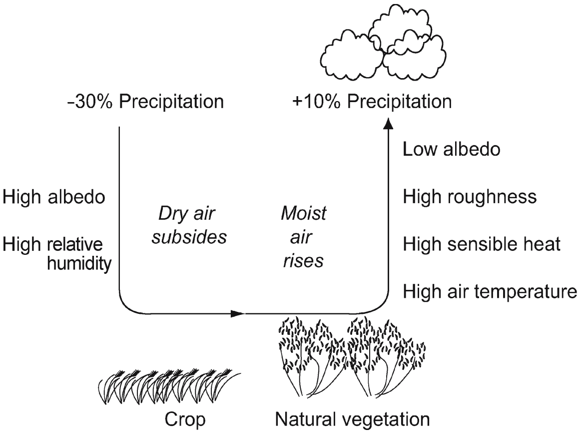

Fig. 7.3. Effects on regional climate of conversion of heathland to croplands in southwestern Australia (Chambers 1998) (reproduced from Chapin et al. 2002, with permission from Springer-Verlag)

The diversity of patches on a landscape exerts an additional impact on biophysical coupling between land and atmosphere. Patches that are larger in size than the depth of the planetary boundary layer (i.e., their smallest dimension is at least 10 km) and which differ in albedo or surface temperature from neighboring patches create convection cells, in which air rises above the warm patch; this air is replaced by cooler moister air that flows laterally from adjacent patches (Pielke 2001). In Australia, for example, the replacement of native heath vegetation by croplands increased regional albedo. As a result, air tended to rise over the dark heathland, drawing moist air from the croplands to the heathlands. The net effect was a 10% increase in precipitation over heathlands and a 30% decrease in precipitation over croplands (Fig. 7.3) (Chambers 1998).

7.3.1.2 *Fd and Land-Use/Disturbance Regime*

Changes in FD brought about by shifting climatic or land-use conditions can in turn produce changes in an ecosystem's disturbance regime and/or resource basis, and thus its ecosystem-service value and suitability for certain land uses. These include, for example, changes in carrying capacity for livestock, capacity for water retention and flood regulation, control of human and domestic animal disease, or amenity values. These processes sometimes start with sharp increases in abundance of native species that were previously non-dominant (e.g., woody encroachment; Scholes and Archer 1997) or the spread over the landscape of exotic species. The latter is the result of the explosive increase in biotic exchanges during the 19th and 20th centuries, often in combination with changes in climate and land use (Fig. 7.1, path 1; see Vilà et al. 2007, Chap. 8 of this volume). Once established, some exotics become invasive and alter ecosystem productivity, resource dynamics, stability, and disturbance regime, often irreversibly (Fig. 7.1, paths 2 and 3). A review of over 150 studies to evaluate the mechanisms underlying the impacts of exotic plant invasions on plant and animal community structure, nutrient cycling, hydrology, and fire regimes revealed that studies examining effects of invaders on ecosystem processes often tend to attribute impacts to differences in important functional traits of the invader as compared to the resident species (Levine et al. 2003). The majority of examples where significant effects on ecosystem processes were reported concerned invasions by a life form previously absent from a native ecosystem (e.g., grasses) and species with traits allowing them to tap into unexploited resources (e.g., nitrogen-fixing, deep rooting). However, life forms readily present in an ecosystem could also have impacts, e.g., on the nitrogen cycle or fuel accumulation for fire, when invaders had attributes conferring them greater efficiency in resource use than the natives.

A recent study illustrates how climate and land-use change and biotic exchanges can alter, and be altered by FD, in a feed-forward, highly irreversible process. The northern Mediterranean basin agricultural land abandonment over the last century (Moreno et al. 1998) and ongoing climate change (Pausas 2004) have resulted in increasing frequencies of very large, intense fires. In Catalonia (NE Spain), higher fire frequency seems to promote the expansion of the large, evergreen, resprouting tussock grass *Ampelodesmos mauritanica* (Vilà et al. 2001). Near-monocultures of *A. mauritanica* now occupy original shrubland sites. Grigulis et al. (2005) tested the hypothesis of a positive feedback between *A. mauritanica* abundance and changing fire regimes by combining measurements across a natural gradient of density of *A. mauritanica* near Barcelona, Spain with model simulations of fire and vegetation dynamics using the landscape modeling platform LAMOS (Lavorel et al. 2000; Cousins et al. 2003). The invasion of shrublands by *A. mauritanica* produced a series of spectacular modifications in community structure and ecosystem properties, which translated to changes in vegetation and fire regimes at the landscape-scale (Fig. 7.4):

1. Aboveground biomass nearly doubled in plots with high vs. low density of *A. mauritanica* (Fig. 7.4a). This occurred because *A. mauritanica* replaced native shrubs, but also some grasses and herbs, and also because the standing biomass of *A. mauritanica* increased significantly. Therefore the morphological/functional composition of the community was considerably modified by the invasion. The quantity of litter also increased significantly, leading to much higher total fuel loads in high invasion plots. The specific aboveground net primary productivity (Garnier et al. 2004) of all components of the community decreased significantly with increasing density of *A. mauritanica*.

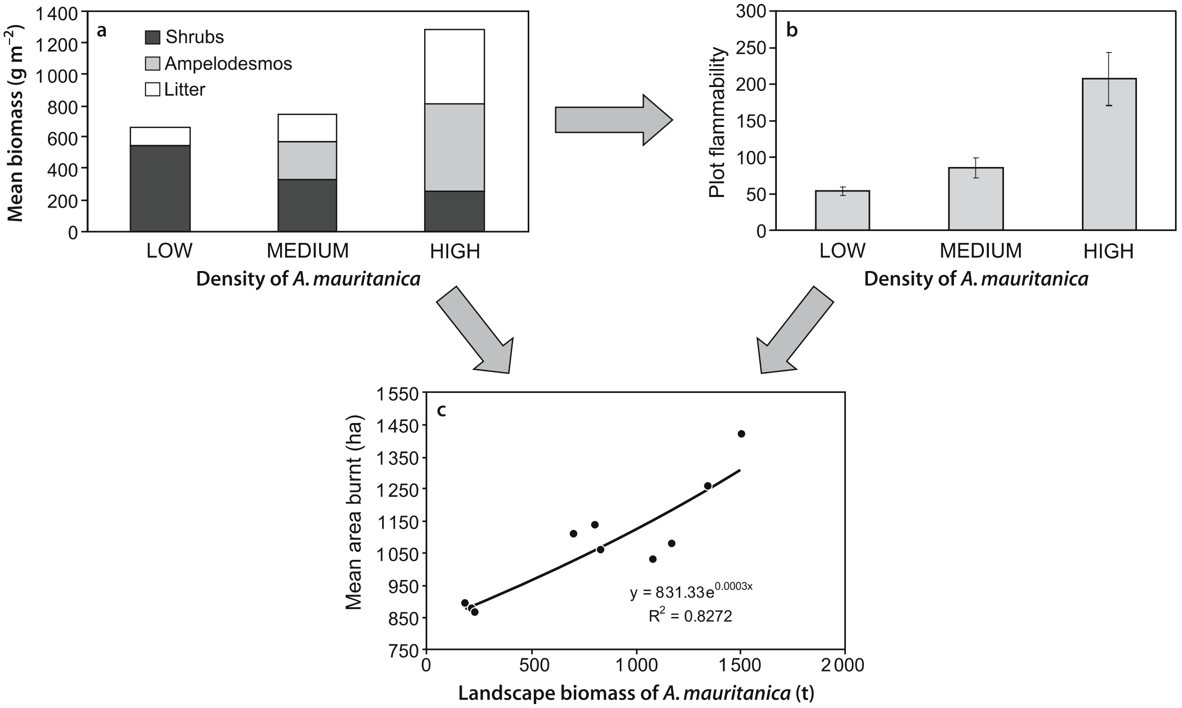

Fig. 7.4. Positive feedback between fire regimes and invasion by *Ampelodesmos mauritanica* in Catalonia. **a** Functional composition of communities with increasing density of *A. mauritanica*. **b** Plot-level flammability calculated from individual flammabilities weighed by the relative biomass contributions of species. **c** Effect of total biomass of *A. mauritanica* on mean area burnt during fire years (reprinted from Grigulis et al. 2005, with permission from Blackwell)

2. The considerable litter accumulation observed with increasing density of *A. mauritanica* was explained not only by the greater production of litter, but also by the fact that its litter decomposed at a 30% slower rate than that of the resident shrubs.
3. Under standardised conditions, *A. mauritanica* ignited much more rapidly than any of the shrub species, especially its dry litter, and once burning produced a more intense flame, again especially as litter. Calculated plot flammability taking into account changes in functional composition and specific flammabilities showed a >40-fold increase from low- to high-density plots (Fig. 7.4b).
4. Simulations of coupled vegetation- fire dynamics parameterised from these measurements of ecosystem properties and life history characteristics of *A. mauritanica* showed that invasion success and contribution to community biomass of *A. mauritanica* increased abruptly with decreasing fire return intervals. Total area burned in the landscape during each fire year was positively and exponentially related to the total biomass of *A. mauritanica* present in the landscape (Fig. 7.4c). Landscapes can hence switch from regimes of small localized to extensive fires as a result of the spread of *A. mauritanica* under decreasing fire return intervals. These patterns were explained by the increasing connectivity of highly flammable vegetation as *A. mauritanica* becomes more frequent in the landscape, coupled with the direct positive effects of fire on the demography of this grass.
5. Hence invasion of Catalan shrublands by *A. mauritanica* threatens a range of services that these natural ecosystems provide to rural and urban populations. Greatest of these is exposure to wildfire, especially in suburban areas that surround the city of Barcelona. Effects on native biodiversity were not yet detectable for plants, but may occur at later stages of invasion, in particular via the notable changes in fire regimes. Finally, invasion by *A. mauritanica* is perceived by the local population and managers as a threat to landscape amenity value.

7.3.2 The Role of Interactions

We have shown above that three components of FD – the *kind*, *relative abundance* and *range* of traits – are important in explaining biodiversity effects on ecosystem processes. In Sect. 7.3.1 we presented strong evidence of the role of the first two components: at any particular location, and within the envelope defined by climatic and disturbance conditions, ecosystem functioning is largely driven by the attributes of the dominant species, which are in turn strongly determined by the action of environmental filters. We know much less, however, about the functional role of the *range* of traits present in any given ecosystem, i.e., does it matter whether the organisms present are very similar or very different in terms of functional traits? The overwhelming evidence in favor of the mass-ratio hypothesis, which states that instantaneous functioning of ecosystems is determined to a large extent by the trait values of the dominant contributors to plant biomass; Grime (1998), might lead to the conclusion that the ecosystem role of subordinate species can be safely considered negligible. However, both theoretical knowledge of interactions and empirical examples tell us otherwise. Subordinate species are known – or expected – to play a significant role in long-term ecosystem stability (see e.g., Grime 1998; Dukes 2001; Lyons and Schwartz 2001; Lyons et al. 2005). Interactions between dominant and subordinate species within a given trophic level, and across trophic levels, are at the core of some of the mechanisms by which biodiversity affects ecosystem functioning (Chapin et al. 2000b). Two mechanisms involving species coexistence within the trophic level of primary producers are based on trait differences (*range* of traits) among species. These are resource use complementarity and facilitation.

Resource use complementarity is based on temporal and spatial niche partitioning (e.g., different rooting depths, phenologies, establishment mechanisms in regeneration gaps, forms of nitrogen that can be taken up from the soil), which reduces interspecific competition (MacArthur and Levins 1967). As a mechanism by which biodiversity influences local-scale ecosystem functioning, resource use complementarity assumes that the larger the functional trait distance between plants, the stronger the complementarity effect, and the more complete the total resource use by the community is expected to be (Trenbath 1974; Ewel 1986; Vandermeer 1989; see Hooper et al. 2005 for a detailed review). Complementarity in resource use is indeed a common coexistence mechanism in plant communities (e.g., Silvertown et al. 1999; McKane et al. 2002; Hooper and Dukes 2004). However, it is still uncertain whether this higher FD consistently leads to higher ecosystem 'performance' (e.g., higher productivity, nutrient retention, stability) beyond combinations of a very small number of species, such as those found in agriculture and forestry. Many cases in which species differences lead to higher biomass production involve nitrogen-fixing legumes, and thus can be interpreted as facilitation (Fridley 2001, see below).

Complementarity in resource use leading to higher ecosystem 'performance' in the absence of nitrogen-fixing legumes has been empirically demonstrated in some cases (e.g., van Ruijven and Berendse 2003), but seems far from universal, and its importance likely depends on the environmental context (Fridley 2003; Dimitrakopoulos and Schmid 2004; Hooper and Dukes 2004; Petchey 2004; Hooper et al. 2005). Grime (2002) has argued that, while resource use complementarity is definitely important as a coexistence mechanism, there is no reason based on natural selection why it should lead to 'enhanced' ecosystem functioning. The admission and persistence of organisms in plant communities and ecosystems depend upon their individual fitness rather than their contribution to community- or ecosystem-level properties, and coexistence and contribution to ecosystem processes often depend on different plant traits. Whereas complementarity facilitates the entry and persistence of species in the community it cannot be assumed that this will necessarily lead to complementary roles in sustaining the ecosystem. For example, Hooper and Dukes (2004), using synthetic serpentine-grassland communities, found that functional trait differences among species lead to strong complementarity in resource use among plants, but these were not sufficient to cause consistent increases in community productivity with increasing number of species. Dimitrakopoulos and Schmid (2004) measured biodiversity effects on plant biomass in synthetic calcareous-grassland communities planted on soil of different depths, and found that the importance of resource use complementarity increased as soil depth increased, suggesting that the biodiversity effect on biomass production may be strongly constrained in shallow soils.

The second interaction-based mechanism by which trait differences between species within the same trophic level can influence local-scale ecosystem functioning is facilitation. Probably the best example of this is the frequent stimulation of total production of species mixtures in the presence of nitrogen-fixing species. This is well known from the agricultural and forestry literature (Trenbath 1974; Vandermeer 1989; Cannell et al. 1992) and has been one of the most consistent effects of FD in synthetic-community experiments on the role of diversity in local-scale ecosystem functioning. Other plant-plant facilitation examples are the nurse effect by which larger plants ameliorate harsh climatic conditions or herbivore pressure for seedlings of other species (see Callaway 1992 and Bruno et al. 2003 for examples and detailed review of other facilitation mechanisms). Despite the increased interest in facilitative interactions in the past few years, there are not many documented examples of effects at the level of ecosystem functioning beyond biomass production (often positive effects, see above) and invasion resistance (both positive and negative effects; see Marler et al. 1999; Stampe and Daehler 2003). The literature on the effects of facilitation or resource use complementarity on ecosystem ser-

Box 7.2. Indirect interactions challenge the FD approach

Indirect interactions are those in which a species, through direct interaction with another species or modification of resources, alters the abundance of a third species with which it is not directly interacting. Such interactions challenge the FD approach, since there is no way to predict the ecosystem-level consequences of species additions or loss on the basis of the kind, range or relative abundance of traits.

Example 1
Facilitation among Woody Invaders in Temperate and Subtropical South America

The glossy privet (*Ligustrum lucidum*) is an evergreen, bird-dispersed and shade-tolerant Asiatic tree that invades seminatural woodlands and grasslands in southern South America. Originally introduced as an ornamental plant, this species apparently does not grow faster than native species, nor can it use soil resources not taken up by the resident communities (Gurvich et al. 2005). Its seedlings are susceptible to grazing by livestock and its recruitment has been reported to be strongly limited by the availability of recruitment micro-sites and by the interference from herbaceous vegetation (Mazia et al. 2001). On these bases, one would hardly predict its aggressive expansion over the landscape in the last decades. In central Argentina open woodlands its success is the result of indirect interactions with the native fauna and flora, mediated by the presence of another woody invader, the fire hawthorn (*Pyracantha angustifolia*). Unlike native species, both exotic shrubs produce fleshy fruits in autumn and winter, thus offering an extra food source to native frugivorous birds during a period of scarcity (Tecco et al. 2006). The branching architecture of *P. angustifolia* is attractive to perching birds, thus facilitating the dispersal of *L. lucidum* seeds under its canopy. Once germinated, *L. lucidum* seedlings grow slowly under *P. angusti-folia*, but as a shade tolerant, survives much better than the herbaceous dicots and grasses which outcompete it in the open (Tecco et al. in press). Also, the thorny, dense, umbrella-like canopy of *P. angustifolia* protects the seedlings from browsing and trampling by livestock. Once established, *L. lucidum* forms dense, shady, almost impenetrable thickets with an extremely poor understorey, both in terms of biomass and species richness (Lichstein et al. 2004). This, in turn, is expected to have important effects on ecosystem processes, services, and the land-use value of the land. For example, the total standing biomass and water uptake of *L. lucidum* near-monocultures are likely to be higher than those of stands dominated by semideciduous native vegetation. Carbon and nutrient cycling may also change by alteration of decomposition processes through altered litter quality and quantity and by a cooler, moister microhabitat. The effect of the winter extra supply of food for frugivorous birds by these two invasive species can have ripple effects on bird communities and the fleshy-fruited species dispersed by them.

Example 2
Gophers and Goatgrass in Californian Grasslands

The expansion of the exotic barbed goatgrass (*Aegilops triuncialis*) over the Californian landscape is also the consequence of several indirect interactions between three trophic levels that can hardly be predicted on the basis of the traits of the dominant species or the range of traits present in the community. According to Eviner and Chapin (2003), gophers are both attracted to patches dominated by goatgrass and negatively affect the latter. Apparently, the root architecture of goatgrass stabilizes the soil and makes it more efficient for gophers to burrow in patches dominated by this species. The negative effects of gophers on goatgrass stem from two processes. First, their burrowing activity buries goatgrass plants and thus slows down its expansion over the landscape. Second, they reduce the infection of goatgrass seedheads by the fungus *Ulocladium*, thus retarding germination and putting this species in a disadvantaged position with respect to native grasses. On the other hand, the presence of gophers decreases with heavy grazing. The expansion of goatgrass in heavily grazed paddocks decreases both the pastoral quality (seedheads can cause injury to livestock and its leaves are very poor nutritionally) and the amenity value (less native biodiversity, spiky seedheads are uncomfortable to hikers) of these Californian landscapes.

vices is scarce (see Díaz et al. 2005), and, to our knowledge, there is no published study explicitly addressing the effects of these mechanisms on global change drivers.

Resource use complementarity and facilitation are based on trait differences between species, i.e., their effects are expected to be maximal when species are very different from each other. Therefore, in those systems where these mechanisms indeed lead to enhanced ecosystem functioning, one should reasonably predict increased or decreased ecosystem 'performance' on the basis of an expanding or shrinking range of plant traits (Hooper 1998; Petchey 2003). However, there are other types of interactions that are both common and play an essential role in the preservation – or disruption – of ecosystem processes and services, and yet are not directly linked to the range of traits present in the local community. Major examples are interactions involving keystone species (Power et al. 1996), interactions involving ecosystem engineers (Jones et al. 1994), and indirect interactions (Box 7.2). 'Ecological surprises' in which the removal or introduction of species has triggered dramatic changes in ecosystem processes and services, often with very high cultural and economic costs, usually involve one or more of these types of interactions (see Díaz et al. 2005 for review and examples of 'ecological surprises'). In all these cases, changes in ecosystem processes and services, and feedbacks to global change drivers, are not easily predictable from species richness or from any of FD components (i.e., neither from the kind, or the relative abundance, or the range of traits present). The functional *identity* (*kind* of traits) of the introduced or removed species is of prime importance in determining these unexpected (and often negative) ecosystem-level impacts. Unlike in the mass-ratio hypothesis however, there is no easy a priori link between the traits of the species in question and putative ecosystem processes or feedbacks onto global change drivers. This represents one of the toughest challenges to the FD approach, and an extremely promising venue for new research.

7.4 Summary and Conclusions

Functional diversity (FD) comprises the *kind*, *range*, and *relative abundance* of functional traits present in a given community. Major global change drivers, including changes in climate, atmospheric composition, land-use/disturbance regime, and biotic exchanges, affect and are affected by FD in a non-random, and often predictable way. There is overwhelming evidence that the *kind* of traits that are present in higher abundance are major drivers of short-term ecosystem processes and their feedbacks onto global change drivers. Both the response of plant traits to environmental filters and their effects on biogeochemical and biophysical ecosystem processes (including simple, direct interactions with herbivores and decomposers) can be predicted with acceptable accuracy, although present theory cannot account for the mutually-neutralizing or synergistic effects of combinations of traits.

The role of the *range* of traits in influencing ecosystem functioning by resource use complementarity and facilitation is less clear, and fewer empirical examples are available, although both theory and some experimental evidence suggest that the role of subordinate species is important in maintaining long-term stability. Finally, there are other biodiversity-related effects, which are the result of indirect interactions, and/or interactions involving keystone species and/or ecosystem engineers, that cannot be predicted on the basis of the kind, range or relative abundance of traits, and remain a major challenge for the FD approach.

Non-linearities that are triggered by changes in climate, land-use regime and/or biotic interactions that involve altered FD, and in turn affect global change drivers and ecosystem services, represent a major threat to the integrity of the life-support systems. There is therefore an urgent need for more theoretical and empirical studies that would lead to better understanding and anticipating their consequences.

The quantification of functional diversity is not free from difficulties, and it is certainly less straightforward than counting the number of species, at least in areas with well-described floras. However, it provides a much stronger insight into the links between community structure, ecosystem functioning, and global change drivers and ecosystem functioning than does the consideration of species richness alone. Major venues for future research in FD are (1) the identification of those functional traits or functional trait combinations that are more likely to trigger ecosystem and landscape-level non-linearities; (2) continued efforts to measure functional traits under a wide range of biomes and regions, following standardized lists and protocols (see Lavorel et al. 2007, Chap. 13 of this volume); (3) more empirical investigation on how important are the roles of resource use complementarity and facilitation in determining ecosystem functioning under different degrees of environmental filtering; (4) more empirical and theoretical work on how FD effects on ecosystem processes translate into changes in global change drivers and ecosystem services; and (5) the design of easily-workable FD indices that could be applied to a wide range of natural situations, and thus broaden the possibilities of empirically testing the functional role of biodiversity.

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Chapter 8

Linking Plant Invasions to Global Environmental Change

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8.1 Introduction

Biotic invasions have been recognized as an important element of global change (Vitousek 1994). Introductions of alien species into novel habitats have increased in tandem with travel and international trade (McNeely 2001). Many species have been introduced accidentally (e.g., in water ballast, in soil, or as crop seed "contaminants"), but some have been intentionally introduced as ornamentals, food, or fiber products.

The introduction of alien species can have many ecological impacts, and contribute to the homogenization of biological systems worldwide (Lockwood and McKinney 2001). Biotic invasions, along with alterations in land-use patterns and disturbance regimes, are among the major causes of biodiversity loss worldwide (Soulé 1991). In cases where alien species have quantitative or qualitative trait differences from native species, invasions can also alter ecosystem processes such as nutrient cycling dynamics and disturbance regimes (Vitousek et al. 1987; D'Antonio and Vitousek 1992; D'Antonio and Corbin 2003; Levine et al. 2003). There are some well known cases of devastating effects of invasive plants on ecosystems such as the invasion of annual grasses in western U.S. (Mack 1981) or the invasion of pines in South-African shrublands (Le Maitre et al. 1996). These dramatic invasions emphasize that invaders often parallel environmental changes that are taking place at the regional scale. Therefore, research on the links between invasions and environmental changes is urgent and timely.

Biotic invasions are capable of interacting with other anthropogenic changes in the environment to alter biodiversity and ecosystem processes in invaded habitats. For example, there is evidence from a variety of ecosystems that N inputs favor alien plant species (Huenneke et al. 1990; Vinton and Burke 1995; Maron and Connors 1996). Furthermore, land-use changes such as clearing for agriculture, road building (Gelbard and Belnap 2003), or alteration of disturbance regimes (Mack and D'Antonio 1998; D'Antonio et al. 1999) have been shown to facilitate plant invasions.

The aim of this chapter is to present evidence of the interactions between several components of global environmental change and plant invasions. We focus on the effects of increasing atmospheric CO_2 concentrations ($[CO_2]$), climate change, terrestrial eutrophication, and changes in land-use/cover on the distribution and performance of plant invasions. We focus on plant invasions because in terrestrial ecosystems plants interact most dramatically with environmental and landscape changes, often reverberating to higher tropic levels. We do not consider the interactions between changes in disturbance regimes "per se", such as wildfires and invasions, because they have been extensively reviewed elsewhere (Mack and D'Antonio 1998; D'Antonio et al. 1999).

8.2 Plant Invasions and Elevated CO_2

Atmospheric CO_2 concentration has increased ca. 35% since pre-industrial times, and is predicted to rise to double the preindustrial concentration by the end of this century. A great deal of research has shown that plant photosynthesis and growth are stimulated by elevated $[CO_2]$. Although invasive and native plant species responded similarly across a wide range of controlled-environment experiments, i.e., the average invasive species does not respond more strongly than the average native, several problematic invasive species are nonetheless strong responders (Dukes 2000). Indeed, recent research has highlighted several cases in which invasive species may be favored by the $[CO_2]$ increase (Moore 2004).

Results from several controlled-environment studies found growth of invasive species to be more strongly stimulated by elevated $[CO_2]$ than growth of native species that were either closely related or sympatric in the same habitat. The average E/A ratio (ratio of growth or final biomass at elevated/ambient $[CO_2]$) for an experimental doubling of $[CO_2]$ was 1.82 in non-native species vs. 1.28 in native species – 2.35 in the non-native vine *Lonicera japonica* vs. 1.40 in native sympatric vines (Sasek and Strain 1991); 1.56 in the non-native *Rhododendron ponticum* vs. 1.12 in native understory plants in a Swiss forest (Hättenschwiler and Körner 2003); and 1.54 in *Bromus tectorum* vs. 1.31 in native Great Basin grasses (Smith et al. 1987).

Most elevated [CO_2] research has examined responses of plants to projected future concentrations, but it is important to note that the present [CO_2] already represents a significant increase over pre-industrial times. Ziska (2003) found an average stimulation of biomass of six invasive species of 46% in response to a doubling of [CO_2]. However, the growth response among these species to the increase in [CO_2] during the 20th century (from ca. 280 to 370 μmol mol^{-1}, a 30% increase) was significantly higher, averaging 110%, and was much higher than in native species. This indicates that many plant invasions that have occurred in the 20th century have probably been stimulated by rising levels of [CO_2]. In addition to increased branching and leaf area, Ziska and colleagues also observed significantly higher pollen production in common ragweed (Ziska and Caulfied 2000) and higher spine production in Canada thistle (Ziska 2002), both in the past century and projected into the next century. This indicates that elevated [CO_2] may increase pollen counts from non-native weeds to the detriment of human health, and that weeds such as Canada thistle may become even more invasive at elevated [CO_2].

In a community context, Dukes (2002) found *Centaurea solstitialis* (yellow starthistle) to increase in biomass and seed production by ca. 70% in response to a doubling of [CO_2] in both monoculture and polyculture, whereas total biomass of the polyculture (made up primarily of native species) increased by less than 30%. This suggests a differential success of *Centaurea* in a community dominated by native species. Although the response of a species in a whole community is less straightforward than the response of individual pot-grown plants, the response of the monocultures and polycultures as a whole were similar in the Dukes (2002) experiment. In a similar vein, *Lonicera japonica* (Japanese honeysuckle, a C_3 vine) increased ANPP 2.9-fold and cover 2.2-fold at the Oak Ridge FACE site, whereas the total understory community did not show increased ANPP and only a 1.3-fold increase in cover (Belote et al. 2003).

At the Nevada Desert Free-air CO_2 Enrichment (FACE) Facility, an annual invasive grass (*Bromus madritensis* ssp. *rubens*; red brome) exhibited higher differential photosynthesis, productivity and seed production than native annuals at elevated CO_2 during an extremely wet (El Niño) year (Smith et al. 2000). *Bromus madritensis* is closely related to *B. tectorum* (cheatgrass), an annual Eurasian grass that has invaded most of the intermountain west of the U.S.A. (Mack 1981). *Bromus tectorum*, whose growth has also been shown to be differentially stimulated over native species at elevated [CO_2] (Smith et al. 1987), is well known to stimulate large grassland fires in this region (Knapp 1998), which in turn has converted large areas of diverse shrublands to annual grasslands (Young and Evans 1978). Similarly, the non-native *B. madritensis* has been shown to stimulate wildfires in the Mojave Desert (Brooks 1999), a region with no evolutionary history of wildfire on a recurring basis. This led Smith et al. (2000) to conclude that elevated [CO_2], through a differential stimulation of growth in *B. madritensis*, could potentially convert large areas of desert scrub to an alien-dominated annual grassland.

Why are invasive species more responsive to elevated [CO_2] than are natives in some of these recent studies? Three trends have been observed. First, there are potential plant architectural differences. Ziska (2003) examined the underpinnings of increased growth, namely the production of leaf area and net assimilation rate (NAR, a growth-related index of photosynthetic CO_2 assimilation) in six non-native species. Interestingly, increases in leaf area were consistently responsible for the stimulation of growth in these non-native species rather than increases in NAR. Similarly, Huxman and Smith (2001) found that elevated CO_2 stimulated growth of a Mojave Desert invasive grass much more than that of a native forb, even though both species had similar increases in photosynthesis. In a study of a non-native and native vines, Sasek and Strain (1991) observed that the differentially increased growth in the non-native vine at elevated [CO_2] was due to accelerated branching (up to 3-fold higher) that in turn resulted in a greater increase in leaf area. The precise mechanism for such a response is not presently known.

Second, there may be differences in plant construction cost between invasive and native plants. Several studies have shown invasive species to have lower construction costs than sympatric natives (Baruch and Goldstein 1999; Nagel and Griffin 2001), and elevated [CO_2] exacerbates this difference. In *Bromus madritensis*, plant construction cost is significantly lower at elevated [CO_2] than at ambient [CO_2], a response that was not observed in a native annual grass, *Vulpia octoflora* (Nagel et al. 2004). Lower construction cost allows *Bromus* seedlings to grow more quickly and assume larger size and greater seed rain than the native *Vulpia*, with *Bromus* exhibiting differentially greater growth than *Vulpia* at elevated [CO_2] (Table 8.1); this should give *Bromus* a strong competitive advantage during the short time window that soil resources are available in this desert ecosystem. Similar to *Bromus*, lower construction cost of the wetland macrophyte *Lythrum salicaria* (purple loosestrife) at elevated [CO_2] resulted in over a 200% increase in carbon fixation per unit of energy invested in leaf biomass, a much higher rate than in sympatric native species (Nagel and Griffin 2004). This dramatic increase in carbon assimilation efficiency occurred in *Lythrum* despite only modest increases in photosynthesis and no change in leaf respiration per unit leaf area.

Third, elevated [CO_2] may bring about changes in reproductive allocation, specifically investment of carbon and nitrogen in seeds. *Bromus madritensis* makes more seeds per unit carbon and nitrogen investment at elevated [CO_2] than in ambient [CO_2] (Huxman et al. 1998, 1999),

Table 8.1. Construction cost, relative growth rate (*RGR*), final plant biomass and total seed number in the native annual grass *Vulpia octoflora* and the invasive grass *Bromus madritensis* growing during a wet year at the Nevada Desert FACE Facility in the Mojave Desert. Elevated [CO_2] = 550 µmol mol^{-1}. Also included is the ratio of the invasive-to-native species (*I*/*N*) for each parameter at each [CO_2] (data are from Nagel et al. (2004))

Parameter	[CO_2]	*Vulpia octoflora*	*Bromus madritensis*	*I*/*N*
Construction cost (g g^{-1} d^{-1})	Ambient	1.95	1.75	0.9
	Elevated	1.78	1.55	0.87
RGR (g g^{-1} biomass d^{-1})	Ambient	0.054	0.068	1.26
	Elevated	0.062	0.108	1.74
Biomass (g)	Ambient	0.08	0.51	6.4
	Elevated	0.11	0.89	8.1
Seed number $plant^{-1}$	Ambient	128	231	1.8
	Elevated	226	533	2.36

thus significantly increasing their differential abundance in community seed rain (Smith et al. 2000).

Our current knowledge concerning the effects of elevated [CO_2] on invasive plant species has mainly focused on plant performance and plant ecophysiology. However, we are still poorly prepared to predict the consequences for communities and ecosystems. This is because most studies that have examined the effects of elevated [CO_2] on plants have been conducted on potted plants grown in glasshouses, a problem that has been alleviated in recent years by the advent of various technologies (e.g., FACE and Open-Top Chambers (OTC's)) that have allowed natural communities of plants to be continuously exposed to elevated [CO_2]. Additionally, relatively few studies have examined the CO_2 responses of invasive species grown in competition with the communities that they invade. Responses of individual species do not consistently predict the success of species grown in competition. Future research efforts need to prioritize (1) the mechanistic underpinnings for the differential success of invasive species to elevated [CO_2], and (2) responses of invasive species grown under "realistic" circumstances.

8.3 Plant Invasions and Climatic Change

As fossil fuel burning and tropical forest clearing increasingly change the composition of the atmosphere, the Earth's climate is expected to change in tandem (IPCC 2001). Model predictions suggest that the future climate will be warmer, and that precipitation patterns will change. Although the rate and extent of these changes will depend largely on future human actions, even the mildest of expected changes would likely lead to range shifts among plant and animal species, along with changes in plant and animal phenology (IPCC 2001). Indeed, many species are already responding to changes in temperatures and growing season lengths (Peñuelas et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Will some invasive plant species be favored by these climate changes? If so, which ones?

Clearly, invasive species whose native ranges are warmer than their introduced ranges would be at an advantage. Two mechanisms would favor these species: first, the species should withstand the increasingly hot extreme temperatures better than natives, and second, they should experience less mortality due to extreme cold events. Examples of the first mechanism can be found among the C_4 species. The higher optimum temperature for photosynthesis found in C_4 species would provide an advantage over C_3 plants in a warmer environment (Ehleringer et al. 1997). Increases in warm extremes could help native C_4 grasses invade C_3 grasslands in New Zealand (White et al. 2000, 2001). Patterson (1995) provided examples of several tropical and warm-temperate agricultural weeds that are likely to become more problematic in the United States as temperatures increase. In an example of the second mechanism, warming may already have benefited cold-sensitive (i.e., frost-sensitive) invasive plants in Swiss forests. There, as the frequency of frost return intervals has declined over the past century, the abundance and diversity of alien evergreen broadleaved species have increased (Walther 2002).

Species interactions may be as sensitive to changes in precipitation patterns as to warming. In regions where precipitation increases, ornamental species that had been restricted to gardens by water limitation could become more problematic. In western North America, a wetter climate could cause several invasive grasses to become denser, with negative consequences for native plant and animal species (Dukes and Mooney 1999). On the other hand, a drier climate in this same general region could increase the prevalence and impacts of shrubby *Tamarix* species that invade riparian zones (Zavaleta and Royval 2002).

Certain properties are likely to confer advantages under any type of climate change. These properties include the ability to tolerate a wide range of climates, the ability to shift ranges rapidly, and the lack of dependence on other organisms for pollination and seed dispersal. Invasive species tend to have all of these favorable properties (Dukes and Mooney 1999).

Several studies of herbaceous plants have shown that the native ranges of invasive species span greater latitudinal distances or geographic ranges than the native ranges of non-invasive species (Rejmánek 2000). While debate continues about the cause for this pattern, a consequence is that many successful invaders tolerate a wide range of climates, and should be relatively insensitive to climate shifts over most of their ranges. Malcolm et al. (2002) presented evidence that the rate at which climatic zones shift under projected warming may, in some locations, exceed maximum rates of plant migration observed in post-glacial time periods, which suggests that the most mobile species will be favored by rapid warming. Indeed, several traits favoring long-distance dispersal are commonly found in invasive species (Rejmánek 1996), suggesting that these species will be among the fastest to migrate to newly suitable habitats. Finally, the ranges of invasive species are rarely limited to the range in which coevolved pollinators or seed dispersers exist. In fact, invasive species seem particularly adept at forming new mutualisms (Richardson et al. 2000a). Therefore, while some native species may be disadvantaged if mutualistic relationships are disrupted by climate change, most invasive species will not.

A handful of case studies have examined how climate change could alter the success of particular invasive species by combining climate model predictions with inferred environmental constraints. Based on two future climate scenarios, Beerling et al. (1995) predicted northward shifts of the European range of *Fallopia japonica*, which is native to Asia. In both scenarios, the new potential distribution moved from central Europe into Scandinavia, and into Iceland. This model was purely based on climate suitability, and did not limit ranges based on soil types or interactions with currently established species. In a climate envelope exercise carried out by Richardson et al. (2000b), potential ranges of five of South Africa's more noxious invasive plants decreased to 63–92% of their starting range under a ~2 °C warming. In this analysis, plant ranges were restricted to suitable soil types. Kritikos et al. (2003a,b) predicted potential ranges of a tropical woody vine, *Cryptostegia grandiflora*, and a woody legume, *Acacia nilotica*, under several future climate scenarios. Although the two invaders had not yet filled their current potential ranges in Australia, the studies suggest both species' ranges would expand under warming, and especially with decreased drought stress.

8.4 Plant Invasions and Land Eutrophication

Though N is the most abundant component of the Earth's atmosphere, it is unavailable for most vegetation unless it is "fixed", or converted from inert atmospheric N_2 into other forms of N, through such processes as lightning or biological fixation. As a result, it is frequently the nutrient most limiting primary productivity in the temperate region (Vitousek and Howarth 1991). Human alteration of the N cycle, however, has increased the rate of N fixation to such an extent that human-derived N now exceeds natural processes (Vitousek et al. 1997). Today, ecosystems in eastern North America, northern Europe, and localized habitats downwind of large sources of N such as urban areas receive orders of magnitude more N in wet and dry deposition than they would receive from natural sources (Aber et al. 1989, 1998; Galloway et al. 1995, 2003; Fenn et al. 1998).

Increasing N inputs have had important consequences for species composition and diversity of plant communities (e.g., Kellner 1993; Wedin and Tilman 1996). A number of European communities have changed dramatically as a result of increased N deposition. For example, the diversity of vascular plants, bryophytes, and lichens has declined in British acid grasslands (Stevens et al. 2004) and Dutch chalk grasslands (Bobbink 1991) as a result of decades of increased N inputs. Species composition has also shifted toward species characteristic of N-rich habitats in forests in France (Thimonier et al. 1992), the Netherlands (van Breemen and van Dijk 1988; DeVries et al. 1995), and Sweden, Norway and Finland (Falkengren-Grerup 1986; Hogbom and Hogberg 1991; Rosen et al. 1992).

Against the general background of changes in species composition and diversity following atmospheric N deposition, increased availability of N may facilitate the establishment and success of alien species (Jefferies and Maron 1997; Fenn et al. 2003b). Enhancement of N availability has been shown to favor establishment and success of fast-growing invasive species in a variety of habitats (e.g., Huenneke et al. 1990; Vinton and Burke 1995; Maron and Connors 1996). Therefore, the potential impact of N deposition would be expected to be greatest in relatively infertile habitats, by permitting the invasion of species characteristic of high-N conditions into formerly low- or moderate-N habitats.

The role of elevated N inputs in facilitating species invasions has been shown most clearly in infertile desert, grassland, and shrubland habitats of western and southwestern North America. Urban centers in the Southwest, including Phoenix and Tucson, AZ, Las Vegas, NV, and Los Angeles, CA have contributed to N deposition rates as high as 29 kg ha^{-1} yr^{-1} (Fenn et al. 2003a). Alien annual grasses, such as *Bromus madritensis* ssp. *rubens* and *Schismus* spp., and an alien forb, *Erodium cicutarium,* have invaded *Larrea tridentata* (Creosote bush) shrublands in the Mojave and Sonoran deserts. Brooks (2003) found that N and NPK fertilization (32 kg N ha^{-1} yr^{-1}) increased dominance of alien species in the Mojave Desert. While alien biomass increased in fertilized plots by 52–56% relative to controls, the density, biomass and diversity of native annual species decreased in fertilized plots. In contrast, fertilization (10 kg N ha^{-1} yr^{-1}) of a Mojave Desert annual plant community before the invasion of the alien grasses and forbs led to an increase in the biomass of native annual species (Romney et al. 1978). Brooks (2003) hypothesized that increased competition with alien species for soil water and other nutrients led to the decline in native species. Thus, native desert annuals are apparently able to take advantage of N inputs when aliens are scarce, but not when aliens are abundant (Brooks 2003).

Alien annual grasses have also invaded coastal sage scrub communities and serpentine grasslands in California. The increasing abundance of grass species such as *Avena* spp., *Bromus* spp., and *Vulpia* spp. in southern California coastal sage scrub ecosystems has coincided with increasing N deposition rates to >45 kg N ha^{-1} yr^{-1} (Allen 2003). In order to tie grass invasion to N inputs, Allen (2003) added N (60 kg N ha^{-1} yr^{-1} for 10 years) to a shrubland receiving low deposition rates. Annual grasses responded positively to N fertilization, though there was no effect on shrub growth or mortality, suggesting that changes in shrub cover requires many years to take place. The invasion of annual grasses such as *Lolium multiflorum*, *Avena* spp., and *Bromus mollis* into serpentine grasslands in the San Francisco Bay Area has also coincided with elevated N deposition (>10–15 kg N ha^{-1} yr^{-1}) (Huenneke et al. 1990; Weiss 1999). Serpentine soils in California have served as refuges for native grass and forb species because their low levels of N, P and K, coupled with high Mg/Ca ratios and high heavy metal content, have historically acted as barriers to alien species invasions (Murphy and Ehrlich 1989). Responses of serpentine vegetation to experimental N fertilization indicate that increasing N inputs are a driving factor in the invasion (Huenneke et al. 1990). Without active management to reduce the competitive effects of fast-growing alien species, native grasses and annual forbs, including rare serpentine endemics, may be lost from these communities with cascading effects to other trophic levels (Weiss 1999).

Elevated atmospheric N deposition may also increase the susceptibility and/or impacts of introduced pathogens or disease in forests (Brown 1995; Bobbink et al. 1998; Throop and Lerdau 2004). In eastern North America, introduced pests and pathogens such as the gypsy moth (*Lymantria dispar*), beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.) and the hemlock woolly adelgid (*Adelges tsugae*) have had substantial impacts on the community composition and ecosystem functioning of forests (Liebhold et al. 1995; Jenkins et al. 1999). The role that N inputs play in these invasions is not well-established, but there are indications that elevated foliar and bark N concentrations in trees experiencing N deposition have led to increased susceptibility to attack (Latty et al. 2003). Future research should consider the interactions between atmospheric N deposition, pathogen invasion and forest health.

8.5 Plant Invasions and Changes in Land Use/Cover

Man-induced transformation of natural systems is leading to a major biodiversity crisis in recent times (Vane-Wright et al. 1991; Reynolds et al. 2007, Chap. 8 of this volume). In the last century, land transformations have been extensive, rapid, and in most cases irreversible. Changes in land-use/cover (LUC hereafter) can be defined as land transformations from one ecosystem "state" to another in terms of ecosystem structure, composition and function (Hobbs 2000). Because plant invasions occur across landscapes, their dispersal and spread depends on landscape structure and dynamics (With 2002). For this reason, it is surprising that few studies have examined interactions between invasion patterns and changes in LUC.

There is a general presumption among ecologists and managers that changes in LUC directly increase biological invasions. Human population density has been used as a surrogate of LUC transformation, and it has been shown that there is a positive relationship between human population density and regional plant species density (Vilà and Pujadas 2001) or frequency distribution of species (Pysek et al. 1998). Moreover, observational analyses of the current relationship between invasions and LUC types almost always conclude that the most invaded habitats are the ones which directly or indirectly suffer major environmental fluctuations or changes and/or are "less natural" (e.g., urban, agricultural). Although these approaches support the notion that changes in LUC are drivers of invasion, we should emphasize that changes in LUC include a broad range of ecosystem degradation and ecosystem recovery changes (Hobbs 2000; Reynolds et al. 2007, Chap. 20 of this volume). Therefore, land transformation does not necessarily have a sole directional effect on plant invasions. Furthermore, differences in the distribution or abundance of an alien plant within a LUC type are not amenable to the static analysis of contemporary LUC if differences are due to differences in LUC history. For example, in Catalonia (NE Spain), shrublands and woodlands invaded by prickly-pear cacti, *Opuntia* spp., are the ones that were croplands 30 years ago (Vilà et al. 2003).

There are two main reasons why, in general, changes in LUC can influence invasions. First, LUC changes are frequently accompanied by disturbances. Disturbances are unanimously acknowledged to favor plant invasions because they provide "open windows" to the entrance of propagules and better conditions (i.e., more light, space and nutrients per capita) for seedling establishment and growth (Hobbs and Huenneke 1992). Regional surveys and flora screening for alien species often find higher alien species richness in altered ecosystems (e.g., ruderal and anthropogenic ecosystems) than in unaltered ones (e.g., forests, shrublands). For example, edges of highly used roads enhance dispersal and increase light levels and disturbance, which promote establishment of alien herbs (Parendes and Jones 2000).

Second, changes in LUC include modifications in landscape composition and structure, such as fragmentation, which increases the length of edges and the prevalence of corridors that can facilitate invasions. There is clear evidence that fragmentation creates more edge, which facilitates the spread of invasive species to habitat remnants within a man-modified land matrix. For example, in Quebec (Canada), forest fragments surrounded by agricultural fields that have been intensively farmed with the use of commercial fertilizers and herbicides contain a higher percentage of alien weeds than forests surrounded by low intensity farms (Boutin and Jobin 1998). In the same way, transportation corridors increase the spread and the opportunity of establishment of alien plants. In European countries, the density of alien plant species is positively correlated to the length of transport networks (Vilà and Pujadas 2001). The influence of transportation corridors on invasions is positively related to their improvement and frequency of use. For instance, in Utah there is higher cover and richness of alien plant species in semiarid grasslands and woodlands adjacent to paved roads than in graded or 4WD tracks (Gelbard and Belnap 2003). Likewise, in Glacier National Park (Montana-US), grasslands adjacent to primary and secondary roads have higher species richness than along back trails (Tyser and Worley 1992).

To properly test if changes in LUC directly increase invasions, we must relate spatially and temporally explicit knowledge of LUC changes to the presence, abundance and population performance of alien species. We propose the following LUC attributes as land transformation parameters for analysis: direction, intensity, number of stages and number of stage types (Table 8.2). Direction refers to the trajectory of the change, which can be to a more degraded or to a more recovered or restored state than the initial LUC; intensity means the magnitude of the change; number of stages means the number of steps analysed in the whole time series and; finally, the number of stage types refer to the identities of the LUC types that have characterized a given location through time. We expect invasions to be more frequent where the direction of LUC changes leads to greater degradation, where intensity is higher, and where more types of LUC changes have taken place. For example, we might expect higher abundance and diversity of alien species in oldfields than in mature woodland, in areas where the LUC changes have been large in extent or very extreme, and where repeated LUC changes have offered multiple openings for invasion to occur. To our knowledge, there are very few studies aimed to test this hypothesis. A positive relationship between intense habitat degradation over the last 50 years and high diversity of alien plants has been observed in several wetland and dune communities around the Mediterranean Basin (Pino et al. 2006).

Overall, despite the wide interest in biological invasions at a variety of scales, studies exploring invasion patterns and their main landscape correlates from a geographically explicit point of view are scarce. Moreover, interactions among plant invasions and the type, magnitude, trajectory, and direction of landscape changes remain to be explored.

8.6 Multiple Interactions

Most research on the effects of global environmental changes on biological invasions has examined effects of single environmental factors. Although different elements of global change act at different spatial scales, and their impacts are different depending on the biome considered, environmental changes interact in complex ways, complicating predictions of ecosystem responses (Norby et al. 2007, Chap. 3 of this volume). For example, the success of broad-leaved alien trees in Switzerland can be related to both recent climate shifts and elevated atmospheric [CO_2] (Hättenschwiler and Körner 2003).

Ongoing changes on land and in the atmosphere decrease our capacity to predict which introduced species are most likely to become invaders and which ecosystems are most vulnerable to invasion. To overcome this uncertainty, regional-scale studies from a geographically explicit point of view appear to be relevant to identify invasion hot spots and to compare the relative role of climatic, edaphic, landscape and socioeconomic factors on invasion patterns. Preliminary studies in Catalonia, a high diversity ecosystem region of 32 000 km^2 in NE Spain, point out that mean annual temperature influences plant invader diversity, which is also favoured by landscape diversity and regional disturbances (Pino et al. 2005). Ecological niche modeling, a technique in which georeferenced occurrences of alien species are linked to geographically explicit environmental datasets (Peterson

Table 8.2.
Proposed attributes of changes in land-use/cover (LUC) and their influence on plant invasions. *S* represents stages of LUC changing thought time from more (S_0) to less natural (S_n)

LUC attributes	Increasing invasion scenario		Decreasing invasion scenario	
Direction	Degradation:	($S_0 \rightarrow S_n$)	Restoration:	($S_n \rightarrow S_0$)
Intensity	More intense:	($S_0 \rightarrow S_n$)	Less intense:	($S_0 \rightarrow S_{n-1}$)
Number of stages	3 stages:	($S_0 \rightarrow S_{n-1} \rightarrow S_n$)	2 stages:	($S_0 \rightarrow S_n$)
Number of stage types	3 stage types:	($S_0 \rightarrow S_{n-1} \rightarrow S_n$)	2 stage types:	($S_0 \rightarrow S_{n-1} \rightarrow S_0$)

et al. 2003), is another recent, reliable approach used to predict the potential distribution of invasions on a species-by-species basis. In essence, the ecological niches are modeled by combining occurrence points and environmental information of species in their native distribution area using a selected set of environmental datasets and diverse algorithms. These models are then projected onto potential receptor areas to identify geographic regions showing ecological conditions inside and outside of the species' niche. A number of recent examples including vertebrates, plants, and insects are available in the literature (Peterson and Vieglais 2001; Peterson et al. 2003; Roura-Pascual et al. 2004). Both approaches offer the hope that realistic predictions of future plant invasion patterns are possible.

Moreover, as changes in land-use cause vegetation changes and alter ecosystem biogeochemistry (Jackson et al. 2007, Chap. 19 of this volume; Reynolds et al. 2007, Chap. 20 of this volume), plant invasions transform vegetation structure, and can directly or indirectly affect ecosystem functioning (Ehrenfeld 2003; Levine et al. 2003), and consequently can exacerbate changes in land-use or environmental changes. Research on the feedbacks of plant invasions on environmental change has been scarce, and has mainly focused on how certain fire prone invasive plant species increase fire risk (D'Antonio et al. 1999), or whether invaders that expand their populations in tandem with land degradation limit restoration efforts back to former community composition (Corbin and D'Antonio 2004). There are many research areas which deserve greater attention. For example, it remains to be explored if plant invaders, responding with fast growth and high fitness to elevated [CO_2] and N deposition, increase soil respiration and N availability. Factorial field experiments comparing the responses of native and alien species to multiple environmental changes could provide answers to these questions.

8.7 Summary and Conclusions

Invasion by alien species is one of the most conspicuous human driven ecological changes, often with undesirable effects on biodiversity and ecosystem functioning. However, few studies have addressed how environmental change (i.e., elevated [CO_2], climate change, N deposition and changes in LUC) can influence the success of plant invaders, invasion impacts and feedbacks. Because global change components are interacting in multiple ways, increasing the uncertainty of species and ecosystem responses (Norby et al. 2007, Chap. 3 of this volume), there is an urgent need to increase research in this area.

While studies of invasive species' responses to elevated [CO_2] have mainly focused on ecophysiology and growth, studies examining responses to changes in climate, N deposition and land-use have examined patterns of plant distribution and abundance in the context of community structure. When comparing invasive with closely related or coexisting native species, the invasives often perform better than the natives or the alien but non-invasives. The mechanisms through which aspects of global change benefit invasive species and harm native species have begun to be explored. A particularly promising direction is to consider whether specific life-history traits, such as those that confer fast growth, broad ecological niches, high seed production or long-distance dispersal, offer hope in the development of predictions of future invasions (Grotkopp et al. 2002). We suggest that the exploration of plant invasions in the context of plant functional types (Lavorel et al. 2007, Chap. 13 of this volume) deserves further consideration. We also propose that exploring the multifactor effects of global change on plant invaders would increase our predictive power on habitat vulnerability to invasion.

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Chapter 9

Plant Biodiversity and Responses to Elevated Carbon Dioxide

Catherine Potvin · F. Stuart Chapin III · Andrew Gonzalez · Paul Leadley · Peter Reich · Jacques Roy

9.1 Ten Years of GCTE Research: Apprehending Complexity

The general assumption, in the first phase of elevated carbon dioxide (CO_2) research, was that increasing atmospheric CO_2 concentration would act as a fertilizer for plant systems. Under this "large-plant-scenario" (Fig. 9.1), increased photosynthesis at elevated CO_2 would lead to higher plant biomass which would induce a negative atmospheric feedback loop that would offset anthropogenic carbon (C) emissions.

A second general assumption in early research was that the effects of elevated CO_2 on plant community structure could be predicated using a C-based perspective with clear "winners" and "losers" based on species' ability to take advantage of the increased atmospheric CO_2 concentration (e.g., plant with C_3 vs. C_4 photosynthetic pathways). The reality unveiled by a decade of research proved more complex and the "large plant scenario" largely untenable.

9.1.1 Effects of CO_2 on Plant Diversity Through Alterations of the Physical Environment

A large number of studies on plants growing in pots, monoliths and *in situ*, now yield a broad perspective of responses to elevated CO_2 (e.g., Bazzaz 1990; Poorter 1993; Körner 2001; Navas 1998; Woodward 2002; Poorter and Navas 2003). Reviews have used meta-analysis to identify statistically significant trends (Curtis and Wang 1998; Wand et al. 1999; Kerstiens 2001). Pot studies have generally confirmed the C-based perspective of the differential response of functional groups of plant species to elevated CO_2: plants with the C_3 photosynthetic pathway generally respond more that C_4 plants (due to greater stimulation of net C fixation), fast-growing plants more than slow-growing plants (due to stronger C sinks), and N-fixing plants more than non-fixers (because the high C cost of N fixation is overcome). However, an important revelation of *in situ* experiments, both within and outside of the GCTE network, is that this C-based perspective gives an incomplete understanding of how plants respond to elevated CO_2 in multi-species communities. Apparently C-based functional groupings of plant response to CO_2 break down (Poorter and Navas 2003) while the effects of CO_2 on ecosystem water balance and nutrient cycling often play a larger role on plant community structure than previously suspected (Fig. 9.1).

Elevated CO_2 can modify soil nutrient availability, nutrient uptake capacity, and nutrient use efficiency (Bassirirad et al. 1996; Hungate 1999; Körner 2001) all of which are likely to modify plant community structure in

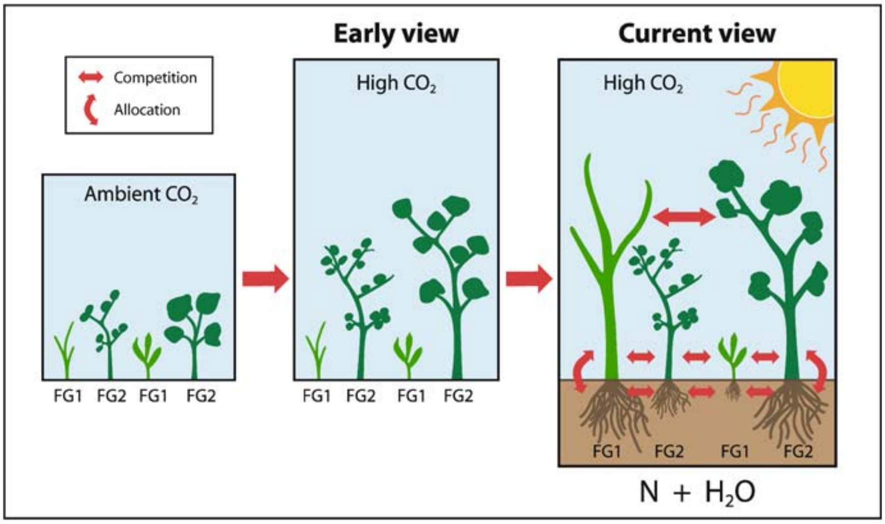

Fig. 9.1. Simple cartoon illustrating the early and current views of the effect of elevated CO_2 on plant ecosystems. Current knowledge suggest that elevated CO_2 is likely to affect, minimally, photosynthetic carbon uptake, plant growth and allocation, N and water uptake leading to differential above- and belowground competition. Moreover response to elevated CO_2 is not consistent within functional groups. Here *FG1* and *FG2* refer to two hypothetic functional groups

nutrient limited ecosystems. Yet, the effects of CO_2 on plant community structure acting indirectly through nutrient availability are poorly studied. On the other hand, several studies indicate that soil water status is often key in determining species-specific responses to elevated CO_2 *in situ* (e.g., Owensby et al. 1993; Volk et al. 2000; Morgan et al. 2004), although there are also a number of studies where this is not the case (e.g., Arp et al. 1993; Zavaleta et al. 2003a,b; Nowak et al. 2004). The effects of CO_2 on soil water balance may help explain why many of the expected direct CO_2 effects on diversity, such as the encroachment of C_3 woody plants into C_4 savannas (Walker 2001) or the increase in competitive ability of C_3 species compared to C_4 species in grasslands, are not consistently observed (Morgan et al. 2004). Species-specific responses in calcareous grasslands may also largely depend on CO_2 effects on water balance. In study of CO_2 effects on calcareous grassland, Leadley et al. (1999) found that *Carex flacca* had a greater growth response to elevated CO_2 than the dominant grass *Bromus erectus*. Volk et al. (2000) provided compelling evidence that the large differences in response of *Carex* and *Bromus* to elevated CO_2 may be explained by the effects of elevated CO_2 on soil water content. More generally, Stocklin and Körner (1999) identified the functional group of mesophytic species as the most responsive to increased CO_2 in monoliths of these calcareous grassland communities. Apparently, reductions in stomatal conductance at elevated CO_2 that lead to modifications in soil water status can play a key role altering plant community structure.

Climate apparently also modulates community responses to elevated CO_2. Roy and collaborators (unpublished) compared the CO_2 response of Mediterranean annual herbaceous species over several growing seasons. Their experiment documented large inter-annual variability in the response of individual species to CO_2. The response of most annual species to elevated CO_2 switched from being highly negative in some years to being highly positive in other years. For example, in the community composed of 2 grasses, 2 composites and 2 legumes, the biomass response of the annual grass *Bromus madritensis* (Fig. 9.2) changed from a 70% reduction to a 300% increase depending on the years. Because the planting was repeated similarly every year for 5 years in greenhouses tracking outside temperature and precipitation, the results suggest that climatic conditions might drive the outcome of this elevated CO_2 experiment. Similarly, the presence of an interaction between climatic variability and response to CO_2 for perennial herbaceous communities was reported by Owensby et al. (1996) for a Kansas tallgrass prairie. On wet years, there was no significant biomass response to CO_2, while on dry years, the C_4 species *Andropogon gerardii* was stimulated and drove a positive community biomass response.

Roy (unpublished) further noted that CO_2 interacted with the diversity level of the community: year to year variability was less in the communities with the higher number of species. Several experiments both in the field and in microcosms suggest that increasing diversity increases the stability of ecosystem properties (Hooper et al. 2005). Tilman and Downing (1994) reported for example that, in the Minnesota grassland, plots with a high diversity resisted drought better then plots with low diversity. An issue that remains largely unanswered is the extent to which elevated CO_2 and diversity would interact to either increase or decrease the stability of eco-

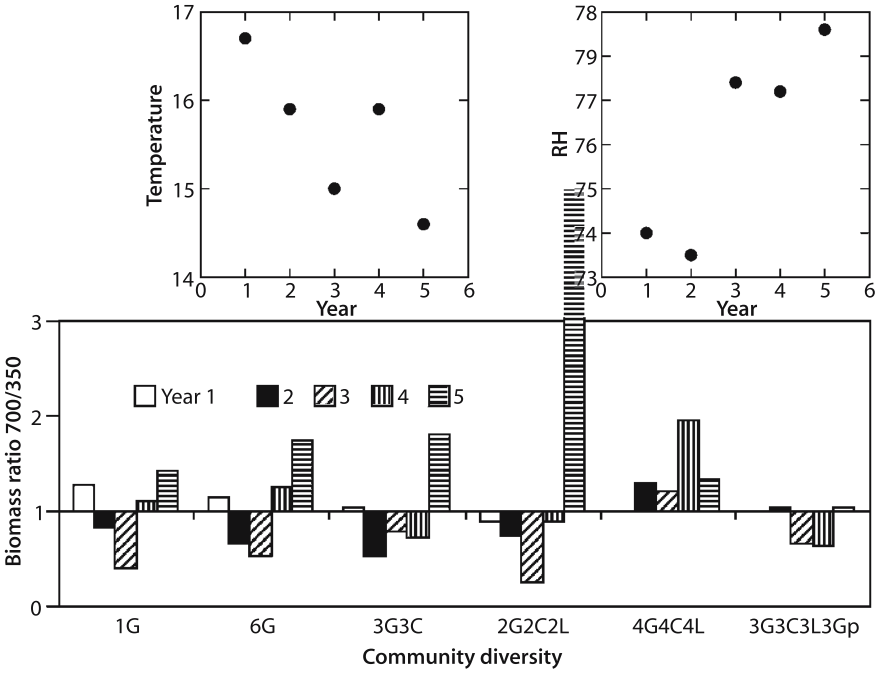

Fig. 9.2.
CO_2 response of the annual grass *Bromus madritensis* (total aboveground biomass at senescence) when grown for 5 successive years in communities of various complexity established by planting young seedlings of annual or perenial grasses, composites and legumes in a predefined pattern (annual grasses: *G*, composites: *C*, legumes: *L*, perennial grasses: *Gp*). Each *bar* is the average of one to four 0.5 m^2 model ecosystems at each CO_2 level, with 360 to 30 individuals of *B. madritensis* per model ecosystem depending on diversity level. Two greenhouses were run at 350 µmol CO_2 mol^{-1} and two at 700 µmol CO_2 mol^{-1}. Average annual temperature and relative humidity in the greenhouses for the five years of the experiment are given in the *small panels* above the main figure

system properties. Clearly responses to elevated CO_2 are modulated by climate, water and nutrient availability with different feedback loops:

- Changes in atmospheric CO_2 alter the relative availability of resources (C, water, and nutrients), which in turn alters competitive interactions among plants potentially leading to changes in diversity or dominance patterns.
- Environmental variability affects species-specific responses to elevated CO_2 while community diversity and composition in turn influences both the inter-annual variability and the direction of the response to elevated CO_2.

9.2 Temporal Variation and Response to Elevated CO_2

9.2.1 Reproductive and Evolutionary Aspects of the Response to Elevated CO_2

Adding to complexity, researchers recognized that the response of vegetative biomass to elevated CO_2 is not sufficient to understand long-term community responses. CO_2 induced differences in number and quality of seeds should have strong impact on the diversity of plant communities over the long-term. In a meta-analysis covering 79 species, Jablonski et al. (2002) reported a stimulation of the number of reproductive organs or their weight by about 20%. Crop species were more responsive (+25%) than wild species (+4%) despite a similar stimulation of vegetative biomass. Variability is very high between genera (–26% in *Ipomea* sp to +30% in *Brassica* sp.) as well as within genera (from +2% to +60% in *Raphanus* sp.). Individual seed size was marginally increased but seed nitrogen content was reduced by about 14% in both wild species and crops. In a single experiment in the field with 17 species, Thürig et al. (2003) found a significant increase in the number of flowering shoots (+24%) and seeds (+29%) with very large responses in some species (flowering shoot +236% in *Trifolium pratense* and +1 000% in *Carex flacca*). In perhaps the first field experiment to compare tree species reproductive output, Stiling et al. (2004) found a four-fold increase in acorn density for two oak species and no change in the third one.

Furthermore, rising atmospheric CO_2 concentrations may alter the genetic structure of plant populations through directional selection; i.e., within a population, those individuals that have the greatest response to CO_2 in terms of growth and reproduction will tend to exclude those individuals of the same species with weaker responses. If such evolutionary responses occur responses of plant species observed in short-term experiments may not be representative of the response of plants to long-term, slowly rising atmospheric CO_2 concentrations. Several studies have demonstrated genetic variation in responses to CO_2 concentration (Wang et al. 1994; Stewart and Potvin 1996; Schmid et al. 1996; Roumet et al. 2002; Spinnler et al. 2003; Mohan et al. 2004; Bidart-Bouzat 2004; Ward and Kelly 2004) suggesting that elevated CO_2 may drive rapid directional selection. However only a few studies experimentally tested the evolutionary responses to controlled selection under various CO_2 levels. *Brassicae juncea* did not show genetic adaptation to a combined CO_2 and temperature increase, possibly due to inbreeding depression in a stressful environment (Potvin and Toussignant 1996). Derner et al. (2004) found that the increase in CO_2 responsiveness from the first to the third generation of wheat was not driven by genetic changes but by CO_2-induced changes in seed quality. Andalo et al. (1996) reported a decrease in seed germination of *Arabidopsis thaliana* when grown in two successive generations under elevated CO_2. Ward et al. (2000), also on *A. thaliana*, is the only report of a selective effect of CO_2 but genetic adaptation was found only under selection at low Pleistocene-like CO_2 concentration. Evolutionary responses at elevated CO_2 resulted in a shortened life cycle that did not allow for increased biomass accumulation. It appears that:

- Variations in the response of growth, allocation, phenology, or ontogeny (Kinugasa et al. 2003; Ward et al. 2000; LaDeau and Clark 2001) can explain the observed large interspecific differences in reproductive responses.
- In principle, it is critical to incorporate the effects of evolutionary processes in our predictions of ecosystems responses to global change (Ward and Kelly 2004). However, too few studies exist to give us a clear idea of the evolutionary potential in the face of elevated CO_2.

9.2.2 Communities at Equilibrium Versus Dynamic Systems

Community dynamics also has to be taken into account to determine whole systems response to elevated CO_2. Changes in the relative contribution of individual species under elevated CO_2 could alter community production with consequent changes in community composition (Körner 2001; Potvin and Vasseur 1997; Reynolds et al. 2001; Chapin et al. 2000). Several experiments have focused on understanding the impact of elevated CO_2 on community composition. We use three long-term CO_2 enrichment studies conducted on grasslands to illustrate this point: the calcaeous grassland experiment of Switzerland (Leadley et al. 1999; Niklaus and Körner 2004), the grazed pasture of Southern Québec, Canada (Potvin and Vasseur 1997; Vasseur and Potvin 1997) and the annual grassland of the Jasper Ridge Biological Preserve in California (Zavaleta et al. 2003a,b). Floristically the richest of those grassland sites was the Swiss grassland with a total of 70 vascular species (Leadley et al. 1999), followed by the Californian site with a total of 43 species (Zavaleta et al. 2003a) then the Québec site with about 10 species (Potvin and Vasseur 1997). CO_2 enrichment lasted six years in Switzerland, five years in Québec while Zavaleta et al. (2003a,b) reported three years of CO_2 enrichment. These three experiments provide a unique opportunity to examine the extent to which elevated CO_2 might alter species composition with a possible feed-back loop on community biomass accumulation.

In the Swiss grassland, the number of species present in the plots increased through time, 1996 vs. 1999, but exposure to elevated CO_2 had no significant effect on species richness. In contrast elevated CO_2 significantly enhanced evenness estimated as the modified Hill ratio E^* (Niklaus and Körner 2004). At the same time, community productivity increased under elevated CO_2 and the increase in aboveground biomass could be predicted by precipitation. The highest biomass enhancement was observed after five years of enrichment (+31%) and the effect seemed to decrease thereafter (+18% enhancement on year 6). At the Québec field site, between 1992 and 1996, total species number was reduced by 10% under elevated CO_2, 47% in the ambient open-tops and 31% in the control plots (Potvin unpublished). Through time evenness, measured as Simpson's index, decreased under ambient CO_2 while it increased under elevated CO_2 (Potvin and Vasseur 1997). Destructive harvest, carried-out at the end of the five years of CO_2 enrichment, showed that biomass accumulation was not statistically different between the high (360 g m^{-2} ±125) and the ambient (486 g m^{-2} ±152) open-tops nor the control plots (435 g m^{-2} ±118) (Potvin unpublished). Three years of elevated CO_2 over California grassland led to a reduction in species number of 8% (Zavaleta et al. 2003a) however no information was given on evenness. The Californian study examined the effect of N deposition, precipitation and warming on diversity. Interestingly the effect of these different global change drivers on diversity was purely additive. The two enrichments (N and CO_2) reduced diversity, while precipitation increased diversity and warming had no effect. Norby et al. (2007, Chap. 3 of this volume) provides an exhaustive analysis of the results from the Jasper Ridge Global Change Experiment (JRGCE). In the JRGCE, elevated CO_2 led to increased plant biomass when acting alone but to a reduction in NPP when applied in conjunction with other global change drivers: temperature, N deposition and precipitation.

Together these results suggest that elevated CO_2 will elicit changes in biodiversity, whether negative or positive, and that these changes may or may not be associated with changes in community biomass. This observation is supported by other studies. An experiment combining elevated CO_2 with sward management of temperate grassland monoliths (Teyssonneyre et al. 2002) showed that cutting frequency modified the biodiversity response of the monoliths. At low cutting frequency the decline in species diversity was partly alleviated by elevated CO_2, a result with much resemblance to the Québec experiment. Furthermore, elevated CO_2 may interact with a number of other components of global change including N deposition, changes in precipitation, and temperature. CO_2 is thought to stimulate production and C storage primarily in areas of nitrogen deposition (Schimel 1995; Nadelhoffer et al. 1999). In these nutrient-rich environments, enhanced productivity is often associated with reduced species diversity (Tilman and Downing 1994). However, in the JRGCE, Zaveletta et al. (2003a,b) found no interactions between CO_2, N, precipitation and temperature on plant diversity. The diversity responses of any combination of treatments could be predicted from the sum of the responses to individual treatments. Additive responses of this type would make prediction of CO_2 responses in the future much more tractable, but additional multifactor experiments will be essential for testing the generality of this pattern.

The three field experiments discussed above differ fundamentally from those using growth chambers, in which a fixed set of species is exposed to elevated CO_2, because the communities under study were moving targets where species richness, identity and dominance were

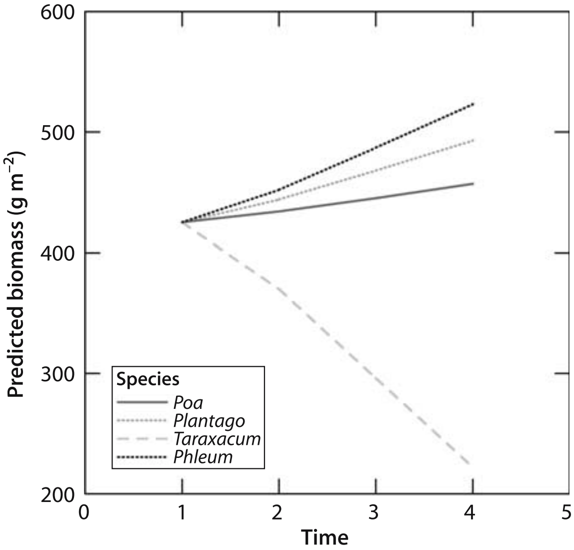

Fig. 9.3. Predicted changes in community biomass due to changes in dominance and identity of dominant species for the Québec experiment. The model assumes an arbitrary time scale leading to changes in dominance in the community. Predicted biomass was calculated as $PB = S_a b_a + S_b (b_i + b_j + b_k)$ where S_a is the area occupied by the dominant species, S_b is the area occupied by each of the other species, b_a is the biomass per area of the dominant species and b_{i-k} the biomass per area of the three companion species. At time 1, community biomass was modeled for even stands where Simpson's index, $D = 4$. Dominance increased through time to a maximum, $D = 1.53$, when 80% of the area was occupied by a single species. The model was run four times with either *Phleum pratense*, *Plantago major*, *Taraxacum officinale*, or *Poa pratensis* as dominant species. The scenario in which *Poa* becomes dominant is analog to observations from the Québec elevated CO_2 experiments

constantly changing. As such they might provide a more realistic appraisal of the effect of elevated CO_2. The study of dynamic communities raises the possibility that biomass response to elevated CO_2 could be hard to detect in early successional sites if large changes in biomass associated with a shift in species composition are taking place. A simple model was built to examine the effect of shifts in dominance of the four most common species on community biomass at the Québec site. The simulation shows that both changes in dominance pattern and in the identity of the dominant species strongly affect community biomass (Fig. 9.3). Community biomass decreased by 47%, when *Taraxacum* became dominant, while it increased by 23%, when *Phleum* became dominant. Biomass in the high CO_2 chambers was 25% lower then that of the ambient CO_2 chambers after five years of enrichment. The simulation shows that succession-mediated changes in biomass could either mask or amplify changes in biomass due to CO_2 enrichment. Leadley et al. (1999) reported vast differences in responsiveness to elevated CO_2 between *Lotus corniculatus, Bromus erectus* and *Carex flacca* and the other species during the first three years of results for the Swiss grassland experiment. In fact, the authors explain the observed lag in the response of aboveground biomass by the growth rate of these species; implicitly suggesting that successional pattern is important for an understanding of biomass responses to CO_2. Bolker et al. (1995), using an individual-based forest model, similarly reported that changes caused by successional sequence were larger than direct CO_2 responses. In their simulation, they identify red oak as a species driving many of the patterns observed. Two years of CO_2 enrichment in the Nevada Desert FACE Facility (NDFF) reported a 42% reduction in density for the native annual species coupled with a 40% increase in aboveground biomass. *Bromus madritensis*, an invasive exotic species, became a higher proportion of total plant density at elevated CO_2 (Smith et al. 2000). Those changes in community biomass associated with a shift in composition illustrate the challenge facing ecologists in predicting the effect of elevated CO_2 on dynamic communities (Díaz 2001).

An important legacy of the last ten years of elevated CO_2 research is the recognition that natural communities must been studied as dynamic systems. Studies of the dynamic responses of communities to elevated CO_2 indicate that:

- Elevated CO_2 might elicit changes in community diversity both in term of species richness or evenness. In dynamic communities, species identity and dominance patterns can drive the response to CO_2.
- Community biomass can change regardless of the effect of CO_2 due to succession alone. As both effects can be of similar magnitude, it may be difficult to partition the effect of CO_2 and succession on transient communities.
- Although the effects of elevated CO_2 on biodiversity may be less pronounced than those of other global change drivers such as land use, climate, N deposition, and biotic exchange, elevated CO_2 will likely interact with these drivers in ways that differ among biomes (Sala et al. 2000).

9.3 Biodiversity Loss and Response to Elevated CO_2

9.3.1 Species Diversity and Response to Elevated CO_2

The studies reported in the previous section suggest that elevated CO_2 has the potential, at least under certain circumstances, to alter biodiversity. The interaction between CO_2 and diversity must therefore be examined in the context of the diversity-productivity relationship. The GCTE decade has witnessed an enormous effort by ecologists to try and disentangle the links existing between diversity and ecosystem functioning (e.g., Chapin et al. 2000; Tilman et al. 2001; Spehn et al. 2005). As pointed out by Hooper et al. (2005) biodiversity has often been confounded with species richness although other components of biodiversity such as evenness, composition and presence/absence of key species all exert strong effects on ecosystem properties. Loreau and Hector (2001) suggested that a diversity effect might be due to either sampling or complementarity. Sampling refers to the likelihood that a key species be present in a community while complementarity describes interactions among species. Research on elevated CO_2 suggests that the response to elevated CO_2 is largely mediated by species identity and competitive interactions (see Körner et al. this volum;, Hanley et al. 2004; Navas et al. 2002; Ramsier et al. 2005). It is thus likely that elevated CO_2 could modify the diversity/productivity relationship. Three projects explicitly addressed this question by manipulating CO_2 concentration and plant diversity: the Swiss calcareous grassland study (Stocker et al. 1999; Niklaus et al. 2001), Roy's annual herbaceous communities (see Sect. 9.2.1) and the Minnesota, USA, BioCON project (Reich et al. 2001a,b, 2004) (Fig. 9.4).

To answer the question: "How does species loss influence biomass and its response to elevated CO_2?" the BioCON project relied on plots planted with 16, 9, 4 and 1 species while the Swiss experiment involved plots of 31, 15 and 5 species. In the BioCON project, total biomass of plots with 9, 4, and 1 species was, respectively 2, 13, and 50% less than that of plots with 16 species (Reich et al. 2001a,b; Reich et al. 2004). The enhancement of biomass resulting from elevated CO_2 decreased with declining diversity. In ambient plots, the average stimulation of total biomass in response to elevated CO_2 was 22%, 18%, 10% and 7% in, respectively, the 16-, 9-, 4- and 1-species plots (Reich et al. 2001a,b). Differences in diversity accounted for a five-fold difference in the effect of CO_2 enrichment Whereas elevated CO_2 increased biomass by

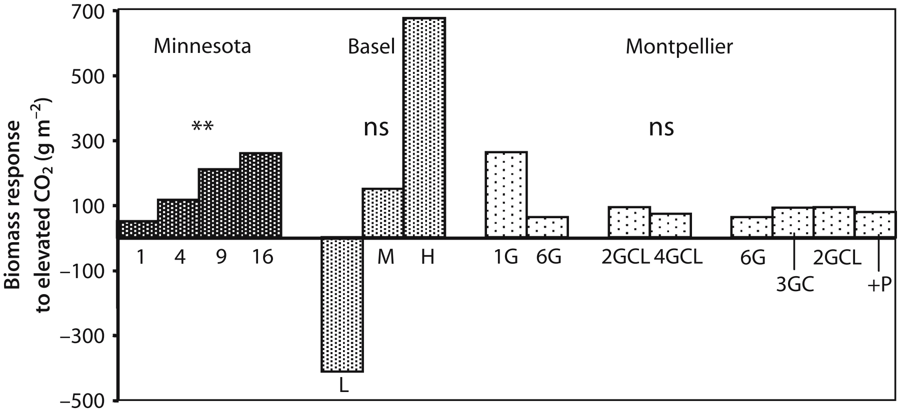

Fig. 9.4. Comparison of three experiments studying the interactions between CO_2 and plant diversity. In all cases, the CO_2 effect is expressed as the absolute change in total plant biomass at elevated vs. ambient CO_2 concentrations. *Minnesota:* Effects of diversity on total plant biomass response averaged over two years of CO_2 exposure in the field using FACE rings (Reich et al. 2001). Communities were planted with 1, 4, 9, or 16 plant species. *Basel:* Biomass response of calcareous grassland communities after five years of CO_2 exposure in the field using screen-aided CO_2 exposure (Niklaus et al. 2001). Communities were planted with 5 (L = low diversity), 12 (M = medium diversity) and 31 (H = high diversity) species, but species richness declined over the duration of the experiment in all treatments. *Montpellier:* CO_2 response of planted Mediterranean grassland communities of various complexity (G = annual grasses, C = composites, L = legumes, P = perennial grasses, where the number indicates the number of species within each functional group). Each bar is the average of four 0.5 m^2 model ecosystems grown in climate-controlled greenhouses (J. Roy, unpublished data)

258 g m^{-2} in the most diverse plots, it increased biomass by only 47 g m^{-2} in the monocultures. Likewise, the Swiss experiment found a significant effect of diversity on biomass; this effect, however, declined with time (Niklaus et al. 2001). Elevated CO_2 had a significant but highly variable effect on the biomass of high-diversity plots but no such effect on the medium and low-diversity communities. Conversely, Roy and collaborators found a significant increase in plant biomass production at elevated CO_2 in Mediterranean grassland communities, but the addition of species within functional groups did not alter this response.

Two complementary BioCON experiments allow further partitioning of the effect of functional groups and species within functional groups on CO_2 responses. These experiments include plots with *(i)* 1 or 4 species from single functional groups (C_4 grasses, C_3 grasses, N-fixing legumes and non-N-fixing herbaceous species) and *(ii)* four species varying from 4 to 1 in functional groups. All these plots were replicated across four CO_2 and N levels. Biomass increment in response to elevated CO_2, enriched N, or their combination was greater in 4-species than in 1-species plots (Fig. 9.5). Furthermore, plots planted with each forb species grown in monoculture had, on average, 44% less total biomass than plots with all four forbs species. Across all four functional groups, single functional group plots with one instead of four species had 29% less biomass on average (Reich et al. 2004). Decreasing the number of groups from 3 or 4 to 1 or 2 resulted in 20% lower total biomass on average, even with species richness constant at 4. Total biomass responses to CO_2 and N reflect effects on fine root biomass (Fig. 9.5). For instance, on average, in plots with four functional groups, elevated CO_2 increased fine root biomass by 191 g m^{-2}, but as the number of groups decreased to 3, 2, and 1, elevated CO_2 increased fine root biomass by 91, 90, and only 14 g m^{-2}, respectively.

In the BioCON project, functional group diversity was not a prerequisite for species richness to have significant effects and this effect was seen in disparate functional groups. This contrasts with the Mediterranean grassland study that did not find evidence that reductions in the number of functional groups altered the growth response to elevated CO_2 In the Swiss experiment, species responding positively to CO_2 enrichment did not follow common functional type classification. Thus while elevated CO_2 might well influence community composition, it is difficult to predict changes. Together, the BioCON, Swiss grassland, and Mediterranean grassland experiments provide insights on how a species poor world would respond to elevated CO_2:

- Decreases in diversity can lead to lower total plant biomass and to reduced responsiveness to elevated CO_2. This diversity effect is highly variable ranging from very pronounced (BioCON), relatively small (Swiss grassland) to nil (Mediterranean grassland).
- In the BioCON project, holding species richness constant, plots with decreasing functional group richness had less biomass and smaller enhancements of biomass in response to CO_2, when compared with plots with greater functional group richness. This was not the case in the Mediterranean grassland study.

9.3.2 Ecosystem C Fluxes in a Species-Poor World

The previous section suggests that species-poor communities could accumulate less biomass and be less responsive to elevated CO_2 with the magnitude of responses

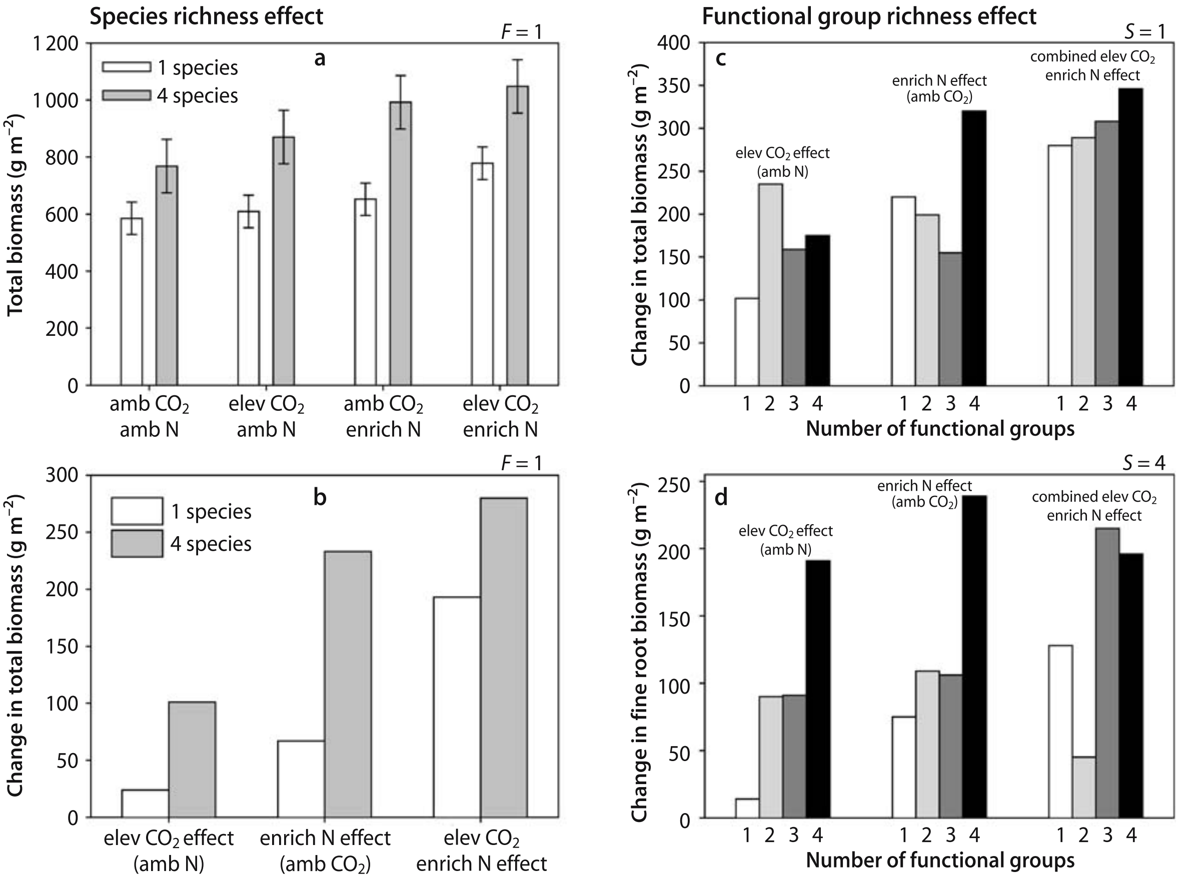

Fig. 9.5. Effects of species richness and functional group richness on biomass accumulation and response to elevated CO_2. **a** Total biomass and **b** change in total biomass (above- and below-ground, 0–20 cm depth) (+1 S.E.) for plots planted with one functional group and either 1 or 4 species, grown at four combinations of ambient (368 µmol mol^{-1}) and elevated (560 µmol mol^{-1}) CO_2, and ambient or enriched N (4 g N m^{-2} yr^{-1}). Data averaged over two harvests in each year from 1998 to 2001. **c** Change in total biomass and **d** in fine root biomass in plots with 4 species, and either 1, 2, 3 or 4 functional groups, grown at four combinations of ambient and elevated CO_2, and ambient and enriched N

modulated by resource availability. This raises a question: Would a species-poor world become a less efficient C sink? If this were the case, the initial assumption of elevated CO_2 research, coined earlier as “the large-plant-scenario”, would be invalidated. In fact, we know little about the effects of species loss on the capacity of ecosystems to take up C in the long term. So, where does the future of research on elevated CO_2 and diversity lie?

First, if we want to understand the consequences of species loss on the ability of ecosystem to sequester C, we need to develop better ways to estimate C cycling. Although it is widely acknowledged that C sequestration and net primary production (NPP) are not equivalent (Körner 1995; Karnosky 2003) most experiments examining the diversity/productivity relationship have used either NPP or biomass accumulation to report on ecosystem function. Catovsky et al. (2002) emphasize the urgent need to move beyond estimates of NPP toward better estimations of net ecosystem exchange (NEP). It is important to understand the diversity effects on plant biomass, on litter decomposition as well as on soil respiration (both autotrophic and heterotrophic) in order to estimate appropriately C fluxes in and out of the system. In the only published measurements of the effects of plant diversity on NEP, Stocker et al. (1999) found that reductions in plant diversity did not alter whole ecosystem CO_2 fluxes in calcareous grasslands at elevated or ambient CO_2 concentrations. At the ecosystem level, Chambers et al. (2004) modeled the response to elevated CO_2 of tree biomass and wood litter for a Central Amazon forest. An important conclusion of their study is that coarse litter is important in determining the forest carbon balance and should be considered as a C flux. They argue that under elevated CO_2, the gains in carbon due to increased growth would be roughly balanced by the increased stock of coarse litter. Using microcosms, Van Voris et al. (1980) proposed that the complexity of CO_2 efflux time series, i.e., the number of cyclic components required to compose a time series, might provide useful information regarding ecosystem C cycling. In laboratory microcosms of an old-field ecosystem, they demonstrated that the complexity of CO_2 flux time series was negatively related to the amount of calcium lost in the leachate, an indicator of system disturbance in their experiment. This result suggests that the analysis of CO_2 fluxes may be a useful integrative measure of the effects of disturbance (e.g., species loss) on the C cycle.

Second, we need to better understand the impact on community disassembly on C cycling. Habitat destruction and climate change are and will continue to be the major drivers of species loss and subsequent ecosystem responses (e.g., Lawton and May 1995; Thomas et al. 2004a). For example, using an area-based extrapolation of climate envelopes, Thomas et al. (2004b) suggested that climate change might lead to up to 35% of the taxa being "committed to extinction" in their study regions over the next 50 years. To date, experiments addressing the functional consequences of species loss have typically been performed over small spatial and temporal scales relative to the size, generation times and possible extinction rates of the organisms involved (e.g., Sect. 9.3.1, Tilman et al. 1997; Hector et al. 1999; Lepš et al. 2001). Because extinction in response to habitat destruction and climate change is a non-random process dominated by non-equilibrium population dynamics (Kareiva and Wennergren 1995), we need to better understand the long-term effects of community disassembly.

Community disassembly and its affects on C uptake and on the response to elevated CO_2 have received relatively little attention (Lawton 1994; Sala et al. 1996; Grime 1998; Gonzalez and Chaneton 2002). For example, the identity of species extinctions (e.g., rare vs. dominant; Grime 1998) and the rate at which such extinctions occur could generate non-linear ecosystem responses (Lamont 1995). Furthermore, long-term temporal changes in the abundances and biomass of remnant populations (e.g., Laurance et al. 1997; Didham et al. 1998) have been largely missing from biodiversity-C cycling studies conducted to date. The first Ecotron experiment (Naeem et al. 1994) reported that higher diversity communities consumed more CO_2 than lower diversity communities. It was suggested, however, that the experimental design could not separate diversity and composition effects (Huston 1997), but an additional shortcoming was the limited duration of the experiment. McGrady-Steed et al. (1997) studied microbial communities that exhibited greater inter-community variation in CO_2 flux at low diversity than at high diversity. However, this effect seemed to be due to differences in species composition among low diversity communities (Morin and McGrady-Steed 2004), and not to diversity effects per se.

The results obtained to date do not demonstrate whether a species-poor world will become a less efficient C sink or not. We might however be able to flip the question around and propose management strategies to increase C storage at the landscape level. GCTE is coming to an end at the same time as the Kyoto Protocol is coming into effect. The Nations of the world are now seeking ways to promote the uptake of C through land-use changes while ensuring the stability of these sinks. Hooper et al. (2005) summarized our knowledge to date by indicating that community composition is at least as important as species richness to determine ecosystem properties. Therefore management strategies that incorporate biodiversity will have to pay attention to the identity of species and their interactions (Hiremath and Ewel 2001). Furthermore estimates of the potential for C sequestration need to incorporate a precise assessment not only of C stocks but also of C losses. For example, C accounting methodologies proposed for afforestation and reforestation projects under the Clean Development Mechanism (www.unfccc.org) need to inventory coarse woody debris as well as living biomass.

Many questions remain for the next generation of global change research:

- How is the relationship between net primary productivity and net ecosystem productivity affected by biodiversity, elevated CO_2 and other global change drivers?
- Can we predict which species are most likely to be lost by habitat fragmentation or climate change?
- How will the process of species loss, driven by habitat fragmentation and climate change, affect CO_2 fluxes and the response of ecosystems to elevated CO_2?
- In what ways, if any, will future species loss alter the C source and sink capacities of different ecosystems?

9.4 Summary and Conclusions

In situ studies of communities suggest that the interactions between biodiversity, atmospheric CO_2 concentration, and C cycling are very complex. Rising CO_2 will probably act on plant diversity through a number of very indirect pathways; e.g., by altering the relative availability of resources such as water and nutrients thereby altering competitive interactions among plants. Second, changes in plant community structure due to rising CO_2 concentrations, particularly in highly dynamic systems, may be as or more important in determining biomass responses than the direct effect of elevated CO_2. Finally, species loss resulting from global change might reduce productivity as well as responsiveness to elevated CO_2, although the response will largely depend on species identity.

Over all, simple scenarios invoking a clear and simple biospheric loop between atmospheric CO_2 and terrestrial biomass due to CO_2 fertilization need to be abandoned and replaced by an understanding of a complex system involving both biotic and abiotic feed-back loops. Our ability to either manage or predict the relationship between diversity and ecosystem function is still limited.

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Chapter 10

Predicting the Ecosystem Consequences of Biodiversity Loss: the Biomerge Framework

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10.1 Biodiversity and Ecosystem Functioning: a Synthesis

10.1.1 Why Biodiversity Matters to Global Change Ecology

Global change ecology has become increasingly concerned with understanding how linkages between changes in biological diversity (henceforth, *biodiversity*) affect ecosystem functioning (Chapin et al. 2000; Loreau et al. 2001; Hooper et al. 2005). By biodiversity we mean, "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." This definition, because it has been adopted by the Convention on Biological Diversity and the Millennium Assessment probably has the broadest subscription in comparison to the many other definitions proposed for biodiversity (Duraiappah and Naeem 2005). It clearly defines biodiversity as more than just species or taxonomic diversity ("variability of living organisms from all sources"). It includes variability in biotic interactions ("ecological complexes") and geography (diversity within and among populations, species, and ecosystems).

The relationship between biodiversity and ecosystem functioning is important in global change ecology for several reasons. First, biodiversity is experiencing unprecedented declines in virtually all ecosystems due predominantly to anthropogenic processes such as the conversion of natural ecosystems to less diverse managed systems (e.g., farms, plantations, aquaculture), biological invasions, enhanced rates of N deposition, habitat fragmentation, and climate change (Ehrlich 1988; Wilson 1988; Soulé 1991; Groombridge 1992; Hawksworth 1995; Heywood 1995; Wilcove et al. 1998; Sala et al. 2000; Balmford et al. 2002; Raven 2002). Several studies have shown that biodiversity loss can significantly lower primary production, which is critical to all other ecosystem functions (e.g., Naeem et al.1994; Tilman et al. 1996; Hector et al. 1999).

Second, biosphere-geosphere feedbacks in Earth System processes are a critical component of climate change biology (Díaz et al. 1993; Mooney et al. 1993; Walker and Steffan 1996; Woodwell 1995; Andreae 2002), thus understanding what roles biodiversity may play in these feedbacks is important given widespread declines in biodiversity. For example, carbon sequestration by terrestrial plants represents an important feedback in climate change, and CO_2 impacts on production are affected by plant species composition and diversity (e.g., Bolker et al. 1995; Zavaleta et al. 2003; Reich et al. 2004).

Third, the Convention on Biological Diversity (CBD), signed and ratified in the early 1990s by the vast majority of the world's nations, declared that biodiversity underpins Earth's ecosystems and that biodiversity conservation is fundamental to achieving environmental sustainability and sustainable development (http://www.biodiv.org/). Establishing a scientific basis for the relationship between biodiversity and ecosystem functioning would facilitate the development and implementation of science-based policy for the CBD to achieve its goals of biodiversity conservation and, ultimately, sustainable development.

An additional consideration of the importance of biodiversity in global change ecology is its relationship to ecosystem services, most of which are governed by ecosystem functions. Ecosystem services are defined as the benefits people obtain from ecosystems (Daily et al. 1997; Costanza et al. 1997; Naeem 2001a). The importance of biodiversity to ecosystem services is highlighted in the Millennium Assessment (MA), a consensus of nearly 1 400 experts from 95 countries, by the following statement:

> Biodiversity represents the foundation of ecosystems that, through the services they provide, affect human well-being. These include provisioning services such as food, water, timber, and fiber; regulating services such as the regulation of climate, floods, disease, wastes, and water quality; cultural services such as recreation, aesthetic enjoyment, and spiritual fulfillment; and supporting services such as soil formation, photosynthesis, and nutrient cycling. The MA considers human well-being to consist of five main components: the basic material needs for a good life, health, good social relations, security, and freedom and choice and action. Human well-being is the result of many factors, many directly or indirectly linked to biodiversity and ecosystem services while others are independent of these.

10.1.2 Linking Change in Biodiversity with Change in Ecosystem Functioning

In spite of the logical inseparability of biodiversity and ecosystem functioning, in that neither exists in the absence of the other, little theoretical or empirical work prior to 1992 had explicitly addressed whether changes in biodiversity could have predictable impacts on ecosystem function. Traditionally, biodiversity was largely considered an epiphenomenon or dependent function of abiotic factors, such as climate, greography, or edaphic factors (Naeem 2002; Naeem et al. 2002). Intercropping studies (e.g., Vandermeer 1989; Vandermeer et al. 2002), the study of keystone species (e.g., Power et al. 1996, and studies of ecosystem engineers (e.g., Jones et al. 1994; Wright et al. 2002), had demonstrated that species could potentially have large impacts on ecosystem function (Statzner and Moss 2004), but these were viewed as local or secondary effects. Over the last decade, however, this view has changed. Theoretical and small-scale (e.g., <10 m^2) experimental studies have introduced the idea that biodiversity can regulate abiotic factors through its control over ecosystem function, although whether these findings apply at larger scales (>1 km^2) typical of natural systems remains unclear (Naeem 2002; Loreau et al. 2002; Hooper et al. 2005).

That biodiversity was seldom linked to ecosystem functioning prior to the 1990s is not surprising in light of the fact that the study of biodiversity and the study of ecosystem functioning have been, and continue to be, largely independent lines of ecological research (McIntosh 1985; Likens 1992; Schulze and Mooney 1993; Grimm 1995; Díaz and Cabido 2001). To link biodiversity with ecosystem functioning, in particular making the latter a dependent function of the former, required a synthesis that would bring together community and ecosystem ecology.

10.1.3 Lessons Learned from Early Debates

Like syntheses in most scientific disciplines (Kuhn 1962), considerable debate surrounded early findings (Naeem et al. 2002). Three important lessons emerged from this debate, arising mostly from sources of confusion. First, the idea that ecosystem function is controlled, at least in part, by biodiversity does not imply that taxonomic or species richness, in and of itself, somehow controls ecosystem function. Biodiversity refers to both taxonomic (e.g., species or genetic) *and* ecological (e.g., life history or functional) diversity over all spatial and temporal scales and of these components, it is functional diversity that matters. Functional diversity refers to the diversity of species traits rather than taxonomic diversity, where traits are those that either govern how a species responds to environmental change or how it effects ecosystem processes. For example, a grassland may have 200 species of herbaceous plant species, but with respect to nitrogen fixation, it may be considered to have only two functional types – legumes (N fixers) and non-legumes (see Chap. 7 and 13). Thus, biodiversity can control ecosystem function when changes in biodiversity involve changes in functional diversity (number and relative abundance of functional types) over space or time (Smith et al. 1997; Hooper and Vitousek 1998; Díaz and Cabido 2001; Lavorel and Garnier 2002; Petchey and Gaston 2002; Naeem and Wright 2003; Symstad and Tilman 2001). Change in taxonomic diversity affects ecosystem functioning only in so much as it correlates with change in functional diversity.

Second, because biodiversity and biomass are often related, in the sense that larger expanses of ecosystems often contain more individuals and more species than smaller expanses, there is an additional conflation of biodiversity loss with biomass loss. For example, removal of a forest by clear cutting will significantly alter watershed discharge, but it is not the loss of biodiversity *per se* that is responsible for this change in ecosystem function – it is the loss of vegetation, or more simply, the loss of biomass. If, however, one replaced a functionally diverse forest with an equivalent biomass of a monoculture plantation and watershed discharge was affected, then in this case, the change in biodiversity led to the change in ecosystem function.

Third, the associations between biodiversity and ecosystem functioning derived from large-scale observational studies are often different both in magnitude and sign from those derived from small-scale experimental studies. Many of the debates have concerned seeming conflicts between findings from within-ecosystem experiments and those of cross-ecosystem correlational studies (e.g., Levine 2000; Naeem 2001b). Such contrasts in findings are not surprising given that larger scale studies include variation in ecosystem function due not only to variation in biodiversity, but variation in many other factors, such as climate, nutrient supply rate, and history, that are held constant in experimental systems (Troumbis et al. 2000; Troumbis and Memtas 2000; Chase and Leibold 2002; Fridley 2003). The lesson learned is that if one wants to predict ecosystem response to change in biodiversity across large scales, one has to understand how other factors (controlled in experiments and uncontrolled in observational studies) affect both biodiversity and ecosystem function.

These sources of confusion that fueled the early debates have since become active research areas in the study of how biodiversity and ecosystem functioning are linked. Indeed, the framework we discuss below is an outcome of research in theses areas.

10.1.4 What We Have Learned about the Relationship between Biodiversity and Ecosystem Function

Although the history of research on biodiversity and ecosystem functioning (BEF) is one of point-counterpoint debate, a consensus has emerged (Loreau and Hector 2001) and syntheses and directions for future research identified (Loreau et al. 2002; Hooper et al. 2005). Numerous experiments and much theory have accumulated over the last decade and BEF research continues to be one of the most active areas in ecological research. Space does not permit reviewing this enormous literature, but much of it is covered in several reviews (Chapin III et al. 2000; Loreau et al. 2002; Hooper et al. 2005). Briefely, however, BEF research has demonstrated that

- change in biodiversity has significantly altered ecosystem functioning and the services it provides in many well-documented studies,
- species' functional characteristics strongly influence ecosystem functioning,
- the mechanisms and pathways by which biodiversity loss impacts ecosystem functioning vary among systems,
- species vary in their impact on ecosystem functioning from slight to relatively subtantial,
- and, whereas a small number of species may provide levels of ecosystem functioning similar to species-rich communities, more species are needed to insure continued provisioning of ecosystem function over longer periods of time (Hoppe et al. 2005).

For this chapter, it is important to note that while theory (e.g., Hughes et al. 2002; Loreau 2004; Petchey et al. 2004), grassland experiments (e.g., Fridley 2003; Foster and Dickson 2004; Zavaleta and Hulvey 2004; Roscher et al. 2005; Spehn et al. 2005), microcosm research (e.g., Fox 2004; Heemsbergen et al. 2004; Wohl et al. 2004), and marine/aquatic studies (e.g., Duffy et al. 2001; Emmerson et al. 2001; Stachowicz et al. 2002; Solan et al. 2004), have all contributed significantly to advancing the frontiers of BEF research, only a few have considered the implications of applying BEF to the scales typical of most ecosystems (e.g., Emmerson and Raffaelli 2000; Troumbis and Memtas 2000; Bai et al. 2004; Cardinale et al. 2004; Statzner and Moss 2004). The purpose of this chapter is to establish a framework by which BEF research can expand to larger scale investigations.

10.1.5 The Scientific Framework for Linking Biodiversity and Ecosystem Functioning

The initial BEF framework was developed over a decade ago, but has stimulated a tremendous amount of research. Vitousek and Hooper (1993) developed a graphical framework for linking biodiversity and ecosystem functioning that captured the heart of the synthesis, but was insufficiently detailed to avoid the controversy that would eventually emerge. They plotted biodiversity on the x-axis and ecosystem functioning on the y-axis then postulated several possible relationships between the two. As simple as this might seem, it represented a radical departure from traditional ecology. By plotting biodiversity on the x-axis, it portrayed biodiversity as the *independent* factor while portraying ecosystem functioning as the *dependent* factor, traditionally the y-axis. Almost always, in ecology, one plots biodiversity as a dependent function, usually of abiotic factors such as temperature, precipitation, or productivity (e.g., Gaston 2000). A wide variety of relationships between biodiversity and ecosystem functioning have been proposed in accordance with the Vitousek-Hooper framework (Martinez 1996; Schläpfer and Schmid 1999; Naeem 2002).

Graphical approaches such as the Vitousek-Hooper framework are heuristic devices that motivate and facilitate scientific discourse, but adapting such frameworks to the real world is seldom straightforward (Naeem et al. 2002). In particular, the most significant challenge to adapting abstract frameworks to the real world requires dealing with scale (Naeem 2001b; Symstad et al. 2003). Both biodiversity and ecosystem functioning are complex, scale-dependent terms that are not readily quantified by single variables and therefore not readily related to each other by simple bivariate plots. "Ecosystem function" refers to a virtually limitless set of processes associated with ecosystems ranging from global (e.g., global sequestration of atmospheric CO_2) to local processes (e.g., grassland productivity). Likewise, "biodiversity" refers to an equally limitless set of ecological measures that quantify biodiversity from large-scale (e.g., biome) to small-scale (e.g., genotypic variability within a population for the expression of a single gene) properties of ecological systems. Consider Fig. 10.1 in which the scales of biodiversity and ecosystem functioning are presented as a bivariate plot. Plotting ecosystem function against biodiversity across such a plot would yield an enigmatic figure that is almost impossible to interpret mechanistically even though conceptually it captures the central idea.

When experimental tests of the Vitousek-Hooper framework were conducted, in reality, only a small region of the bivariate plot shown in Fig. 10.1 was explored, but interpretations of these studies were seldom constrained to the region explored. Much of this experimental research crossed out "biodiversity" and wrote in "plant species richness," crossed out "ecosystem functioning" and wrote in "primary production," and then plotted data collected from combinatorial experiments whose units (pots and plots) were seldom more than a few meters on a side and seldom conducted for more than one or a few years (Naeem et al. 1994; Naeem and Li 1997; Hooper and Vitousek 1997; Tilman et al. 1996; Tilman et al. 1997;

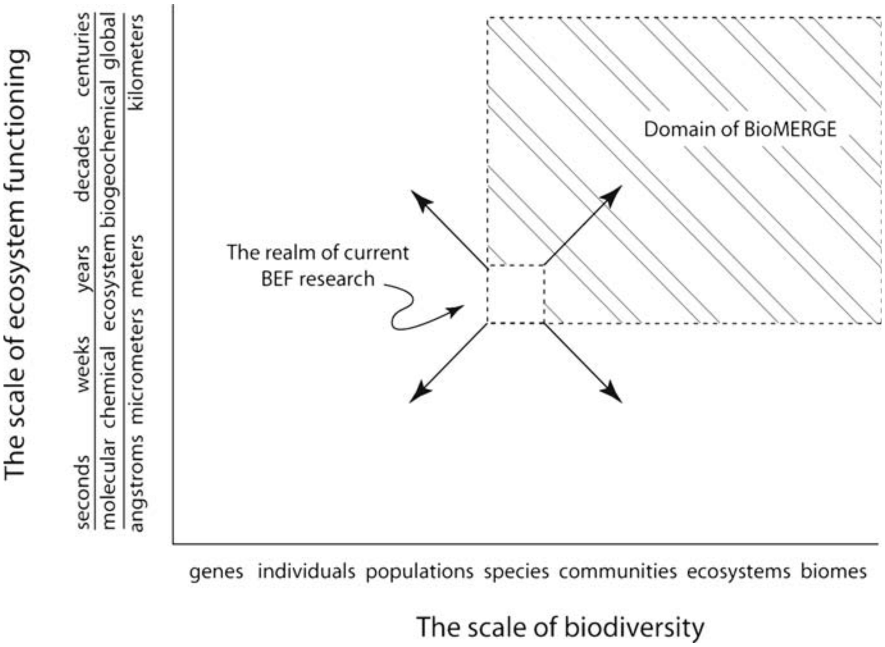

Fig. 10.1.
The realm of current research in Biodiversity and Ecosystem Functioning (BEF) and the realm of BioMERGE. Each *axis* abstractly and approximately represents the scales of biodiversity and ecosystem functioning, illustrating the latter as a dependent function of the former. The *center box* illustrates the average domain of current BEF research, which has focused on relating species diversity to ecosystem functioning at small spatial (in the realm of square meters) and temporal scales (in the realm of weeks to years). The *arrows* indicate directions of new research necessary for the expansion of BEF research. The *larger box* encompassing the *upper right quadrant* represents the domain of BioMERGE, which seeks to extend BEF research to larger scales

Wardle et al. 1997; Symstad et al. 1998; Hector et al. 1999; Mulder et al. 1999; Sankaran and McNaughton 1999; Spehn et al. 2000; Symstad 2000; Symstad and Tilman 2001; Engelhardt and Ritchie 2001; Hooper et al. 2002; Petchey et al. 2002; Schmid 2002; Schmid et al. 2002; Fukami and Morin 2003). Microcosm studies (e.g., Naeem and Li 1997; McGrady-Steed and Morin 2000; Petchey et al. 2002; Fukami and Morin 2003) were often conducted for longer periods of time in terms of numbers of generations, but they were still small in spatial scale (small with respect to the typical size of aquatic ecosystems, though in terms of organism size, the spatial scale was probably larger than most experimental studies).

In spite of the limited scope of this research, because a positive, saturating or asymptotic (or linear in a semi-logarithmic plot) relationship between biodiversity and ecosystem functioning was often found (e.g., Naeem et al. 1994; Tilman et al. 1996; Hector et al. 1999), the claim was made that biodiversity enhances ecosystem functioning. This claim ignited a strong debate (Guterman 2000; Kaiser 2000). Even though the findings themselves were not questioned, the mechanisms were unclear, the use of species richness as a proxy for biodiversity and primary production as a proxy for ecosystem functioning seemed questionable, and the findings often appeared to be the inverse of what was known from correlative studies of biodiversity and ecosystem functioning conducted at larger scales (e.g., Wardle et al. 2000). Finally, these early experiments lacked considerations of functional diversity and trophic structure. Although later experiments would examine these issues, the initial lack of treatment of these issues offered only limited applicability of such findings to worlds that were functionally (not just taxonomically) diverse, multitrophic, and much larger in scale.

The new framework we discuss here brings biogeography into the picture, and by so doing, allows for the expansion of BEF research beyond its currently limited domain of small-scale studies to large-scale evaluations of ecosystems and environmental consequences of biodiversity loss (Fig. 10.1). Biogeography, broadly defined, is the study of past and present distributions of species and populations. As such, it encompasses many topics including evolutionary ecology, community assembly, species saturation, species area curves, ecogeographic rules, zonation, endemism, environmental heterogeneity, allometry and scaling rules, historical factors and paleoecology, and much more. In this framework we use the term *biogeography* in a narrow sense to specifically refer to geographic patterns of distribution and abundance, and we use the term macroecology (*sensu* Brown 1995) to refer more specifically to allometry and scaling rules, though the biogeography and macroecology are closely linked (Blackburn and Gaston 2003).

This chapter reviews the most recent conceptual framework for BEF research. The framework we discuss is being developed by a research coordinating network (RCN) whose acronym is BioMERGE (Biotic Mechanisms of Ecosystem Regulation in the Global Environment). For convenience, we simply refer to this framework as the BioMERGE framework.

It is important to note at the outset that *BioMERGE is not a research agenda*, such as those periodically established by the Ecological Society of America (Lubchenco et al. 1991; Palmer et al. 2004) or by international agencies such as GCTE or DIVERSITAS. Rather, it is a synthetic research framework that develops and evolves through participation by any and all interested individuals.

10.2 The BioMERGE Framework

The BioMERGE framework consists of three sub-frameworks. The first framework is structural, one that links species (taxonomic diversity), trophic groups, and functional diversity with ecosystem functioning. The second is an expansion of the Vitousek-Hooper BEF framework to include biogeographic principles. The third is a research implementation framework that serves as a guide for conducting an effective large-scale BEF research program. These three sub-frameworks reflect a summary of the previous decade of BEF research, identify existing bodies of ecological knowledge that can be brought into the BEF synthesis, and point to needed research and future directions that will enable us to better understand the ecosystem consequences of biodiversity loss.

10.2.1 The BioMERGE Structural Sub-Framework

The structural framework for BioMERGE outlines how species and ecosystems are linked and provides the ecological foundation for the conceptual and empirical frameworks discussed below. This structural framework differs little from previous frameworks and serves only to focus attention on the key elements of BEF research. An ecosystem is considered to be a collection of species representing four trophic groups (autotrophic species, autotrophically-derived species, decomposer, or decomposer-derived species, see Fig. 10.2) that cycle material between organic and inorganic forms. Omnivory or other complex trophic interactions are acknowledged, but left out of the graphic for simplicity.

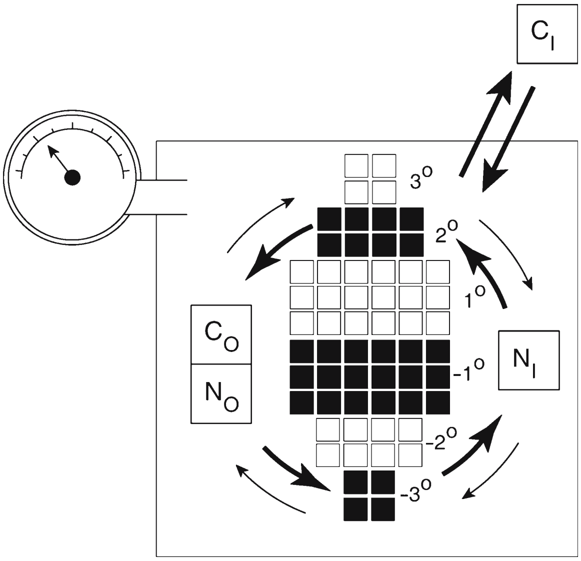

Fig. 10.2. The BioMERGE conceptual framework. Species are represented by *small squares* that are either autotrophs (here limited to photo-autotrophs or 1° producers), and either autotrophically derived heterotrophs (2° and 3° consumers) or microbial decomposers (–1°) or consumers of microbial decomposers (–2° and –3°). The autotrophs draw down inorganic carbon (C_I) (e.g., atmospheric CO_2 for terrestrial plants) and uptake inorganic nutrients to produce organic material that is distributed throughout the trophic groups of species. All contribute through mortality to a pool of dead organic material (C_O and N_O) that is decomposed into its inorganic constituents. There are many other routes (*thinner arrows*), but the overall pattern consists of internal cycling and carbon exchange that tracks energy acquisition through photosynthesis. Ecosystem functioning therefore involves any of the *broad arrows* while biodiversity represents taxonomic diversity, trophic structure, and functional diversity (not shown) within trophic groups

Graphically, this framework is illustrated by portraying an ecosystem as a box within which an assemblage of species with a specific trophic structure resides. Within this box, nutrients are represented as two organic (living species and dead organic matter) and one inorganic pool. The box (ecosystem) draws down and returns inorganic carbon (CO_2) to the atmosphere, but much of the nutrient cycling is considered to be confined to the ecosystem itself. To this system, a meter or measuring device that monitors ecosystem function (e.g., net primary production or total ecosystem respiration) is connected. This framework illustrates BEF research as the study of how ecosystem function, or the attached meter, responds to species loss. Traditional ecosystem ecology would not pay much attention to the species within the box, but would instead focus primarily on how changes in cycles and fluxes affected the meter, whereas traditional community ecology would pay little attention to the cycles, fluxes, or the meter associated with the system.

The main points of this structural framework are,

- it draws significant attention to the decomposer community, which is frequently ignored,
- traditionally defined trophic groups, such as primary consumers, herbivores, and carnivores, are not considered functional groups,
- ecosystem function refers only to organic-inorganic matter transformation (i.e., not invasion resistance or aesthetic properties).

10.2.2 The BioMERGE BEF Sub-Framework: an Expansion of the Vitousek-Hooper Framework

The Vitousek-Hooper BEF framework presented a number of alternative trajectories that ecosystem function could trace (e.g., linear, asymptotic, or logistic) as biodiversity declines. In contrast, the BioMERGE framework assumes an asymptotic trajectory that represents an average for a range of possible trajectories that ecosystem function could follow as biodiversity declines (Fig. 10.3). The asymptotic curve reflects the perspective that the loss of species does not, on average, dramatically impact ecosystem function until functional (*F*) and taxonomic diversity (*S*) are equal (i.e., species are singular rather

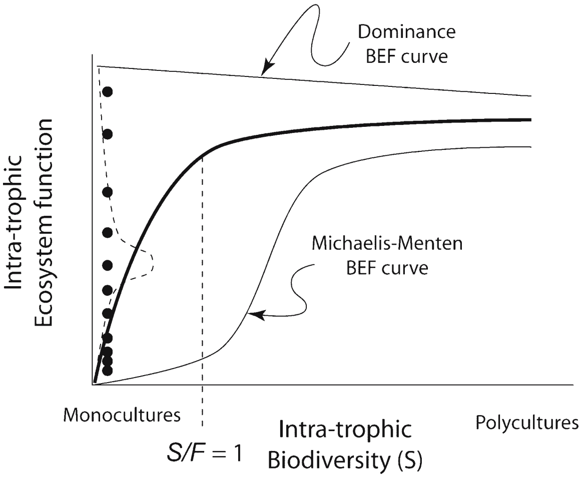

Fig. 10.3. The BioMERGE expansion of the Vitousek and Hooper framework. At the monoculture end, the majority of species (each represented as a *closed circle*) exhibit small levels of functioning whereas a few exhibit high levels following a general log-normal like pattern. The x-axis plots biodiversity as intra-trophic species richness (S), such as species richness of plants or species richness of herbivores. The maximum species richness (*right-most portion of curve*) represents an ecosystem in which species richness is stable and high. The asymptotic, *solid line*, represents the general BEF relationship based on the assumption that a significant portion of the species in an ecosystem are redundant with respect to specific ecosystem functions. That is, once at least one species is present per functional group ($S/F = 1$, where $F =$ the number of functional groups), additional species have significantly smaller impacts on ecosystem functioning. The *dashed lines* indicate boundaries of combinatorial variants in species composition. The lower boundary is based on a Michaelis-Menten like model of ecosystem function, which assumes that biodiversity acts like a catalyst for biogeochemical processes. The upper boundary is based on a dominance model in which no species can achieve higher ecosystem functioning than that of the species with the dominant level of functioning among the monocultures. The *line* is illustrated as a slightly negative slope to allow for the fact that in multi-species assemblages, at least some of the resources are controlled by other species, no matter how rare they are. These boundaries represent the range of possible expressions of ecosystem functioning for a specific level of species richness. Note that many alternative boundaries are possible

than redundant)(Naeem 1998). The "elbow" in the curve therefore occurs when $S/F = 1$.

The rationale for using a range of trajectories rather than a single trajectory is to acknowledge the fact that different sequences of biodiversity loss will result in different patterns of change in ecosystem functioning. A community will trace a specific path through the diversity-by-function bivariate space for a specific sequence of biodiversity loss, but there are many different paths possible – that is, history, or the pattern of disassembly (or assembly) matters (Fukami and Morin 2003).

The multiplicity of pathways a trajectory can take in biodiversity-function space therefore describes two distinct, but important properties of biodiversity change. The first property is the combinatorial nature of change. A step towards decreasing (or increasing) biodiversity implies an enormous number of possible changes in community structure and composition. The second property is temporal contingency or the historical component of disassembly (or assembly). One can get to any community composition or structure from another by an enormous number of possible pathways and how one gets there affects ecosystem function. Consider, for example, that a BEF experiment that constructs replicate communities of 1, 8, and 16 species to determine the relationship between biodiversity and ecosystem function, there are 26 292 possible species combinations between a 16 species community and an 8 species community and 26 316 between an 8 species community and a monoculture. Thus, the problems are not simply the inability to replicate all 8 species communities, of which there are 12 870 different kinds, but the inability to know how the ecosystem functioning observed for 8 species communities might have been affected if they were the result of a staggering number of possible disassembly (or assembly) pathways. Obviously, for practical reasons, unless the community itself is very small (<10 spp.), experimental studies can only explore such an enormous number of possible communities in a very limited way.

The BioMERGE framework also considers that among the possible single species (or monoculture) treatments only a few species exhibit high levels of ecosystem function while the rest show lower levels (Fig. 10.3). That is, species with higher abundance (in terms of biomass) are assumed to make larger contributions to ecosystem functioning. This portion of the framework derives from the common, lognormal-like pattern of distribution and abundance observed at the large spatial scales more appropriate for communities than what has been typically employed in experimental research (Preston 1962; May 1975; Hughes 1986; Adler 2004). While debate continues concerning whether the canonical lognormal (Preston 1962), sequential breakage (Sugihara 1980), neutral (Bell 2000; Hubbell 2001) or other models best explain biogeographical patterns in relative abundance at larger scales, the fact remains that lognormal-like abundance patterns are common. An important part of this exercise, which we discuss below, is to use species traits to derive relative abundance. It is at this point that biogeography, in the form of incorporating patterns of commonness and rarity, enters the BioMERGE framework. There are many other aspects of biogeography that could be included, but they are beyond the scope of our chapter.

Using a lognormal-like distribution of abundance to describe the distribution of monoculture ecosystem functions leads to the null expectation that only a few species will dominate ecosystem function while many others (the rare species) will make lesser contributions. For example, in the case of plants, the null expectation would be that dominant species in polyculture will be the most productive species in monoculture and rare species in polyculture would have the smallest abundance as monocultures. In the absence of experimentation, of course, one cannot know for certain if a rare species in polyculture is rare because of suppression by competitive dominants, but could be quite abundant if released from suppression by extinction of the dominants. For example, while it is difficult to imagine that a rare orchid in a tropical rainforest would completely replace the biomass of the rainforest if it were the only species left, it is less clear whether any one of 900 species of trees in an Amazonian rainforest would replace the bulk of the biomass of that forest in the absence of the other 899.

The issues surrounding dominance, relative growth rates, and the relationship between monoculture and polyculture production are many and complex and have been a central part of the debates surrounding BEF literature (Garnier et al. 1997; Hodgson et al. 1998; Lepš et al. 2001; Loreau and Hector 2001; Adler and Bradford 2002; Schmid 2002). We will not review these issues here, but they do point to the need for a contemporary BEF framework to explicitly include dominance.

The main points of this expanded Vitousek-Hooper BEF framework are,

- an emphasis on a *range* of possible pathways ecosystem function can take in the face of biodiversity loss rather than a single pathway
- the inclusion of both functional and taxonomic diversity reflected by an average asymptotic trajectory, with the asymptote occurring where ecological redundancy is lost
- dominance (commonness and rarity) is integrated into the framework by the assumption of a lognormal-like distribution of function among the monocultures

Like previous BEF research, this framework assumes that environmental influences over community composition and structure (e.g., gradients, frequency of disturbance, seasonality, and so forth) are constant.

10.2.3 The BioMERGE Research Implementation Sub-Framework

The third BioMERGE sub-framework is one in which we have outlined the necessary steps in an evaluation of the ecosystem consequences of biodiversity loss at scales much larger than experimental work generally encompasses. There are three steps. First, establish an operational biota using what is known to set the stage and using ecological principles to estimate what is unknown (i.e., fill in the missing species, their abundance, and their function). Second, establish diversity-function transition matrices for estimating changes in ecosystem function given changes in diversity. Third, select an extinction scenario to determine the realm of possible expressions of ecosystem function that could occur during the course of biodiversity loss. These steps are detailed below.

Step 1: Establish an Operational Biota

Virtually no biota for any ecosystem is fully known nor is likely to be known in the near future if for no other reason than the fact that microbial diversity remains, in spite of many advances in molecular methods, still impossible to determine fully (Øvreås 2000; Torsvik et al. 2002). Given a location on Earth, however, one can establish an *operational* biota, or a biota derived inventories, surveys, and from ecological principles such as biogeographic theories of relative abundance solely for the purposes of BEF analyses. Like climate modeling to understand ecosystem or Earth System responses to elevated CO_2, understanding the range of responses of ecosystems or Earth Systems to biodiversity loss provides valuable insights into the potential consequences of such change. We propose several steps.

Step 1.1. Estimate species richness for major taxa in the community. Global patterns in biodiversity are not random so, at least in principle, there are some predictable elements for species richness and relative abundance given the geographical position of the ecosystem. For example, even in the absence of taxonomic information, such as floral and faunal surveys, we can estimate species richness for various taxa (plants and vertebrates) using the environmental correlates of species richness such as potential evapotranspiration, elevation, latitude, and so forth). This information provides an approximate magnitude for the biodiversity axis on the BEF curve.

Step 1.2. Establish relative abundance. This step requires employing a lognormal-like distribution, as discussed earlier, to derive the expected relative abundance for the number of species in the ecosystems. For example, to derive the relative abundance of an ecosystem containing S species (N_i, where N equals the maximum number of individuals of the i^{th} species supported by the ecosystem) we draw S numbers from a log normal distribution with its shape determining coefficients (mean and variance) based on what is known for the region, what is known from similar regions, or from the estimated S from step 1.1.

To derive the relative biomass of species based on abundance we could use the allometric scaling formula,

$$M_i = 9\,191\,N_i^{-1.341}$$

(Enquist et al. 1998), where M_i is the biomass and N_i the density of the i^{th} species. This is not necessarily a universal law, but it is a strong, empirically robust relationship that can be used to approximate relative biomass.

While use of such methods has long been a tradition in ecology (Horn 2004; Statzner and Moss 2004), they are not without its controversies (e.g., Cyr and Walker

2004; Li et al. 2004; Marquet et al. 2004; Tilman et al. 2004). For example, allometric coefficients from the metabolic theory of ecology (MTE) (Brown et al. 2004), such as that used for M_i above, are often derived across enormous taxonomic (e.g., cyanobacteria to giant redwood trees), spatial (across biomes), and temporal scales (data collected over decades). Not surprisingly, the predictive power of scaling rules based on MTE declines rapidly as one reduces the taxonomic, spatial, and temporal scales of investigation. Indeed, they may be practically useless for predicting function for a small system typical for most ecological research (Tilman et al. 2004). The BioMERGE approach is at an intermediate scale – providing predictions at the ecosystem level for multitrophic communities over moderate time scales – thus such caution in applying MTE is appropriate.

Step 1.3. Establish species relationships to ecosystem functioning. Step 1.1 and 1.2 provide species richness and relative abundances, but response- and effect-functional traits (*sensu* Lavorel and Garnier 2002) are needed to convert changes in the estimated biota to changes in ecosystem functioning. Response traits are species traits that govern ecosystem response to environmental change (e.g., drought tolerance traits), whereas effect traits are traits that govern change in ecosystem function as a consequence of change in species abundance or metabolic activities (e.g., hosting symbiotic N-fixing prokaryotes). The study of functional traits and functional diversity is a rapidly growing field (Smith et al. 1997; Hooper and Vitousek 1998; Díaz and Cabido 2001; Symstad and Tilman 2001; Lavorel and Garnier 2002; Petchey and Gaston 2002; Naeem and Wright 2003), but acquisition of this information is still difficult. Even in the absence of any information, an extensive and rapidly growing list of ecological patterns may be usable for providing, at least to a first approximation, trait information for estimating BEF relationships. For example, leaf, stem, and root biomass are strongly correlated with one another, often with regression r^2 values >0.80 (Enquist and Niklas 2002). This means one can estimate biomass allocations for species even if they have not been determined empirically.

Another example of the utility of allometric traits comes from Wright et al.(2004) who found that leaf mass per area, photosynthetic assimilation rates, leaf nitrogen, leaf phosphorus, dark respiration rate, and leaf lifespan all showed strong patterns of associations for plants from an enormous range of habitats covering most of the range of conditions experienced in terrestrial ecosystems. Once again, even if the only information available is from herbarium sheets, one might be able to estimate important plant traits such as those studied by Wright et al. (2004).

One final example is the estimation of biomass production (primary or secondary) from growth rates using the following allometric scaling formula:

$$G_i = M_i^{0.763}$$

(Niklas and Enquist 2002), where G is the growth rate of the i^{th} species in kg dry matter yr^{-1}. There are many other examples for which physiological or functional traits of species may be estimated from density or biomass data.

While these examples are illustrative, we repeat a caution we raised earlier. The scales over which scaling coefficients are derived should match the scales over which predictions are being made. If they do not, then prediction errors associated with such mismatches (e.g., Tilman et al. 2004) should be stated.

Step 1.4. Establish patterns for trophic structure. Again, for many ecosystems, trophic structure is unlikely to be known, but even so, some efforts can be taken to include this important aspect of an ecosystem's biota. Given autotrophic biomass, one can use empirically derived relationships between the biomasses of different trophic groups or, in the absence of any empirical information, use approximate efficiencies of energy transfer across trophic groups. In many ecosystems, for example, carnivore diversity and even abundance are likely to be known, and Carbone and Gittleman (2002) have shown that about 10 000 kg of prey supports about 90 kg of a given species of carnivore for a wide range of species. The purpose of this step is to determine how much autotrophic biomass is being consumed by herbivores and how much herbivores are regulated by carnivores, an important aspect of ecosystems studied since the 1960s (e.g., Hairston et al. 1960; Polis and Strong 1996).

Below-ground food webs are much tougher to deal with, especially microbes, which may represent the dominant biomass and diversity in many ecosystems (Torsvik et al. 2002). Some studies argue that soil organisms occur in functionally redundant assemblages (Andren et al. 1995; Beare et al. 1995; Liiri et al. 2002), while others argue that redundancy may not be prevalent in stressed systems (e.g., Freckman and Virginia 1997) or in microbial communities (Cavigelli and Robertson 2000). Experimental studies argue for idiosyncratic responses or no response to biodiversity loss in soil communities (Mikola and Setälä 1998) while studies of mycorrhizal fungi argue the opposite (Van der Heijden et al. 1998). The linkages between plant diversity and soil communities and processes are also complex (Setälä and Huhta 1991; Harte and Kinzig 1993; Wardle and Nicholson 1996; De Mazancourt et al. 1998; Bardgett and Shine 1999; Naeem et al. 2000; Mikola et al. 2000; Spehn et al. 2000; Joffre and Ågren 2001; Mikola et al. 2001; Stephan et al. 2001; Mulder et al. 2003; Wardle et al. 2004). In the BioMERGE framework, we assume that the linkage is positive – that soil communities positively affect plants by mineralizing nutrients and that their diversity-function relationships follow the same pattern for other trophic levels (i.e., a positive, asymptotic BEF curve). This is an untested assumption with important consequences and requires considerable caution in interpreting results. One can relax this assumption by using several different BEF curves, but perhaps the most important point to make here is the need to find out if biodiversity in other trophic groups follows patterns similar to what has been observed for plants.

Step 2: Establish Diversity-Function Transition Matrices

A common approach to relating species to ecosystem functioning is to classify species into functional groups, but the wide variety and somewhat eclectic classification schemes make them difficult to use in BEF research (Lavorel and Garnier 2002; Naeem and Wright 2003). Rather than using functional groups, we propose directly using the functional traits of species that are the basis for forming functional groups in the first place (Lavorel and Garnier 2002; Naeem and Wright 2003).

Every organism possesses traits that characterize its response to environmental change and its effect on ecosystem processes. For example, in the face of a drought, plants with traits such as tap roots, persistent dormant seeds, thick cuticles, and greater water-use efficiency are more likely to persist than species that lack these traits. With respect to nitrogen cycling, plants with traits that facilitate microbial fixation of atmospheric nitrogen, either by harboring *Rhizobia* in nodules or supplying carbon to N-fixing bacteria in soils, impact soil N and N cycling in a variety of ways. If legumes lacked drought-tolerant traits in an ecosystem, then, based on response-traits, we could predict that a drought might negatively impact net N fixation.

To translate changes in biodiversity to changes in ecosystem functioning at large spatial scales requires four steps, each of which is illustrated in Fig. 10.4. First, a matrix of environmental variables and a matrix of species' abundances is constructed that reflects conditions prior to the application of a driver. Second, formulae are derived for adjusting each species' density or biomass according to its response functional trait. Third, using the effect functional traits, changes in ecosystem functioning are derived. Fourth, each trophic group is treated separately and the influence of one trophic group upon another is applied (see discussion above). These trophically adjusted, post-biotic-change abundances are then used to estimate what the resulting impacts on ecosystem function would be. Steps 2–4 yield the post biotic-change environmental matrix.

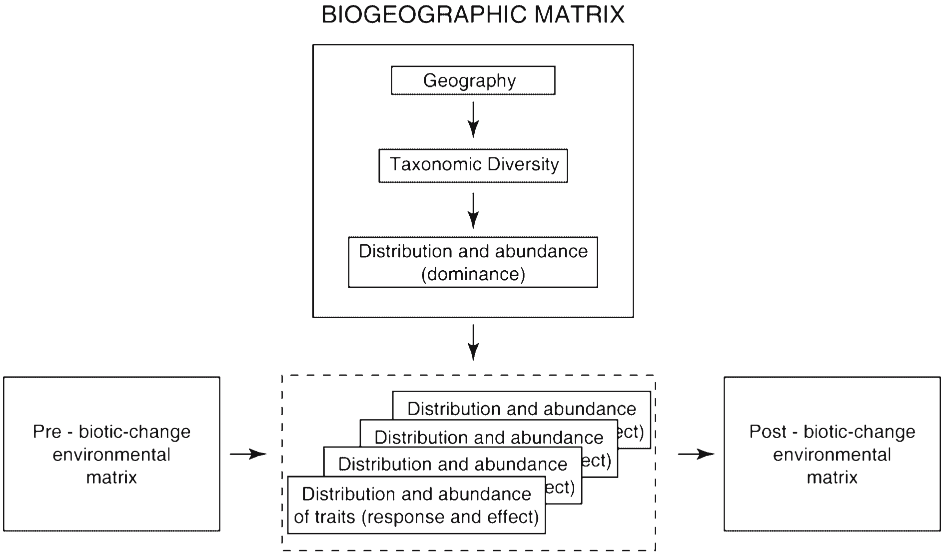

Fig. 10.4. The BioMERGE BEF implementation framework. BioMERGE develops methods of expanding from small-scale BEF research to landscape level predictions of the ecosystem consequences of changes in biodiversity. There are four basic steps; *(1)* designation or construction of a biota, *(2)* development of diversity-function transformation matrices, *(3)* application of driver scenarios for biodiversity change (most often local-extinction scenarios), and *(4)* estimation of the post-driver consequences of the selected driver(s). Constructing a biota (*top most box*) consists of using biodiversity information (i.e., species richness) developed for specific geographic locations. If distribution and abundance patterns (i.e., dominance patterns) are unavailable, then biogeographic principles are used to estimate likely patterns of distribution and abundance. Under the assumption that dominance patterns apply to all trophic levels, diversity-function matrices are developed (*boxes within dashed box on bottom*). These matrices consist of response- and effect-functional trait transformation matrices developed for each trophic group. The right most-box consists of the driver selected for investigation of ecosystem response to biodiversity change (e.g., drought, fire, increasing habitat fragmentation, elevated levels of N deposition, etc.) while the right-most box consists of the predictions for the outcome of the driver applied to the model system

Step 3: Select a Trait-Based Extinction Scenario for Change in Biodiversity

Once one has the model for converting changes in the environment to changes in ecosystem functioning (Fig. 10.4), one can explore how this model behaves when biodiversity is lost, but one has to chose a scenario for how biodiversity loss will occur. One can choose two routes for exploring biodiversity loss. First, as is done in experimental and theoretical BEF research, one can employ a neutral scenario, a combinatorial approach in which all possible compositions due to all possible sequences of species loss are examined. This neutral approach treats extinction probabilities for all species as a random variable.

The second is to employ trait-based extinction scenarios. By this we mean selecting an extinction driver (e.g., climate change, habitat fragmentation, or invasion) and varying extinction probabilities based on species' traits. For example, if the driver is habitat fragmentation, higher probabilities of extinction might be applied to rare species, species with small range sizes, species with small body size, or species in higher trophic levels. Extinction scenarios (based on expert opinion) were used by Sala et al. (2000) to derive predictions for the future of global biodiversity. This framework both extends and narrows this approach by using field-derived data rather than expert opinion on species' traits and drivers to predict specific changes in biodiversity for specific ecosystems rather than the globe. Note that it is at this point that environmental change, when treated as a driver, is incorporated into the analyses.

The main points of this implementation BEF framework are,

- instead of functional groups, response and effect traits are used
- biodiversity is as an explicit part of the conversion of changes in environmental factors to changes in ecosystem functioning through trait-based extinction scenarios

10.3 Discussion: Towards a Large Scale BEF

Initial work in biodiversity and ecosystem functioning focused on simply demonstrating that changes in biodiversity, however defined by researchers, could, in fact, change ecosystem functioning even if all other conditions were held constant. Confirmation of the hypothesis, formalized by the Vitousek-Hooper framework, was a critical first step in bringing biodiversity into our considerations of global change ecology. The next phase, to go beyond the confirmation of the Vitiousek-Hooper framework to one in which predictive applications of BEF principles can be employed in environmental problem solving, is even more critical. The BioMERGE framework is a suggestion for how to pursue this second phase. It does so by embedding much more ecology into its frameworks. By "more ecology," we mean that the BioMERGE framework

- uses patterns from biogeography (i.e., log-normal like projections) to estimate to estimate relative abundance,
- uses allometric scaling and macroecological principles to ascribe function to species,
- uses material and energy-efficiency transfer rates and trophic dynamics to estimate the influence of trophic structure on ecosystem function
- and uses trait-based extinction scenarios to link environmental change with changes in biodiversity.

Rather than supplying specific predictions of ecosystem response to biodiversity loss, it provides boundaries and central tendencies of ecosystem response to biodiversity loss. It also allows for different scenarios of biodiversity loss.

Like other synthetic frameworks, BioMERGE brings with it both the strengths and the limitations of the individual frameworks it incorporates. BioMERGE follows in the footsteps of many other synthetic frameworks, such as the Vitousek-Hooper framework, ecological stoichiometry (Elser and Sterner 2002), the unified neutral theory of biodiversity and biogeography (Hubbell 2001), the metabolic theory of ecology (Brown et al. 2004), island biogeography (MacArthur and Wilson 1967), each of which have tremendous predictive power, but whose limitations have made them each sources of much controversy. For example, in plant ecology, the continuum concept (Austin 1985) is a synthetic framework that combines autecology and biogeography to predict ecosystem function from biodiversity (Austin 1985, 1999). This framework, however, stands in conflict with frameworks that emphasize biotic interactions and system complexity (e.g., trophic-level dynamics, competition, facilitation and indirect and higher-order interactions) (Austin 1985; Callaway 1997). The inclusion of interactions in empirical work based on the continuum concept, however, is readily achieved (e.g., Garnier et al. 1997; Navas et al. 1999; Groves et al. 2003). The way forward is to embrace more complexity when necessary, but resist it when the gains in predictive power outweigh the costs of the added complexity. The BioMERGE framework goes beyond the continuum concept by the inclusion of intra- and inter-trophic interactions, metabolic theory, and biodiversity and ecosystem functioning, thereby incorporating the strengths of the continuum concept and other frameworks but at the cost of increased complexity.

For the reader, and to be honest, for the authors as well, the BioMERGE frameworks require us to conduct research that seems at first glance to be broad, imprecise, and far afield from traditional ecology. We urge, however, that ecologists not be deterred. Consider that early attempts to model global climate and the global carbon cycle began with equally coarse approximations, but the desire as well as the need to understand global warming led to concerted efforts by researchers to model climate change as best they could. Over time, data, models, and methods improved, and while climate change research is still not a precise science, it provides valuable insights into the potentials for anthropogenic forcing of climate processes to lead to significant and detrimental climate change. Given this history for climate change research, certainly understanding "biodiversity change" warrants equal attention.

The experimental and theoretical BEF research spurred by the growth of global change ecology led to a robust set of results that strongly suggest that within-trophic level changes in diversity are associated with changes in the magnitude and variability of ecosystem processes (Loreau et al. 2002; Loreau and Hector 2001). To be sure, many questions remain unanswered. To what extent are experimental results due to facilitation, niche complementarity, or sampling? Which components of biodiversity (is it functional diversity, the identity of species, or dominance) are the most important in determining the impacts of biodiversity loss? Compared to abiotic controls, do biodiversity controls over ecosystem functions matter? Is stability (low variability in ecosystem function in high diversity treatments) due to insurance (Yachi and Loreau 1999), statistical averaging (Doak et al. 1998), or other causes? These questions are not readily addressable by the small-scale experimental approaches that have typified BEF research, but large-scale experiments are impractical. Perhaps answers to these questions may come using observational studies and the BioMERGE frameworks.

Lessons learned from the controversies surrounding early phases of BEF research warn against indiscriminate employment of the BioMERGE framework. The BioMERGE framework has been partially and successfully employed by Solan et al. (2004) to predict ecosystem function (specifically, biogenic mixing) in a marine (estuarine) ecosystem. Similar studies are under way for North American and European grasslands and New World tropical rainforests. Clearly, BEF is scaling up. Perhaps the next step should be to combine a traditional combinatorial BEF experiment with a BioMERGE study and compare their findings.

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Part C

Landscapes under Changing Disturbance Regimes

Chapter 11

Plant Species Migration as a Key Uncertainty in Predicting Future Impacts of Climate Change on Ecosystems: Progress and Challenges

Guy F. Midgley · Wilfried Thuiller · Steven I. Higgins

11.1 Introduction

The prediction of climate change impacts on ecosystems is a challenging problem that has been addressed by both modeling and experimental approaches. The many varied experimental (e.g., Beier et al. 2004) and observational approaches (e.g., Parmesan and Yohe 2003) to investigating ecosystem and species responses to climate change are not addressed here. Modeling approaches also vary widely in approach and scale, from local "patch" scale simulation of system processes and competitive interactions (Shugart et al. 1992; Solomon 1986) to global scale simulation of vegetation functional and structural types (Prentice et al. 1992; Woodward et al. 1995). At "intermediate" geographic scales of landscapes and regions one modeling approach taken has been species-based, with the unit of simulation being the species' geographic range (Guisan and Zimmermann 2000; Huntley et al. 1995; Peterson 2001). Simulation approaches at local and global scales mentioned above are strongly process-oriented. They ignore species range preferences evident at the intermediate landscape and regional scale, and by default assume that a global species or functional pool is available to colonize each site, should environmental conditions be suitable at that site. This has largely concealed a key uncertainty in predicting ecosystem responses to climate change – that which is governed by the underlying spatial rearrangements of species' geographic ranges.

It is widely accepted that climate change impacts on natural species and communities will affect the geographic ranges of species (Parmesan and Yohe 2003; Walther et al. 2002). Indeed, early signs of climate change may be identified by species range shifts (Walther et al. 2001), strongly supporting the idea that range shifts are likely to continue in a larger number of species, and enhancing the possibility for new species invasions (Mooney and Hobbs 2000). What are the implications for predicting vegetation change in response to climate change? Importantly, species in existing plant communities are unlikely to possess similar migration capabilities, and as a result of differential migration and persistence, the communities of the future are unlikely to maintain the composition of those of today with novel communities likely to emerge (Neilson et al. 2005; Pitelka et al. 1997). Clearly, predictions of changing ecosystem function need to account for the species-specific range shifts that may result, apart from the direct conservation need to identify which species are not likely to migrate, and may therefore suffer range reductions and the threat of extinction (Thomas et al. 2004; Thuiller 2004). Considerations of migration and geographic range shift therefore have two direct applications – to modellers of ecosystem function whose models are underpinned by the presence of species with particular functional traits as ecosystem components, and to conservation planners who need to assess threats to biodiversity (Hannah et al. 2002).

The migration capabilities of organisms depend fundamentally both on the distances offspring move from their parents (dispersal) and on the number of offspring a parent produces (Skellam 1951). A great variety of processes is responsible for moving diaspores (Ridley 1930), hence predicting the distances that diaspores move is no trivial task (Higgins et al. 2003; Nathan et al. 2003). Similarly, the diverse range of processes that determines the number of offspring that individuals produce means that forecasting rates of population increase is a complex task (Neubert and Caswell 2000). Research on predicting migration rates has more recently sought to understand the extent to which migration rates are demographically or dispersal limited (Clark et al. 2003).

It is clear that the structure and composition of the world's vegetation can be broadly correlated with climate regime, but it is far more complex to derive from this observation the mechanisms that may drive range shifts as climate changes. This is for three main reasons: First, it is not known what proportion of the worlds species have current geographic ranges which are directly controlled by climate and not by other determinants such as disturbance regime (Bond et al. 2003), human land-use (Hobbs 2000), or strong inter-species interactions (either mutualistic or antagonistic) (Davis et al. 1998). Such factors are at most only indirectly linked to climate. Second, even if we knew precisely how climate controlled species ranges, it would remain a substantial challenge to predict how ranges might change dynamically due to lags in adult mortality and range contractions, which might delay range responses as climate changes. Third, human impacts that have fragmented the landscape and altered populations of biological dispersal vectors (Janzen and Martin 1982) have introduced barriers and filters to the dispersal and establishment of propagules. Many of these factors will retard migration rates (Collingham et al. 1996; Higgins et al. 2003; Schwartz et al. 2001). Other human activities, such as human mediated dispersal (Hodkinson and Thompson 1997) may accelerate spread rates. Plant species migration therefore represents a major uncertainty in the prediction of vegetation response to climate change (Higgins et al. 2003).

In spite of the problems identified above, there has been significant progress in modeling plant species' ability to migrate, driven by the need to project threats both of invasions by alien species and climate change to biodiversity (Clark et al. 2003). In this chapter, we review this progress in broad terms, and identify some key challenges and opportunities that remain.

11.2 Will Migration Be Necessary for Species Persistence?

Four broad responses may follow when populations of sessile organisms are confronted with a change in environmental conditions that compromise their physiological performance, namely local extinction, *in situ* persistence, *in situ* adaptation over generations (also termed an orthoselective response), and migration (Barnosky 1987). These responses are not all mutually exclusive, but may occur concurrently. For example, genetic patterns documented in several tree species reveal the synergistic effect of apparently recent (post-glacial) concurrent migration and selection in spatially separated populations (Cwynar et al. 1987; Davis and Shaw 2001).

In situ persistence is essentially a first line of defense for sessile organisms that can be accomplished either through high levels of tolerance and a long life span of the vegetative stage, or longevity and dormancy of propagules. Many species of extreme environments have evolved significant abilities to persist under adverse or unpredictable conditions, such as the propagules of desert annuals (van Rheede van Oudtshoorn and van Rooyen 1999), or long-lived trees (Bond and Midgley 2001). Persistence may allow many species of extreme environments to maintain a presence in the landscape long after suitable climate conditions have changed. Indeed, it now seems as though populations situated at the so-called "rear edge" of a species' geographic range undergoing a spatial shift are particularly important for the persistence of genetic diversity and evolution of species (Hampe and Petit 2005).

Genetic selection and adaptation is possibly an underappreciated control of species response to climate change (Davis and Shaw 2001), bearing in mind that rapid genetic change via selection under future anthropogenic climate change is possibly only relevant for the shortest-lived plant species. Nonetheless, selection by past climate change may determine current-day spatial variation in physiological optima of broad-ranging species in ways which affect predictions of species responses to climate change. For example, the response of the evergreen gymnosperm *Pinus contorta* to climate change and atmospheric CO_2 rise reverses from being positive throughout its range (if a single optimum genotype is assumed to inhabit the entire species range), to becoming slightly to strongly negative given the current distribution of varying genotypes (Rehfeldt et al. 1999). Nowak et al. (1994) illustrate a range of migration and adaptive responses to Pleistocene-Holocene change in woody plant species of the northwestern Great Basin, and demonstrate the clear existence of "orthoselective" species. These are species that possess high levels of genetic variation that permit their *in situ* persistence during periods of climate change through local selection of pre-adapted genotypes. The factors that determine adaptive plasticity are likely complex and species-specific, and it is too early to be able to generalize about how this response will emerge as anthropogenic climate change continues, but the topic deserves more attention in the context of species persistence.

There is currently no analysis available of what proportion of local, regional or global floras may persist or adapt to climate change *in situ*, but it is widely recognised that migration to keep pace with suitable climate conditions is a necessary response in organisms that lack extreme stress tolerance, longevity or genetic plasticity. Indeed, the rate and amount of climate change may ultimately exceed the capacity of either of these *in situ* responses. Studies of paleo-records strongly suggest that migration has been a widespread response to climate change in Pleistocene floras (e.g., Davis 1976; Davis 1983; Huntley 1990; Huntley and Birks 1983; Webb 1981; Webb 1992) and faunas (Graham 1992) and early monitoring efforts have identified incipient range shifts already occurring in response to recent climatic changes (Parmesan et al. 1999; Parmesan and Yohe 2003).

Spatially distinct genetic patterns in lodgepole pine in western Canada have been ascribed to migration accompanied by selection during post-glacial times (Cwynar et al. 1987), and Davis and Shaw (2001) illustrate several examples of concurrent genetic adaptation and migration, most conclusively for Scots Pine which has migrated extensively in northern Europe since the Last Glacial Maximum, and now shows physiological responses to climate cues that vary depending on the geographic provenance of the species. Thus, a combination of migration and concurrent selection has interacted to allow this species to occupy a range that is potentially wider than if the species had remained genetically homogenous across its range.

It is also apparent that the relative migration capabilities of species are reflected in the global patterns of biodiversity rich regions (e.g., Myers et al. 2000). It seems likely that Pleistocene climatic oscillations between glacial and interglacial climatic conditions have repeatedly sifted local biota according to their migration capabilities, and those regions which were exposed to relatively low rates and amounts of climate change have retained higher numbers of species as endemics (Jansson 2003). This pattern strongly suggests that migration has been a key determinant of the current global distribution of biodiversity, and that high rates of migration across the board are unlikely. Indeed, in the mid-latitude western Cape region of southern Africa, the key characteristics of an endemic include the likelihood of its being ant-dispersed (McDonald and Cowling 1995).

Given expected rates of anthropogenic climate change, what migration rates are required to allow species or species assemblages to keep pace? Two approaches have been taken to address this question. The first is derived from modeling global vegetation types using Dynamic Global Vegetation Models (DGVMs), and the second from modeling individual species ranges.

11.2.1 Vegetation-Type Models

Enhanced DGVMs represent one of the key products of the GCTE project (Cramer et al. 2001), and were designed to model ecosystem processes as determined by interacting vegetation and biogeochemical cycles (e.g., Bachelet et al. 2003; Box 1996; Foley et al. 1998; Holoyac 2000; Kirilenko et al. 2000; Sitch et al. 2003; Smith et al. 2001). Because of their complexity and the resultant computational demands in running them, DGVMs that simulate global vegetation structure and function commonly run at coarse spatial scales – typically more than 2 × 2 degrees of latitude and longitude (although they may be run at a rather fine temporal scale of days to hours and even minutes for some key processes such as photosynthesis). Given that propagule dispersal by plants only approaches distances appropriate to this coarse scale under extremely rare circumstances, DGVMs were clearly never designed to estimate migration requirements under climate change scenarios, but nonetheless have been used to do so (e.g., Malcolm et al. 2002).

Analyses of the required migration rate for ten biome types (representing between 60 and 80% of the Earth's surface) simulated by two vegetation models was estimated to be predominantly in the <300 m yr^{-1} range (Malcolm et al. 2002). For a minority of biome types (representing between 10 and 20% of the Earth's surface) required migration rates of between 1 000 and 10 000 m yr^{-1} were estimated (Fig. 11.1), not exceeding by far rates of migration recorded in the paleo-record (e.g., MacDonald 1993). The lowest required migration rates were found in tropical latitudes, but this increased strongly at latitudes of 40° and higher, such that temperate and circumpolar biomes had higher required rates than did tropical and subtropical biomes.

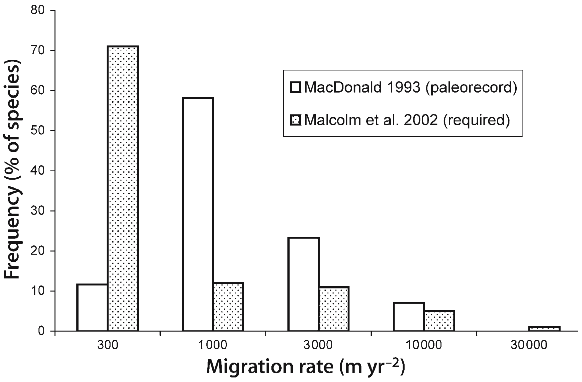

Fig. 11.1. Frequency distribution of post-glacial migration rates (from MacDonald 1993) in relation to required migration rates (from Malcolm et al. 2002). *x*-axis labels represent upper bounds of the migration rate categories

The concept behind Malcolm et al.'s (2002) analysis has been justifiably criticised (Loehle and LeBlanc 1996). Indeed, plant assemblages have never been stable through past variations in climate (Prentice 1986; Webb 1981). Many modern species assemblages do not appear to have long histories (Birks 1993; Davis 1983) and therefore communities or biomes are thought unlikely to move as an entity under changing environment conditions (Birks 1986; Huntley and Webb 1988).

Given the limitation of modeling vegetation types or biomes as whole entities, we analysed, for the purposes of this chapter, the required migration rates of individual plant functional types that define the world's biomes in the Sheffield DGVM (SDGVM, Woodward et al. 1995). In this DGVM, the geographic limits of individual functional types are defined by their physiological tolerances and performance relative to competing functional types. Biomes are then mapped using the relative composition of functional types. This approach is more justifiable than that of Malcolm et al. (2002) for a number of reasons. Most important is the fact that biomes may share functional types (and even species) with adjacent biomes, and the Malcolm et al. (2002) approach therefore overestimates required migration rates of shared functional types.

Our results for SDGVM are presented at a coarse spatial scale (Fig. 11.2) but nevertheless show that all functional types modeled show some migration to new ranges (Table 11.1), and that the most significant required migration rates are for temperate, subtropical and tropical functional types (C_3 shrub/grass, C_4 grass and deciduous broad-leaved tree functional types). Required migration rates are evenly spread with latitude, in contrast to the strong latitudinal patterning predicted by (Malcolm et al. 2002). This lack of latitudinal trend in our analysis is due partly to modeling relatively few functional types, which increases the likelihood of types being shared by

Fig. 11.2.
Global map of 3.75 × 2.5° pixels which experience the arrival of a novel plant functional type as projected by the SDGVM (Woodward 1995) using a climate change scenario for ~2050 according to the GCM HadCM3 (different *colours* represent the number of novel PFTs migrating into a cell, *green* = 1 PFT, *blue* = 2 PFT, *red* = 3 PFT)

Table 11.1.
Migration rates of 6 major plant functional types in terms of numbers of 2.5° pixels (median shift, mean shift and standard error), as projected by the SDGVM (Woodward 1995) using a climate change scenario for ~2050 according to the GCM HadCM3

PFT	C3	C4	Dcbl	Evbl	Dcnl	Evnl
# pixels	251	56	29	67	55	15
Median shift	4.5	3.75	3.75	2.5	2.5	2.5
Mean shift	8.33	4.50	4.93	3.47	3.77	4.37
Std error	0.47	0.37	0.68	0.20	0.29	0.81

adjacent geographic pixels. As such, these results are not directly comparable with those of (Malcolm et al. 2002). However, despite differences in approach, both analyses underline the central message that biogeochemically-based modeling approaches of vegetation predict a substantial requirement for migration of biomes and functional types to new geographic ranges.

The need to incorporate dispersal limitations into DGVM forecasts has been recognised for some time (e.g., Pitelka et al. 1997), but the challenges are substantial. A recent treatment (Neilson et al. 2005) has reiterated that, apart from the challenge of simulating dispersal realistically at such coarse spatial scale, it is difficult to assign a distribution of potential migration rates to plant functional types. This is because plant functional types group species based on functional or vegetative attributes (Smith et al. 1997), and there are not yet well known relationships between these attributes and attributes of fecundity and dispersal. Several issues need to be considered when trying to generalize species-specific knowledge about dispersal and fecundity. For example, how does dispersal ability relate to traits that define either the response to environmental factors or ecosystem functioning (Lavorel and Garnier 2002), and on what basis should functional types be split to distinguish between poor and good dispersers?

It is clear that by incorporating greater scientific understanding of plant functional types and a necessary increase in computational power, future DGVMs will resolve functional types more finely, and operate at finer spatial scale. It may, therefore, become feasible to assign dispersal and fecundity characteristics to functional types that more closely represent groups of species and even individual species, and model their migration more credibly. This step will be critical to allow DGVMs to account for lags in ecosystem response to climate change induced by migration limitations (Neilson et al. 2005), which currently introduce is ignored as an uncertainty in DGVM simulations.

11.2.2 Species-Based Models

Species-based approaches (also called niche-based models) have received increasing interest in the past decade because of their apparent ability to project the potential geographic range responses of multiple species, finally allowing some quantification of species' range shifts in response to climate change. Several recent studies have applied this class of models to generate and estimate risk of species extinctions (Thomas et al. 2004), as well as species' range shifts, species turnover, and variation in species richness (Iverson and Prasad 2002; Bakkenes et al. 2002; Thuiller 2003; Schwartz et al. 2001; Peterson 2003), under global climate change. Recent steps have included the use of species-based models to select areas for species persistence (Araújo and Williams 2000) and to assess the persistence of species in existing reserve networks in the face climate change (Araújo et al. 2004).

Despite considerable research on statistical models of species-climate relationships and their application to climate change studies, the uncertainties in forecasts of such models arising from ecological and methodological considerations have not so far been estimated. Species-based approaches have primarily been derived by developing statistical relationships between known species ranges and environmental variables taken as surrogates for physiologically relevant variables (Austin et al. 1994; Austin and Smith 1989; Guisan and Zimmermann 2000). The approach relies heavily on the concept of Hutchinson's realized niche, recently clarified by Leibold (1995) and Pulliam (2000). In this regard, the most frequent over-simplification found in the literature is the statement that, due to the observed distributions being constrained by biotic interactions, species-based approaches *de facto* quantify the realized niche of species, and never the fundamental niche (Pulliam 2000). As a direct consequence, projecting these models into climatically changed future conditions is, at least according to theory, likely to generate mistakes (Davis et al. 1998), but see Pearson and Dawson (2003) and reply from Hampe (2004).

The degree of error in predictions of niche-based models should thus be related in some way to the competitive status of the species for a given resource (weak vs. strong competitor), which in turn should allow the prediction of whether the species occupies its full fundamental niche or only part of it. Recent analyses have shown that it may be possible to include inter-specific competition in these models (Leathwick and Austin 2001; Anderson et al. 2002) but the competitive status of species can also be expected to change with a changing climate (Davis et al. 1998; Hughes 2000).

A further source of uncertainty is due to the fact that these models are static in space and time and are conceptually unable to cope with non-equilibrium situations, since they do not distinguish between the transient and equilibrium responses of species to a stochastically and dynamically changing environment (Guisan and Zimmermann 2000). As a direct consequence, they cannot theoretically include migration in a dynamic way. To cope with this limitation, recent risk assessment analyses for future climate change scenarios have commonly used two crude assumptions about migration, namely no migration beyond a species present site ("zero migration" or "null migration") and perfect migration to all sites, or "full migration" (Peterson et al. 2002; Thomas et al. 2004; Thuiller 2004). These approximations bracket the most pessimistic and optimistic estimates of future species range size, but have so far incorporated only the simplest migration limitations (i.e., migration into contiguous elements of the modeled landscape (Peterson et al. 2002)) to refine these estimates. The projected impacts of climate change on species turnover (an index of community compositional change and probably linked with ecosystem function) are very strongly influenced by the contrasting migration assumptions of zero and universal migration (Fig. 11.3), and this clearly demonstrates the current limitation in forecasting climate change impacts on biodiversity, and ecosystem structure and function, induced by uncertainties in migration rate.

11.3 Measurements and Models of Migration Rates

Much of our understanding of plant migration is derived from paleo-botanical studies of northern hemisphere regions (Davis 1976; Huntley and Birks 1983; Webb 1992). These studies indicated that several tree genera appeared to migrate rapidly from equatorward "refugial" populations of the Last Glacial Maximum (LGM), some 20 000 years ago, to occupy their current ranges several degrees of latitude poleward. Although some of these

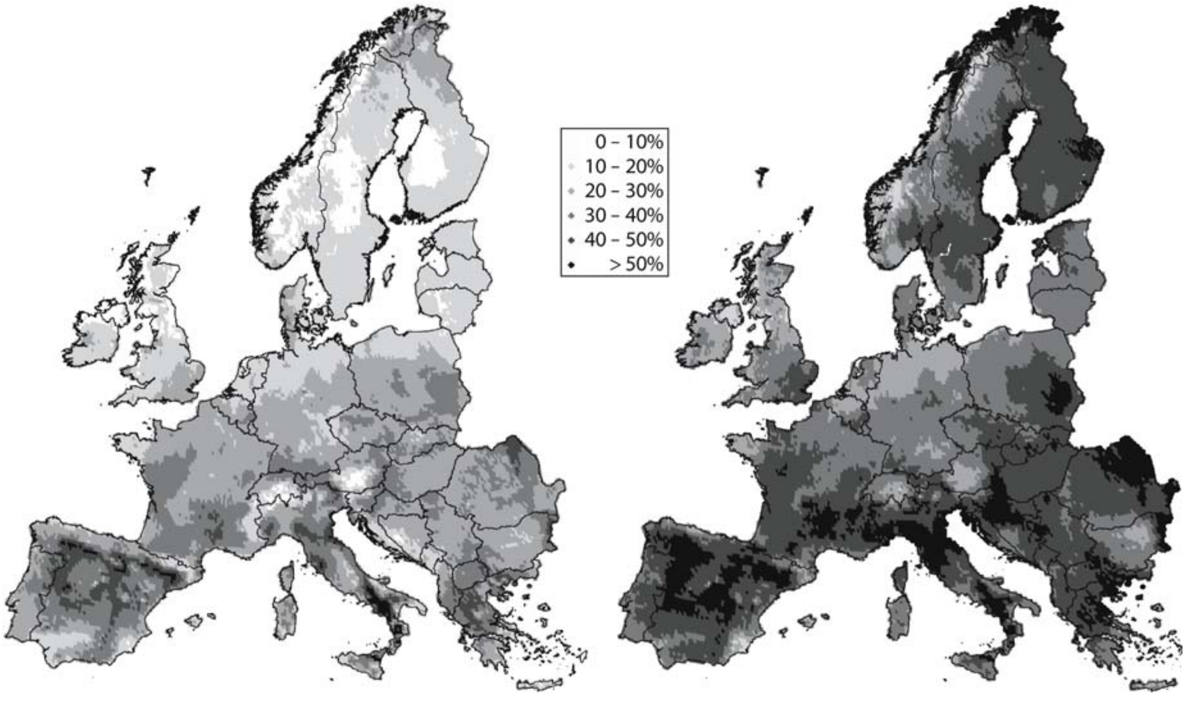

Fig. 11.3. Rate of plant species turnover in Europe for a climate scenario simulated by the GCM HadCM3 under the A1 SRES assumptions (Nakicenovic and Swart 2000), assuming either no species dispersal (*left hand panel*), or universal dispersal (*right hand panel*)

paleo-botanical studies have recently been questioned (e.g., McClachlan and Clark 2004), the balance of evidence suggests that rapid spread ($>100\ \text{m yr}^{-1}$) is possible, at least for some species. This apparent empirical evidence for rapid migration cannot be reconciled with models of plant spread that assumed that dispersal should be approximated as a diffusion process (Skellam 1951). This conundrum (termed "Reid's paradox" by Clark et al. 1998) was resolved by re-examining the simple diffusion assumption that lies at the heart of classical models of spread. Relaxing the assumption that the distribution of seed dispersal distances is Gaussian was found to be consistent with empirical data on the distribution of seed dispersal distances. Moreover, the resulting spread rates were consistent with the rates estimated from the paleo-ecological evidence (Clark 1998; Higgins and Richardson 1999). Hence a new class of spread models have emerged that essentially all treat dispersal as a stratified process (Shigesada et al. 1995). That is, they accommodate the possibility that most diaspores move relatively short distances and that a few diaspores move relatively long distances.

The "resolution" of Reid's paradox has shifted attention away from dispersal and focused it on the other component of spread models, namely the demographic component (Clark et al. 2003). Our empirical knowledge of demographic rates suggest that most populations are neither increasing nor decreasing, that is they have population growth rates close to zero (Franco and Silvertown 2004). A population with a zero growth rate cannot spread, hence most populations for which we have empirical data on demographic rates would be predicted not to spread. However, growth rates could become positive as a result of disturbances caused by climate change, due to the opening up of new geographic areas suitable for occupation by species. Very little is known about how rapidly population growth at the margins of species' ranges will respond to an "improving" climate, and the new availability of space in adjacent areas.

Most data on demographic rates are, for practical reasons, collected from sites where the study species are common (e.g., Sagarin and Gaines 2002), but the demographic rates estimated at such sites are not representative of the conditions to which a spreading population may be exposed. Ideally demographic parameter variation needs to be estimated from the so-called "core" to the edge of species ranges – seldom done, such an approach may yield useful insights into demographic factors controlling range limits (e.g., Brewer and Gaston 2003). It seems especially at range edges that this information could contribute to a fuller understanding of the vulnerability of marginal populations to temporal variability (Vucetich and Waite 2003).

Spreading alien invasive species provide an opportunity to estimate the demographic rates that are appropriate for spread models. For instance, Higgins (2001) estimated demographic and dispersal parameters for spreading invasive plants. While much can be learned from the spread of invasive species about the potential spread of native species under climate change, several factors mean that the knowledge gained is not directly transferable. Notably, spreading alien species are often demographic super-organisms because of predator and competitor release (Keane and Crawley 2002). This suggests that to forecast the spread rate of native species under climate change we need to estimate the likelihood that predators and competitors will accompany the target species, which is clearly a complex task. Nonetheless, studies of invasive plants do reveal the complexities of predicting whether a species that appears to be physiologically suited to a site will indeed invade that site. This subject has both entertained and frustrated invasion biologists for decades, and although significant progress has been made, experience from invasions suggests that our predictive power remains modest (Rejmanek et al. 2004). Studies of spreading invasives also inform us that alien species will migrate rapidly; simple calculations based on the differences in demographic rates between native and alien species with similar life histories suggest that aliens will indeed migrate orders of magnitude faster than native species (Richardson et al. 2000).

A great difference for plants between past episodes of climate change and the current anthropogenic warming is the human alteration of landscapes, involving fragmentation of pristine habitat into patches of varying sizes and connectivity, and the creation of barriers to dispersal. Theoretical models of spread in landscapes influenced by fragmentation and habitat loss show that there may be critical thresholds in landscape connectivity beyond which migration processes cease (Higgins et al. 2003), but the data needed to test these models are far from complete, and will be very challenging to collect. More detailed models of spread that include occasional long distance dispersal have demonstrated that although thresholds may not exist, linear decreases in spread rate with increasing fragmentation and habitat loss are to be expected (Collingham and Huntley 2000; Higgins and Richardson 1999; Lavorel et al. 1995; Malanson 2003). These studies emphasize that additional dispersal traits that define how dispersal will interact with human-transformed landscapes, are needed to predict spread rates in contemporary landscapes (Higgins et al. 2003).

11.4 Linking Migration and Niche Based Models

The previous section has reviewed how an incomplete knowledge of the potential migration rate of species limits our current capacity to predict the impacts of global climate change on the future geographic distribution of species, their range sizes and even potential vulnerability to extinction. Yet very few studies have combined mechanistic models of migration with spatially-explicit models of geographic range shifts. Niche-based models offer a potentially useful tool to predict species range shifts for indigenous species, and even areas susceptible to invasion by alien species (albeit these correlation approaches can only interpolate, not extrapolate into the future). Recent studies (Hoffman 2001; Peterson 2003; Peterson et al. 2003; Peterson and Vieglais 2001; Welk et al. 2002) have shown that this approach could provide a robust alternative to more complex, process-based models (Sutherst et al. 2000). However, despite the usefulness of such niche-based models in drawing potential maps of risk, species migration is not routinely incorporated in this approach.

Some preliminary attempts to integrate niche-based models and mechanistic dispersal models have been carried out. For instance, Iverson, Schwartz and colleagues (Iverson et al. 2004; Schwartz et al. 2001) have recently developed interesting analyses to predict the shift of trees due to climate changing in eastern US, based on the coupling between a niche-based model simulating the future potential suitable area for a species, and a cellular automaton simulating seed dispersal into a fragmented landscape. Such "hybrid" approaches combining different models are promising because they allow inclusion of transient responses of species to changing environments (see also Collingham (2000) and Malanson (2003)). These approaches are also useful in that they encompass a spatial scale within which migration can be simulated realistically, especially by differentiating between long- and short-distance dispersal of propagules, and assessing the relative importance of uncertainty inherent in their estimation. More studies of this kind are needed in order to develop better forecasts of future species range size, distribution and vulnerability to extinction under a wide range of migration rate assumptions (Higgins et al. 2003).

11.5 Summary and Conclusions

As we show above, a failure to incorporate migration limitations into models of vegetation response to climate change greatly compromises their predictive capability, and the uncertainty due to migration is therefore substantial. Species range shifts have been a ubiquitous response by plant species during Pleistocene climate change, and early signs of this response are evident in modern assemblages. Recent work has increased our understanding of the dispersal limitations to migration rate, but there has been far less focus on the issues which govern population establishment and growth rate, especially at the edge of species' ranges.

An overall understanding of community responses to climate change would also benefit from better understanding of *in situ* adaptive responses, as these appear to be significant in some species. Much has been learned from reconstructions of past migration patterns in the paleo-record, and from studies of alien invasive plants, but these "natural experiments" are limited in that they represent special cases where species migration occurs over landscapes unfragmented by human activities (paleo-record), or are experiencing release from predators and pathogens (alien species).

Finally, promising approaches are being developed that address the issue of how human transformation of landscapes will modify migration rates, and that combine mechanistic migration models with spatially explicit models of species geographic ranges at spatial scales relevant to simulating plant propagule dispersal and demographic behavior. These approaches will provide useful insights into biodiversity change under climate and land-use change scenarios. However, the potential increase in spatial resolution of DGVM simulations, and their increasing capacity to simulate more finely defined plant functional types, will allow them to provide an independent alternative assessment of the role of migration in determining the future structure and function of the ecosystems of the Earth.

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Chapter 12

Understanding Global Fire Dynamics by Classifying and Comparing Spatial Models of Vegetation and Fire

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12.1 Introduction

Wildland fire is a major disturbance in most ecosystems worldwide (Crutzen and Goldammer 1993). The interaction of fire with climate and vegetation over long time spans, often referred to as the fire regime (Agee 1993; Clark 1993; Swetnam and Baisan 1996; Swetnam 1997), has major effects on dominant vegetation, ecosystem carbon budget, and biodiversity (Gardner et al. 1996; Lenihan et al. 1998; Ryan 1991; Starfield and Chapin 1996). These effects include cycling nutrients, regulating succession, maintaining diversity, reducing biomass, controlling insect and disease populations, triggering interactions between vegetation and animals, and maintaining important biological and biogeochemical processes (Johnson 1992; Agee 1993; Crutzen and Goldammer 1993; DeBano et al. 1998). Carbon cycles are intimately linked to fire regimes because of the accumulation and combustion of fuel and post-fire vegetation development (Kasischke et al. 1995; Olsen 1981). Fire has sculpted landscapes for millennia by dictating pattern dynamics and community composition (Knight 1987; Swanson et al. 1997).

Modification of the fire regime due to climate warming (e.g., Cary and Banks 1999) may overwhelm many of the commonly investigated ecosystem responses to climate change, including ecosystem productivity, plant migration, and species extinction (Weber and Flannigan 1997; Ryan 1991; Keane et al. 1998). Large nonlinear changes in vegetation composition and structure are likely to occur in response to climate warming and human land use because of the overriding influence of the fire regime (Flannigan and Van Wagner 1991; Crutzen and Goldammer 1993). Carbon storage in some forest ecosystems may significantly decline if fire increases due to climate warming (Kasischke et al. 1995). Because of the inherent complexity of the interactions of fire, climate, and vegetation across multiple scales, simulation modeling is a critical tool for exploring and understanding climate change implications.

A major problem in projecting ecological change and understanding its mechanisms is the lack of non-equilibrium dynamics in many ecological models. The inclusion of disturbance, especially fire, is essential for dynamic vegetation models to simulate transient changes in vegetation composition and structure. Understanding landscape dynamics in relation to fire and how these dynamics may be altered by climate and land-use changes is critical. Additionally, understanding human impacts on the fire regime is essential for projecting vegetation change in human-modified landscapes, which now occupy large proportions of the globe. Using our current understanding of fire behavior, fire ecology and fire-weather, a set of dynamic fire-climate-vegetation models could be developed to simulate fire effects at temporal and spatial scales relevant to vegetation change.

One approach to addressing the effects of changing climate on fire and vegetation dynamics is simulation modeling. At the global scale there appear to be two options: (1) a suite of landscape models that spatially simulate succession and fire dynamics at local scales, or (2) coarse scale vegetation models, called Dynamic Global Vegetation Models or DGVM, that have been developed to predict vegetation response to climate change at global scales (Neilson and Running 1996; Lenihan et al. 1998; Thonicke et al. 2001). However, there are drawbacks to both. The available landscape models are quite different in design and application, developed for different ecosystems and fire regimes, and as such cannot be brought together for comprehensive global simulations. Second, the incorporation of fire into DGVMs to predict these ecosystem responses at global scales has been problematic because of confounding environmental complexities that govern global fire regimes and the general lack of understanding of which fire regime characteristics are important at coarse scales.

This chapter summarizes an effort by the Landscape Fire Working Group, formed under the aegis of the Global Change and Terrestrial Ecosystems Project (GCTE – Task 2.2.2) to identify those fire processes that are essential to dynamically model landscape vegetation changes. This was accomplished by classifying and comparing existing fine-scale, spatial, non-equilibrium process-based ecological models that simulate the dynamic interactions between climate, fire and vegetation, which we called Landscape Fire Succession Models or LFSMs. By classifying all existing LFSMs, we were able to inventory the diverse methods currently used to simulate vegetation, climate, and fire interactions in a spatial domain. We then selected a set of models from a suite of classification categories to perform an extensive LFSM comparison on neutral landscapes to identify the relative importance and sensitivity of simulated fire to terrain, fuel pattern, climate, and weather. Once the important processes were identified, we developed a set of recommendations for including fire dynamics in DGVMs.

12.2 Background

We define LFSMs as models that simulate the linked processes of fire and succession (i.e., vegetation development) in a spatial domain. Although the complexity of spatial relationships of vegetation and fire dynamics may vary from model to model, all LFSMs, by definition, produce time-dependent, georeferenced results in the form of digital maps or GIS layers. Additional processes may have been incorporated into the LFSM simulation, such as timber harvesting and biogeochemical modeling (explicit simulation of the flow of energy, carbon, water, and other elements within an ecosystem or landscape), but the minimum requirement for a LFSM is the explicit linkage between fire and succession. Climatic processes need not be explicitly incorporated into the LFSM, but, because of our interests in climate change, special attention was given to those models that consider the direct effect of weather on fire occurrence and vegetation change.

A series of six GCTE sponsored workshops attended by a wide variety of international ecological modelers and ecologists was held from 1999 to 2003 to synthesize current landscape fire modeling into an organized framework (see Hawkes and Flannigan 2000). One product of these workshops was an objective, quantitative protocol for comparing LFSM simulations across neutral landscapes (i.e., artificial landscapes where topography and vegetation characteristics are controlled) and regional climates to determine the relative sensitivity of predictions to model structure and complexity (Cary et al. 2006). A standardized set of model descriptive elements (MDE) was developed to qualitatively contrast and compare LFSMs, and the values for these elements were estimated by the modelers and entered into a database (Rupp et al. 2001). Information included in the MDE data base included initial purpose of the model, the ecosystem type being simulated, nature of the vegetation being represented and the method of succession, climate variables and drivers, the temporal and spatial scales of predictions, and computing constraints (Keane et al. 2004).

Using workshop findings and the MDE database information, we identified four essential components in LFSMs that represent the primary processes governing the landscape simulation of vegetation and fire: (1) vegetation succession, (2) fire ignition, (3) fire spread, and (4) fire effects. Any LFSM needed to contain all of these components. We assumed any other ecosystem and landscape process simulated by an LFSM, such as harvesting and insect epidemics, could be added as other components or incorporated into one or more of these four primary components. For example, fuel accumulation would be considered part of the vegetation succession component. We debated whether fire extinguishments – when a spreading fire actually goes out – was another component, but decided it should be part of the spread component (i.e., extinguishment is the lack of spread) for simplicity.

Each component for every LFSM was described by the approach, scale, and strategy by the modelers or authors, and this information was also entered into the MDE database (Reinhardt et al. 2001; Keane and Finney 2003; Keane et al. 2004). The approach defines the general design of the model as probabilistic (based on stochastic processes), empirical (based on relationships described by data), or physical (based on fundamental physical processes). Spatial scales are either regional (1 000s of km^2), landscape (10s of km^2), forest stand (<1 ha), or at the level of the individual plant (~m^2). The strategy describes the algorithms, tools, or techniques used to represent a simulation component. Many LFSM components were developed by merging multiple approaches, scales, and strategies.

12.3 Model Classification

The classification effort provided the framework to interpret differences between LFSMs and for stratifying LFSMs for the subsequent comparisons (see Keane et al. 2004 for full details). The classification was based on the four primary processes that influence fire and vegetation dynamics – fire ignition, fire spread, fire effects, and vegetation succession – and the approaches used to represent these processes in the models. The classification space for each component was described in three dimensions by the gradients of stochasticity, complexity, and mechanism that best characterize the simulation of that component. Stochasticity was defined as the amount of randomness inherent in the component design, or the degree at which probabilistic functions influence the simulation of that component. Complexity was defined as the inherent detail incorporated into the design of a simulated component. Models with low complexity have modest sophistication in simulation detail and those with a large number of parameters are considered quite complex. Mechanism was the degree to which fundamental physical or chemical processes are represented in the simulation of a LFSM component. This resulted in 12 evaluation elements (4 components by 3 gradients) for each model. Together, these elements represented a formal description that can be used to objectively compare other models. There is some unavoidable ambiguity in these gradients, but overall we felt these 12 evaluation elements provided a standardized, comprehensive, and somewhat objective context in which to assess LFSMs. In addition, this method can be used to classify and compare other types of models by modifying, eliminating, or adding gradients and components.

We conducted an inventory of existing LFSMs using information gained from workshop participants, a review of the literature, and correspondence with modelers. Only LFSMs that were published in some form were considered, and this search found 44 LFSMs that were used in the classification effort. We contacted the developers of these models and asked them to rate the simulation of the four components (succession, fire ignition, fire spread, and fire effects) by the three evaluation gradients (stochasticity, complexity, and mechanism) using a scale from zero to 10 (zero meant that it was not modeled or applicable and 10 represented the highest level of stochasticity, mechanism, or complexity). Some modelers did not reply, so we assigned our own ratings based on a thorough review of publications on the model. The values assigned to each evaluation element were compiled into a database and then analyzed to identify groups of similar models. To ensure consistency across modeler evaluations of their own models, we created another database with our own assignments of evaluation elements based on published literature and our knowledge of the model.

To identify natural clusters or groups, the evaluation element data were ordinated using principal components analysis (PCA) and clustered using TWINSPAN techniques in the PC-ORD package (McCune and Mefford 1999). The See5 statistical software (Quinlan 2003) was also used to cluster the evaluation element data using Ward's minimum variance hierarchical clustering, which is a divisive clustering technique. The ordination and clustering results alone were not sufficient for developing a comprehensive classification because of the high variance in evaluation elements across models. Therefore, we revised the MDE database created from the workshops so that keywords were used to describe various explanatory categories such as approach, strategy, scale and other descriptive attributes by LFSM component. We then compared the frequency of keywords for each category across all LFSMs to qualitatively identify similar characteristics and natural clusters.

A general LFSM classification was developed from the fusion of the ordination, clustering, and keyword comparison results (Fig. 12.1). This classification has 12 hierarchically nested classes that are distinguished by their scale of application (coarse vs. fine), representation of vegetation (individual plant cohorts vs. framed-based community), simulation of succession (age, empirical, gap-phase, or successional pathway) and the explicit or implicit simulation of fire spread. The locations of all LFSMs and six classification categories are shown in ordination space in Fig. 12.2. A dichotomous key for the classification was constructed from the MDE database using See5 analysis. We then related common keywords to the dichotomous key to name and identify important branches in the dichotomy.

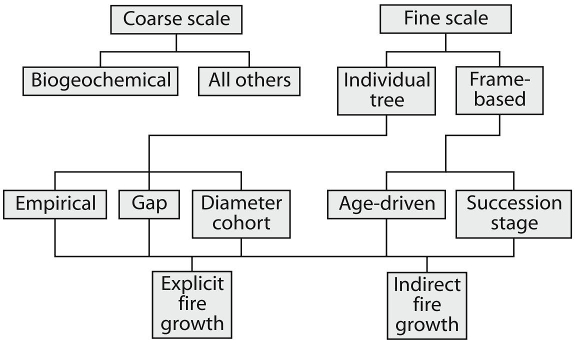

Fig. 12.1. Final set of categories for landscape fire succession models classified using the degree of stochasticity, complexity, and mechanism in the design of the model components of succession, fire ignition, fire spread and fire effects

12.4 Model Comparison

The model comparison was undertaken to identify the relative influence of environmental processes on fire dynamics. It is comprised of three phases of which only results from the first phase are presented in this chapter. In the first phase, we evaluated the sensitivity of fire spread and ignition components without the influence of fire effects and subsequent vegetation development (Phase 2 and 3, respectively). We compared five LFSMs that covered three classification categories for this exercise: LANDSUM, FIRESCAPE, EMBYR, SEMLAND, and a special application of the LAMOS modeling shell called LAMOS-DS (Table 12.1). These models are quite different in many aspects including a wide diversity in their approaches for simulating fire spread and ignition, representation of vegetation, and the complexity of climate and fire linkages (see Fig. 12.2, Table 12.1).

12.4.1 The Models

EMBYR is an event-driven, grid-based simulation model of fire ignition and spread designed to represent the landscapes and fire regimes of Yellowstone National Park (Hargrove et al. 2000). The pattern of forest succession of lodgepole pine forests is simulated by a Markov model, with fuels sufficient to sustain crown fires developing as a function of forest stand age. Fire spread is simulated by examining each burning site and determining spread to the eight neighboring sites as a function of fuel type, fuel moisture, wind speed and direction, and slope. A qualitative index of fire severity of each burned site, estimated as a function of fuel type, fuel moisture, wind speed and burn rate, is used to determine when fire intensity is sufficient to result in a stand-replacing fire.

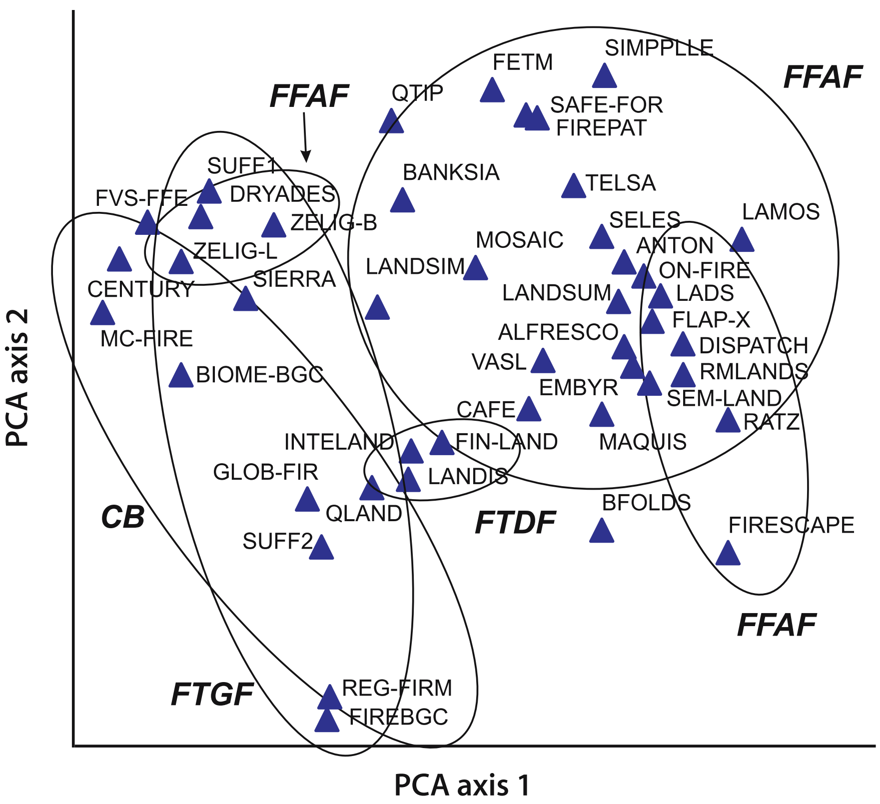

Fig. 12.2.
Delineation of six model classes in ordination space for the developed classification using ratings assigned by the modelers. This shows the relative position between classes and the similarity of models within a class

Table 12.1. Landscape fire succession models included in the model comparison effort with a general description of its application

Model name	References	Ecosystem	Geographic area	Weather database
EMBYR	(Gardner et al. 1996; Hargrove et al. 2000)	Lodgepole pine forests	Central Rockies, USA	Glacier National Park
FIRESCAPE	(Cary and Banks 1999; Cary 2002)	Eucalypts forest	Southeastern Australia	Australian Capital Territory
LAMOS(DS)	(Lavorel et al. 2000)	Any	Portugal	Corsica, Italy
LANDSUM	(Keane et al. 1997; Keane et al. 2002)	Any	Northern Rockies, USA	Glacier National Park
SEM-LAND	(Li 2000, 2001)	Spruce-fir forests	Canada	Edmonton, Alberta

EMBYR propagates fire by user-defined probabilities of fire spread. The probabilities are dependent on the age of the forest stand and the fuel moisture conditions (i.e., probabilities of spread increase with increasing age and decreasing fuel moisture) and are adjusted during the simulation by the local topography, fuel moisture, wind speed and direction.

FIRESCAPE generates spatial patterns of fire regime (Gill 1975) for *Eucalyptus* dominated landscapes in south-eastern Australia (Cary and Banks 1999). It operates on a daily time step that changes to hourly whenever a fire ignites. Daily weather is generated using a type stochastic climate generator (Richardson 1981; Matalas 1967; Cary and Gallant 1997; McCarthy and Cary 2002) and ignition locations are generated from an empirical model of lightning strike locations (Cary 1998). The spread of fire from cells to immediate neighbors is a function of elliptical fire spread (Van Wagner 1969) and Huygens' Principle (Anderson et al. 1982). Head fire rate of spread is determined from the equation form of McArthur's Forest Fire Danger Meter (McArthur 1967; Noble et al. 1980) and fuel loads are modeled using Olson's (1963) model of biomass accumulation which has been parameterized for a range of Australian systems (Fox et al. 1979; Raison et al. 1986). Fire line intensity ($\mathrm{kW\,m^{-1}}$) is calculated for the spread of fire from one cell to the next for characterizing this aspect of the fire regime and for determining the extinction of the individual fire events.

LAMOS-DS is an implementation of LAMOS (Lavorel et al. 2000) with a contagious fire spread model working on a daily time step. It is a simple model, sensible to daily minimum and maximum temperature, precipitation, fuel amount and slope. LAMOS-DS contains two principle functions; one to estimate pan evaporation (Bristow and Campbell 1984; Roderick 1999) which, together with precipitation, produces a moisture budget, and a second equation to modify spread probabilities as a function of slope (Li 2000) and intensity. Fire intensity is the product of three linear functions: fuel load (0–1 kg m^{-2}), moisture (0–200 mm) and temperature (5–25 °C). Temperature during the course of the fire is interpolated between the daily minimum and maximum by a symmetrical sine function. Fires are assumed to begin when temperature is at the daily maximum. Fuel is consumed in proportion to the resulting fireline intensity.

The LANDscape SUccession Model (LANDSUM) is a spatially explicit vegetation dynamics simulation program wherein succession is treated as a deterministic process using a pathway or frame-based community sequence approach, and disturbances (e.g., fire, insects, and disease) are treated as stochastic processes with all but fire occurring at the polygon scale (Keane et al. 1997, 2002). LANDSUM simulates fire spread from user-specified wind speed and direction, slope, and fuel type (burn, no-burn) determined from the succession stage using equations from Rothermel (1972) and Albini (1976).

The SEM-LAND model (Spatially Explicit Model for LANdscape Dynamics) simulates fire regimes and associated forest landscape dynamics resulting from long-term interactions among forest fire events, landscape structures, and weather conditions. A fire process is simulated in two stages: initiation and spread (Li 2000, 2001). The fire initiation stage continues from the presence of a fire ignition source in a forest stand until most trees in that stand have been burned. Once most trees are burned, the fire has the potential to spread to its surrounding cells, and whether a neighboring cell would be burned is a function of the fire spread probability. The fire spread probability is determined by not only fuel and weather conditions, but also by slope in landscape topography. The Canadian Forestry Fire Weather Index system (FWI) (Van Wagner 1987) and the Canadian Forest Fire Behavior Prediction system (FBP) (Forest Canada Fire Danger Group 1992; Hirsh 1996) were used to drive weather, fire spread, and fuel moisture interactions in the model simulation.

12.4.2 The Comparison Design

The comparison involved evaluating the effects of variation in terrain, fuel pattern (i.e., vegetation), climate, and weather on the simulated annual number of fire ignitions and area burned using a set of neutral landscapes and native simulation parameters (i.e., simulation parameters quantified for the region for which the model was developed). The simulation landscapes were represented by a 1 000 × 1 000 array of square 50 m pixels. Variation in terrain was introduced by generating three landscapes with a systematic pattern of valleys and peaks – flat, undulating, and mountainous – characterized by maximum slope values of 0°, 15° and 30° and relief of 0 m, 1 250 m and 2 500 m respectively (Fig. 12.3a) created by a two-dimensional sine function with periodicity of 16.67 km (333.3 pixels).

Two patterns of fuel treatment – finely clumped and coarsely clumped spatial pattern – were evaluated (Fig. 12.3b,c). We created 10 replicates of finely and coarsely clumped fuel maps by randomly allocating values from the series 0.1, 0.2, 0.3, …, 1.0 (inclusive) to either 50 × 50 pixel (625 ha) clumps (coarsely clumped) or 10 × 10 pixel (25 ha) clumps (finely clumped) so that values were evenly represented across landscapes. Fuel maps were transformed differently for each model to produce either fuel or age related maps that were meaningful to individual models (Cary et al. 2006).

Simulations were performed using weather relevant to the location where the model had been previously parameterized and tested, although we attempted to standardize the amount of variability represented across the weather years chosen for each model. Ten, year-long se-

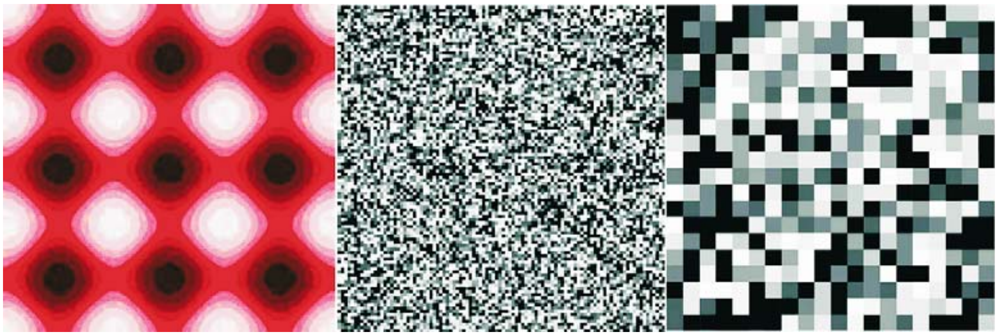
a Terrain **b** Finely clumped **c** Coarsely clumped

Fig. 12.3. Neutral landscapes used as inputs in the model comparison effort. **a** topography is represented by an "egg carton" shape with lowest and highest elevation indicated by *lightest* and *darkest color* respectively, **b** the finely clumped fuel landscape was created by randomly assigning fuel types or associated vegetation types to each pixel on the simulation landscape in 25 ha patches, and **c** the coarsely clumped fuel pattern was created by randomly assigning fuel types within 625 ha patches

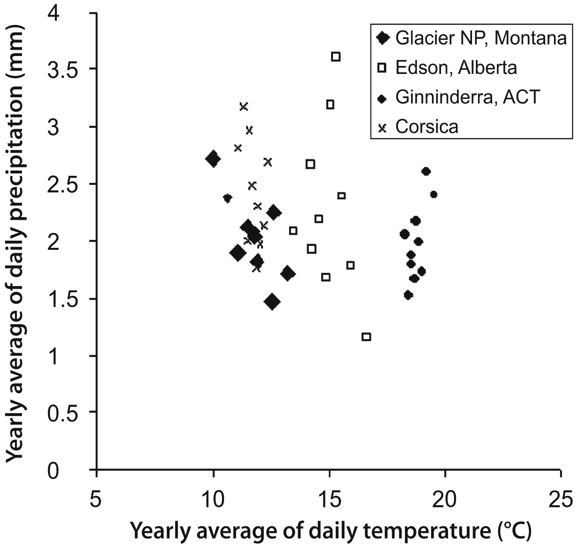

Fig. 12.4. Comparison of average daily temperature and precipitation from Glacier National Park (Montana), Edson (Alberta), Ginninderra (Australian Capital Territory) and Corsica (Italy) weather databases. The temperature data for Glacier National Park and Ginninderra are daily maximum temperatures. The temperature for Corsica is daily average temperature and for Edson it is observed at 1200 LST

quences of daily weather were selected from available data for each model so that the distributions of average annual temperature and precipitation in the selected weather years (Fig. 12.4) matched the corresponding distributions in the available data sets. The differences among the weather set for a particular model represents the weather treatment in our design.

Our design included three climates – observed, warmer/wetter and warmer/drier. The observed climate was comprised of the weather sequences outlined above. The other climates were derived by adding 3.6 °C (mid-range of projected global average temperature increase of 1.4 to 5.8 °C) (IPCC 2001) to daily temperature and by incrementing daily rainfall amounts by −20% (warmer/drier) and +20% (warmer/wetter).

A total of 1800 year long simulations were run for each model from the 18 unique combinations of terrain (flat, undulating, mountainous), fuel pattern (finely and coarsely clumped), climate (observed, warmer/wetter, warmer/drier), and weather (ten one-year replicates), given that there were ten replicate maps of each fuel pattern. Fires affected fuel load/age within each simulation but, since simulations were for only a single year, no vegetation succession algorithms were invoked. The sensitivity of area burned to terrain, fuel pattern, climate, and weather was assessed from the variance explained (r^2) by each variable and their interactions determined from a fully factorial ANOVA performed in the SAS statistical package. Prior to our analyses, we transformed area burned by the natural logarithm to remove highly skewed residuals that resulted from untransformed data.

12.5 Results and Discussion

12.5.1 Model Classification

Results from the model classification effort illustrate the great diversity in model approaches used to simulate vegetation and fire dynamics. This diversity will always preclude a perfect classification because modellers will always emphasize those processes that are important to the local ecosystem or landscape for which the model was developed. For example, many models simulated fire effects as the simple killing of all trees because most fires were stand-replacing for their native landscape. The fire effects component had the least influence in the classification of LSFMs because of the low diversity and low complexity in fire effects simulation across models. In contrast, succession and fire spread were the components that most heavily influenced the clustering and ordination results because of the wide variety of simulation techniques represented. Succession was most important because the three evaluation gradients (complexity, stochasticity, and mechanism) were not closely related in succession simulations. Classification design is nearly always governed by its intended application, so there will never be the ideal LFSM classification for all purposes.

The three gradients used in the classification were not perfectly orthogonal. Highly complex models tend to include many mechanistic functions that tend to have a low degree of stochasticity (Gardner et al. 1999), and they often were built specifically to remove the stochasticity, so that these approaches could be mutually exclusive and the gradients correlated. Some highly complex systems, such as lightning dynamics, must be represented by stochastic functions because of insufficient knowledge and computer resources. We only found significant correlation between the complexity and mechanism gradients ($R^2 = 0.71$, $p < 0.0132$).

The classification can be used for many purposes by providing (1) a common language for communication between managers, modelers, and research scientists, (2) a means to quickly and efficiently characterize or describe a model relative to others, (3) a starting point for managers to select the most appropriate model to implement for their areas of interest, (4) a method for scientists and other modelers to select the most appropriate models for particular situations, and (5) the context to evaluate or compare simulation approaches for each component to build new models or refine old ones. The classification contains 12 categories based on gradients of complexity, stochasticity, and mechanism so it is only useful if these gradients are important to selecting, evaluating, or comparing models. This classification approach can be used for other applications by selecting different evaluation gradients or different components.

12.5.2 Model Comparison

The primary finding of the comparison effort is the overriding influence of climate and weather on fire dynamics (Table 12.2). The natural log-transformed area burned was most sensitive to climate (4 models), weather (4 models), and their interaction (3 models) (Table 12.2). Only FIRESCAPE showed any sensitivity to terrain and only EMBYR showed sensitivity to fuel pattern. The variance explained by weather year was much greater than that explained by the climate treatment for EMBYR, LANDSUM and SEM-LAND simulations. The converse was observed for FIRESCAPE and LAMOS-DS, perhaps because the inter-annual variation between the weather replicates for these locations was lower than for other weather stations despite efforts to standardize this across all models. Differences in variance in area burned explained by the weather replicate treatment may result from differences in inter-annual variability in weather between sites, not differences in model formulation *per se*. Nevertheless, the finding of the importance of inter-annual variability in weather (compared with climate) to fire regime has important implications for the inclusion of fire into higher order models, like DGVMs, because our results indicate increased variability in daily weather may result in greater simulated burned area than large shifts in mean temperature and precipitation.

There are a number of important differences between the models used in this comparison. First, fire regime is an input in LANDSUM whereas it is an emergent property for the other models. Ordinarily, the area burned in LANDSUM would not vary among the climate treatments, however for this comparison the probability of ignition success was made sensitive to the Keetch-Byram Drought Index. For other models, climate affects either the area burned from the same number of ignitions (EMBYR, SEM-LAND) or both the number of ignitions and the area burned resulting from them (FIRESCAPE, LAMOS-DS). Second, there are differences in representation of processes associated with fire ignition and spread. Using the gradient scores from the classification effort, we found that the variance in area burned appeared to be primarily related to the fire ignition module. It was highest for models with complex, mechanistic, deterministic ignition modules (Fig. 12.5).

12.6 Summary and Conclusions

It was clear from the results of the comparison that the inclusion of both climate and daily weather variation into fire models is essential for simulating fire regime. This is especially important if the effects of climate change on fire dynamics are important. Fires burn the most area in warm, dry years, especially when coupled with antecedent drought, and the frequency of these droughty years

Table 12.2. Relative sums of squares attributed to different sources of variation in the comparison of sensitivity of ln-transformed area burned to terrain (terrain), fuel pattern (fuel), climate (climate) and weather replicate (weather), and their interactions. Treatments and interactions considered unimportant (explaining less than 0.05 and 0.025 of total variance respectively are blank). Significant treatments and interactions ($P < 0.05$) are indicated by an asterisk (*). Note that not all significant sources are considered important

Source	DF	Model				
		EMBYR	FIRESCAPE	LAMOS	LANDSUM	SEMLAND
Terrain	2		0.293*			
Fuel	1	0.217*	*		*	*
Terrain × fuel	2		*			
Climate	2	*	0.418*	0.278*	0.178*	0.370*
Terrain × climate	4		*			
Fuel × climate	2	*				*
Terrain × fuel × climate	4		*			
Weather	9	0.329*	0.087*	*	0.333*	0.542*
Terrain × weather	18		0.025*		*	
Fuel × weather	9	0.031*	*			*
Terrain × fuel × weather	18	*				
Climate × weather	18	0.096*	*	*	0.224*	0.046*
Terrain × climate × weath	36		0.025*			
Fuel × climate × weather	18	*				
Terr × fuel × clim × weath	36					
Model	179	0.744	0.905	0.401	0.766	0.971

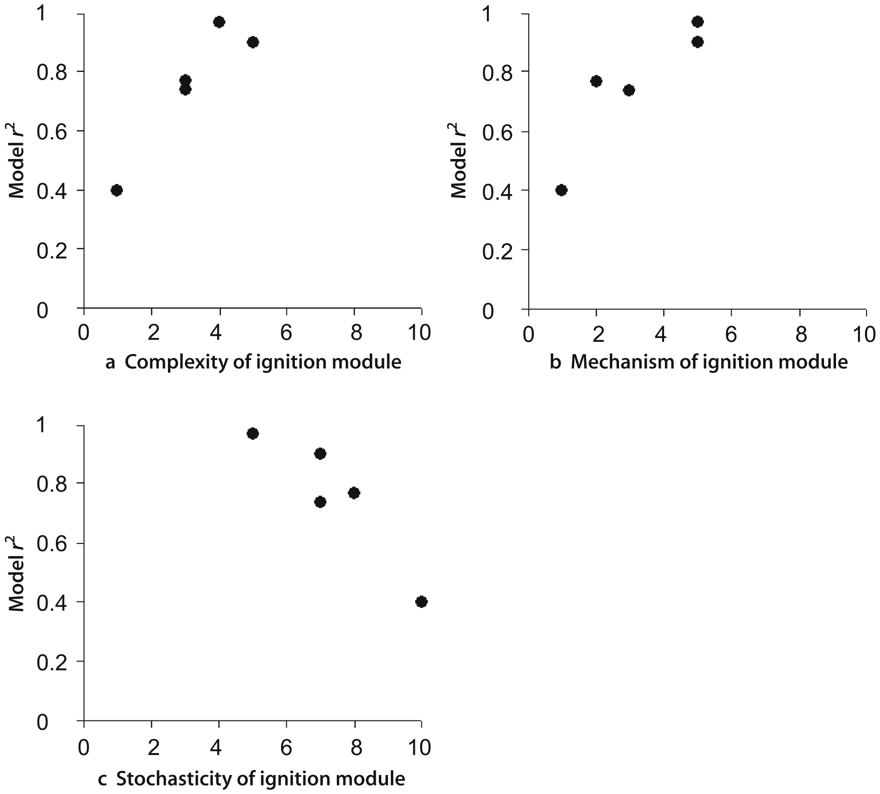

Fig. 12.5. Relationship between level of **a** complexity, **b** stochasticity, and **c** mechanism of fire model ignition modules assessed from the classification effort and model r^2 computed from the comparison effort

eventually defines the fire regime. Furthermore, variation in weather must be adequately captured to effectively simulate climate change responses to fire and vegetation. A surprising result was the relatively low sensitivity of fuel pattern in influencing fire regime. This may mean that coarse scale DGVMs need not be concerned with the pattern of vegetation or the spread of fire within large simulation pixels. The relative insignificance of terrain in determining fire ignition and spread dynamics may also mean that coarse scale models need not account for topographic complexity with the simulation unit when estimating burned area.

The results from the classification can be applied to compare other simulation experiments. Subsequent phases ot he the model comparison need to evaluate ignition and area burned over longer simulation years (100 years) to assess the sensitivity of succession and fire effects on the simulation of fire regime. This should provide a foundation to dynamically represent fire and vegetation in coarse scale DGVMs or LFSMs by taking into account fire plant functional types (Díaz and Cabido 1997). Next, there will be a need to modify the comparison method to evaluate the effect of fuel treatments and fire suppression on fire dynamics by simulating various fuel treatment patterns and management ignition patterns with the weather scenarios for current climate. Results from this effort could provide valuable information on the effectiveness of fuel treatments under severe weather conditions.

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Chapter 13

Plant Functional Types: Are We Getting Any Closer to the Holy Grail?

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Natalia Pérez-Harguindeguy · Catherine Roumet · Carlos Urcelay

13.1 In Search of the Holy Grail

Functional classifications have been seen as a necessary tool for the simplification of floristic complexity in global vegetation models (Neilson et al. 1992; Prentice et al. 1992; Foley et al. 1996; Woodward and Cramer 1996), for mapping vegetation patterns at key times in the past (Prentice and Webb 1998; Prentice et al. 2000), and for monitoring effects of global change or management on vegetation distribution and ecosystem processes (Díaz et al. 2002a; Cruz et al. 2002). Plant functional classifications were first designed by grouping plants a priori based on knowledge of their function, or based on observed correlations among their morphological, physiological, biochemical, reproductive or demographic characteristics (Woodward and Cramer 1996; Smith et al. 1997). It was assumed that these classifications would allow to predict changes in ecosystem processes directly from projected changes in plant species composition in response to global change. This idea was challenged by the recognition that functional effect groups (species with a similar effect on one or several ecosystem functions; e.g., primary productivity, nutrient cycling, Gitay and Noble 1997; Walker et al. 1999) and functional response groups (groups of species with a similar response to a particular environmental factor; e.g., resource availability, disturbance or CO_2; Gitay and Noble 1997; Lavorel et al. 1997) do not necessarily coincide. Although there have been sustained efforts to refine plant functional type (PFT) concepts and terminology (Gitay and Noble 1997; Lavorel et al. 1997; Lavorel and Garnier 2002), the search for a single, functionally comprehensive yet relatively parsimonious, plant functional classification has remained an elusive Holy Grail.

The Holy Grail requires to focus on functional traits of terrestrial vascular plants that (1) can together represent the key responses and effects of vegetation at various scales from ecosystems to landscapes, biomes, and continents; (2) are suitable for relatively easy, inexpensive and standardised measurement over the world; and (3) can hence be used to devise a satisfactory functional classification for global-scale modeling and mapping of the biosphere.

A large amount of research has been initiated on plant furnctional traits and PFTs since the early days of GCTE, where the Holy Grail was formulated largely by modellers. In this chapter we first summarise theoretical and empirical progress on the understanding of the response traits that are relevant to different aspects of environmental change. Recently numerous empirical studies have made considerable progress in elucidating how plant traits can be related to plant function in relation to main environmental constraints (see Sect. 13.2), and how these same traits are then relevant to the distribution of species along gradients of climate, nutrient availability, and disturbance. Additional theoretical (Ackerly 2003) and empirical (Ackerly 2004a) work has also analysed the role of phenotypic plasticity, ecological sorting and natural selection in determining present patterns of association between plant traits and environmental gradients. The correlational approach, which has formed the bulk of that research, has been quite successful in detecting significant associations between particular plant traits and environmental factors (reviewed in Sect. 13.3). Understanding how these traits may then influence biotic interactions, and eventually shape local vegetation through community assembly has however appeared to be a non-trivial scaling exercise, and we review current state of the art in Sect. 13.4. Likewise, scaling from individual plant traits that are affected by environmental changes to ecosystem effects has proved more challenging than initially anticipated because the traits that determine the response to specific environmental factors overlap directly, indirecly, or not at all with the traits that determine ecosystem functions such as biogeochemical cycling or flammability (Lavorel and Garnier 2002; reviewed in Sect. 13.5). Finally, we return to asking how these results have helped modellers working at larger scales, and what key challenges remain.

13.2 Individual Plant Structure and Function

Among all possible traits measurable on an individual plant, those of interest to global syntheses and modeling must fill four conditions: *(i)* bear some relationship to plant function; *(ii)* be relatively easy to observe and quick

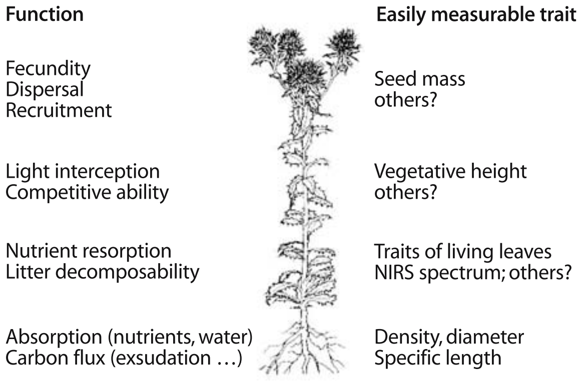

Fig. 13.1. Examples of soft traits and associated functions

to quantify ('soft' traits; Hodgson et al. 1999), *(iii)* using measurements that can be standardized across a wide range of species and growing conditions (Cornelissen et al. 2003b); *(iv)* have a consistent ranking – not necessarily constant absolute values – across species when environmental conditions vary (Garnier et al. 2001; Cornelissen et al. 2003a; Shipley and Almeida-Cortez 2003). Such traits are called 'functional traits' or 'functional markers' (Garnier et al. 2004), and can be morphological, ecophysiological, biochemical, demographical or phenomenological (Fig. 13.1). At this stage, the interest lies in the role of these traits for main plant functions, while their role in ecosystem dynamics is not specified, and they may turn to be response and/or effect traits. Information on soft traits is available for large numbers of species from all types of vegetation (see Díaz et al. 2004; Wright et al. 2004). Over the years, a consensus has been growing about which soft traits are best related to key plant functions such as resource economy or recruitment and how these then become response traits to climate and disturbances (Grime et al. 1997; Westoby et al. 2002; Cornelissen et al. 2003b) (Table 13.1). Comparability of data and global coverage must be ensured by using standardised lists of traits, which are a consensus about which traits are critical for the ecological challenges ahead (Table 13.1), and measuring them with standard methodologies (McIntyre et al. 1999; Díaz et al. 2002b; Cornelissen et al. 2003b), now freely available (Cornelissen et al. 2003b[1]).

Plant functional traits are considered as reflecting adaptations to variation in the physical environment and trade-offs (ecophysiological and/or evolutionary) among different functions within a plant. Co-varying sets of traits have been associated to 'major axes of plant specialization', that are consistent across environments, biogeographic regions and major plant taxa (Grime 1977; Chapin et al. 1993; Díaz et al. 2004). More generally, the analysis of plant functional trait responses to environmental variation, and of their effects on ecosystem function has been guided by the recognition that plants are constrained for performing alternative functions simultaneously, such as resource capture and conservation (Grime 1979; Chapin et al. 1993; Poorter and Garnier 1999), acquisition of several different resources (light and water, Smith and Huston 1989; light and nutrients, Tilman 1988), or growth and reproduction (Silvertown et al. 1993; Solbrig 1993).

A synthesis of empirical and theoretical studies proposed that at least four axes of plant specialization should be considered (Westoby et al. 2002). The first and best understood axis is represented by the specific leaf area (SLA) – leaf life span trade-off and is associated with turnover time of plant parts (including through herbivory), nutrient residence times and rate of response to favourable growth conditions. The global relevance of this axis was confirmed by an analysis across four floras from different biomes and biogeographic regions (Díaz et al. 2004). The second axis, representing the trade-off between fecundity and seed mass addresses establishment opportunities and success in the face of hazards, respectively. Seed mass and fecundity are negatively correlated, even after correcting for plant size. The third axis represented by potential plant height, carries several trade-offs and adaptive elements, and captures multiple constraints such as the density and height of shading competitors, water economy, and response to disturbance. The global relevance of plant height was confirmed by cross-continental analysis (Díaz et al. 2004). Finally, a fourth axis representing the coupled variation between twig size and leaf size determines the texture of canopies. Although a decrease in leaf size is common in dry, high light or cold conditions, the costs and benefits of small vs. large leaves remain to be formalized. Still, identifying an axis relevant to temperature variation, and especially response to extremes, stands as a challenge to ecophysiologists and ecologists.

However, the previous syntheses focused on aboveground traits, which are easily accessible. Recent studies have endeavoured to provide the same kind of information belowground, focusing on the functions of root traits, trade-offs among them, and how they relate to aboveground traits that could then be used as proxies for belowground function. Suites of correlated traits appear to also exist in roots, and represent a trade-off between root longevity and growth rate. Generally, low specific root length (SRL: ratio between root length and root biomass) is associated with thick, dense roots with low nitrogen and high lignin concentrations (Comas and Eissenstat 2004; Craine et al. 2002; Craine et al. 2003), a syndrome usually found in slow growing species or plants grown in limiting conditions (Reich et al. 1998a; Ryser 1998; Comas et al. 2002; Comas and Eissenstat 2004). Available data linking root morphology and plant functioning, and analogies to leaf traits suggest that this suite of traits reflects root longevity (Eissenstat 1991; Eissenstat

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[1] http://www.publish.csiro.au/nid/65/paper/BT02124.htm.

Table 13.1. Association of plant functional traits with (1) plant responses to four classes of environmental change (i.e., 'environmental filters'), (2) plant competitive strength and plant 'defense' against herbivores and pathogens (i.e., 'biological filters'), and (3) plant effects on biogeochemical cycles and disturbance regimes. See also Chapin et al. (1993), Díaz et al. (1999), Weiher et al. (1999), Lavorel (2002) and Lavorel and Garnier (2002) for details, including 'hard traits' corresponding with the soft traits given here. Soil resources include water and nutrient availability. Disturbance includes any process that destroys major plant biomass (e.g., fire, storm, floods, extreme temperatures, ploughing, landslides, severe herbivory or disease). Note that effects on disturbance regime may also result in effects on climate or atmospheric CO_2 concentration, for instance fire promotion traits may be linked with large-scale fire regimes, which in turn may affect regional climates

	Climate response	CO_2 response	Response to soil resources	Response to disturbance	Competitive strength	Plant defence/ protection	Effects on biogeochemical cycles	Effects on disturbance regime
Whole-plant traits								
Growth form	*	*	*	*	*	*	*	*
Life form	*	*	*	*	*		*	*
Plant height	*	*	*	*	*	*	*	*
Clonality	*	?	*	*	*			?
Spinescence	*	?			*	*		?
Flammability		?			*	?	*	*
Leaf traits								
Specific leaf area	*	*	*		*	*	*	
Leaf size	*	?	*		*	*	*	
Leaf dry matter content	*	?	*			*	*	*
Leaf N and P concentration	*	*	*	*	*	*	*	
Physical strength of leaves	*	?	*	*		*	*	
Leaf life-span	*	*	*	*	*	*	*	*
Leaf phenology	*		*		*		*	*
Photosynthetic pathway	*	*			*			
Leaf frost resistance	*				*	*		
Stem and below-ground traits								
Stem specific density	*	?	?	*		*	*	*
Twig dry matter content	*	?	?	?		*	*	*
Twig drying time	*	?	?				?	*
Bark thickness			*	*		*		?
Specific root length	*	?	*		*	*		?
Diameter of fine root	*	?	*					
Distribution of rooting depth	*	*	*	*	*		*	*
95% rooting depth	*	?	*		*			*
Nutrient uptake strategy	*	*	*	*	*		*	
Regenerative traits								
Dispersal mode				*				
Dispersule shape and size				*				
Seed mass			*	*	*	*		
Resprouting capacity								

et al. 2000; Ryser 1996), greater nutrient use efficiency and resistance to herbivore and physical damage (Craine et al. 2001). These traits are thought to minimize nutrient losses, allowing plants to grow larger at low nutrient supply rates. Opposite traits tend to maximize root surface area and length per unit biomass, thereby allowing quick exploration of soil resources and rapid growth. However, root traits are definitely not easily measured. Therefore, there are a number of challenges still to be resolved: *(i)* to identify traits that are closely related to key root functions such as nutrient acquisition, anchoring, rhizospheric activity, decomposition rate; *(ii)* to normalize root traits measurements for broad comparisons; *(iii)* to test relationships between leaf and root traits for later use of leaf traits as easier proxies. Close relationships between leaf and root nitrogen concentration have already been shown at a global scale (Craine and Lee 2003; Craine et al. 2005).

As recognised by early work (Theophrastus ca. 300 BC; Raunkiaer 1934), growth forms are one expression of trade-offs among traits and adaptation to different types of environments. As such, they provide comprehensive links between key traits, plant response to their environment and their effecs on ecosystem function (Chapin 1993), and this is why large scale dynamic models have used them as the basis for their plant functional classifications. However, there is also an important range of variation in trait values and detailed trade-offs among traits within each life form. For instance, the trade-off between leaf lifespan (and underlying protective traits) and traits that promote leaf productivity (e.g., SLA) operates both within and between life forms (Díaz et al. 2004; Wright et al. 2004), but relationships between seed dispersal syndromes and seed size depend on seed size (Westoby et al. 1990).

13.3 Traits and Environmental Gradients

The functional meaning of plant traits for response to environmental variation has been identified through observations of the variations in trait values across environments differing for one or several factors, targeted experiments and modeling. Most of our knowledge is derived from the first approach, and therefore directly applies to spatial variation. Space-for-time substitution is then used to assume that the same changes in trait values would be observed following an environmental change of the same magnitude. Growing numbers of experiments have confirmed this assumption for responses to single environmental factors such as nutrient availability (Dyer et al. 2001) or grazing (Bullock et al. 2001), as do models of community or ecosystem dynamics (Pausas 1999; Colasanti et al. 2001; Ackerly 2003; Boer and Stafford Smith 2003; Hickler et al. 2004).

This combination of approaches has advanced the understanding of the adaptive significance of traits, or combinations of traits, to predict the response of organisms to climate, nutrients and disturbance (Table 13.1). Globally, response to climate, considered in terms of response to extreme low or high temperatures, and to gradients of moisture availability, is associated with variations in life form, leaf traits, rooting depth and lateral root spread, and genome size (McGillivray 1995; Díaz and Cabido 1997; Pavón et al. 2000; Niinemets 2001; Schenk and Jackson 2002, 2005). Specific leaf area (SLA), leaf dry matter content (LDMC) and leaf chemical composition co-vary with soil resource availability (Cunningham et al. 1999; Poorter 1999) as do specific root length, tissue density and diameter (Reich et al. 2003; Robinson and Rorison 1988). Responses to CO_2 depend on life cycle, relative growth rate (RGR), photosynthetic pathway, and stochiometric relationships (Poorter et al. 1996). Response to water availability is associated with variation in SRL, root diameter and root architecture (Fitter 1991; Wright and Westoby 1999; Nicotra et al. 2002). RGR, leaf and root morphology, and seed mass determine response to shading (Leishman and Westoby 1994; Reich et al. 1998b). Response to disturbance is associated with variation in life cycle, plant height, architecture, resprouting and seed traits (McIntyre and Lavorel 2001; Bond and Migdley 2001; Pausas et al. 2004; Díaz et al. in press). Following, we summarise recent progress in the identification of plant traits associated with response to the two simple factors that vary most significantly across communities within a landscape: resource availability and disturbance.

13.3.1 Plant Functional Response to Mineral Resource Availability

Early syntheses on changes in species traits along nutrient gradients (Grime 1977; Chapin 1980) recognised that species from nutrient-rich habitats tend to be inherently fast-growing. This goes along with rapid resource capture and fast turn-over of organs leading to poor internal conservation of resources, while the reverse is true for species from nutrient-poor habitats (Tables 13.1, 13.2). More recently, a series of quantitative traits has been associated with this fundamental trade-off in plant functioning (Reich et al. 1992; Grime et al. 1997; Poorter and Garnier 1999; Díaz et al. 2004; Wright et al. 2004). Fast-growing species from nutrient-rich habitats usually have a combination of high SLA, high SRL and relatively more fine roots, high tissue nutrient (in particular nitrogen) concentration, low tissue density and cell wall content, high rates of carbon and nutrient uptake, and short-lived leaves and roots. Opposite traits characterize species from nutrient-poor habitats, in which the mean residence time of nutrients tends to be maximized through longer-lived organs and/or higher resorption of nutrients from senescing organs (Ryser 1996; Garnier and Aronson 1998; Boot 1989; Aerts and Chapin 2000; Westoby et al. 2002).

13.3.2 Plant Functional Response to Disturbance

Disturbances are defined here as natural or land use related events that remove biomass or individuals (Grime 1977). Although disturbances must be considered for relevant plant functional classifications (Lavorel et al. 1997; Lavorel and Cramer 1999; Pausas et al. 2003), a theoretical framework comparable to that developed for resource economy remains elusive. Moving beyond the well-

Table 13.2. Summary of traits associated with contrasted environmental conditions and their feed forward effects on community structure and ecosystem processes in perennial grasslands

Level of organization	High fertility High disturbance	Low fertility Low disturbance
Individual traits	High SLA, low LDMC, low leaf C : N; allocation to leaves and stems; high plasticity	Large size, long-lived, low SLA, high LDMC, high leaf C : N; allocation to roots; low plasticity
	Numerous, persistent small seeds with high dispersal; selfing	Few larger seeds with low dispersal and no seed bank; outcrossing
Species interactions	Exploitative competitors: rapid depletion of resources; symmetric interactions	Conservative competitors: tolerance to low resource levels; asymmetric interactions
	Predominance of competition	Predominance of facilitation and allelopathy
	High herbivory	High mycorhizal associations
Community	Abundance of forbs and some stoloniferous grasses	Abundance of cespitous grasses
Ecosystem processes	Fast rates of biogeochemical cycling; rapid litter decomposition; high NPP	Slow rates of biogeochemical cycling; slow litter decomposition; low NPP
	High palatability	High fuel loads, high flammability

known ruderal syndrome (Grime 1977) requires better understanding of regeneration traits. There is good evidence that seed size has a fundamental evolutionary and ecological significance for post-disturbance colonization, competitive response and tolerance to abiotic stress (Venable et al. 1988; Westoby et al. 2002). However the role of this trait for seed persistence, dispersal or seedling growth and survival is debated (Marañon and Grubb 1993; Thompson et al. 1993; Hughes et al. 1994). Overall, traits determining population persistence have so far received limited attention in functional trait analyses (Eriksson and Ehrlén 2001). In an analysis of the sensitivity of population growth rate to species demographic parameters, Silvertown et al. (1993) found a correspondence between longevity and resource-rich environments, survival and resource shortage, and fecundity and disturbance. These patterns still need to be matched with variation in soft traits through meta-analyses of large demographic and trait data bases.

Syntheses targeted at specific disturbances organised under the banner of GCTE have highlighted recurrent patterns of plant specialization in relation to soil disturbance, grazing and fire, as well as the nuances that need to be applied to them.

Soil disturbance consistently favours plants with a suite of traits additional to the ruderal syndrome (Lavorel and McIntyre 1999c). Plant species tolerant to soil disturbance by ploughing or mammal digging are characterised by: a short and prostrate stature, with either a stoloniferous architecture in perennial grasses, or flat rosettes in forbs, high fecundity and a small dormant seed pool. Intolerant species are typically larger tussock grasses or dicotyledons, with low fecundity and no seed dormancy mechanisms, and with low plasticity in their morphology. Finally, a group of indifferent species has an architecture characterised by leafy stems, with high morphological plasticity, and high seed dormancy (Lavorel et al. 1998, 1999a,b).

There are few empirically tested generalizations about which plant traits are positively or negatively associated with ungulate grazing, and the validity of some widely recognized trait responses to grazing has remained mostly untested at the global scale. There have been suggestions in the literature, based on pair-wise regional comparisons (Díaz et al. 2001; Adler et al. 2004, 2005), that evolutionary history of grazing by ungulates, as well as habitat productivity, determine what plant traits are favoured by grazing. Díaz et al. (in press) have asked what plant traits are consistently associated with grazing at the global scale, and whether these traits varied with precipitation (a surrogate for resource availability) and evolutionary history of grazing. A quantitative analysis of 195 studies from all over the world confirmed that overall grazing favoured annuals over perennials, short-statured over tall-statured plants, prostrate over erect plants, and stoloniferous or rosette over tussock architecture. This analysis demonstrated for the first time that some of the response patterns disappeared or were substantially stronger or weaker under particular combinations of precipitation and evolutionary history of herbivory. For example, in dry regions with long evolutionary history of ungulate herbivory, grazing did not favor annual plants over perennial plants.

Pausas et al. (2004) analysed regeneration strategies worldwide for woody plant species from ecosystems that are subject to stand-replacement (crown) fires. It is commonly assumed that the main traits allowing persistence after stand-replacement fires are resprouting capacity and the ability to retain a persistent seed bank (termed 'propagule persistence capacity'). Different combinations of these two traits have been preferentially selected in floras with different evolutionary histories. Although all four possible binary combinations appear in most fire-prone ecosystems, the relative proportions of each type (and the dominant type) differ. In Australian heathlands, the proportion of resprouters and non-resprouters is relatively even, compared with other fire-prone ecosystems, though post-fire obligate resprouters (resprouters without a seed bank) are almost absent. In the Mediterranean basin, most resprouters are obligate, while in California shrubs resprouters are evenly segregated among those having propagules that persist after fire (facultative species) and those without propagule persistence capacity (obligate resprouters). Species with neither persistence mechanism are rare in most fire-prone shrublands. Although data was limited, the review also highlighted some clear trade-offs with other traits (e.g., height), as well as the importance of considering the phylogenetic relatedness for a proper understanding of functional traits and trade-offs. For instance, in the Mediterranean basin flora, most resprouters have fleshy fruits and most non-resprouters have dry fruits. However, this pattern is not due to an ecological trade-off, but to a common lineage, as demonstrated by a phylogenetically controlled analysis (Pausas and Verdú 2005).

The data syntheses relating response traits to fire and grazing have still only dealt with individual disturbances. A further challenge lies in the understanding of disturbance regimes. For example, in many grasslands of the world disturbance regimes combine fire, grazing and/or mowing, fertilization and soil disturbance. Because regimes represent fixed combinations of disturbances that recur on the landscape, they can mask the interactions between the individual disturbances within that structure plant communities (Collins 1987). Woodlands and savannas are often shaped by the combination of grazing by wild and domestic herbivores, together with intentional or unintentional fire (Bond et al. 2003). Additional disturbances associated with farming and forestry can co-occur with grazing and fire to structure woodlands and forests (McIntyre and Martin 2001; McIntyre et al. 2002; Dale et al. 2001). Grazing tolerance of a number of species from Australian subtropical grasslands was found to covary with other disturbances (McIntyre et al. 2003), with the grazing tolerance of native species tending to decline in the presence of soil disturbance or water enrichment. Novel combinations of human-induced and natural disturbances are already widespread and are expected to be features of the future. Their effects can range from changes in dominance of different PFTs to dramatic shifts associated to plant invasions (D'Antonio and Vitousek 1992).

Pausas and Lavorel (2003) proposed a unifying framework that may apply to a variety of disturbance types. This framework is based on the recognition that plants can have persistence strategies at different levels of organisation and provides an understanding of the order in which different mechanisms act on plant persistence in disturbed systems. The main parameters to determine persistence in chronically disturbed ecosystems are those related to: **I**ndividual-persistence capacity, **P**ropagule-persistence capacity (persistence at the population level), **C**ompetitive capacity (persistence at the community level) and **D**ispersal capacity (persistence at the landscape level). The approach by Pausas et al. (2004) is a special case of this approach. Much remains to be done to identify traits relevant to different levels of response, and how these may vary depending on context. Nevertheless, sixteen possible functional types could be obtained by assuming a simple binary classification of the four levels of persistence.

13.3.3 Projecting Changes in Plant Functional Traits in Response to Global Change

Natural gradients usually combine variations in climate, resource availability, and disturbance regimes. These underlying simple gradients may be explicit for analyses of plant response to altitude (Pavón et al. 2000) or agricultural disturbance (Kleyer 1999), though again these combinations are likely to not be stable in the future. In many other instances however, the nature and amount of environmental variation underlying complex gradients (*sensu* Austin and Smith 1989) along which traits are studied has not been quantified or formalized. For instance, this is the case of successional gradients (Bazzaz 1996; Prach et al. 1997; Garnier et al. 2004; Richardson et al. 2005) or ecotones (Dodd et al. 2002) which are prime opportunities to obtain time series of plant functional traits.

Interpretation and projections of plant distributions along complex gradients are problematic because traits associated with different factors, such as water and nutrient stress, can overlap (Díaz et al. 2004) or be independent (Cunningham et al. 1999; Dyer et al. 2001). Non-overlapping trait responses are commonly observed when one environmental factor involves adult traits (e.g., nutrient availability) and other regeneration traits (e.g., disturbance) (Shipley et al. 1989; Leishman and Westoby 1992; Thompson et al. 1996; Lavorel et al. 1999b). In addition, the role of genetically-based plasticity of traits in response to environmental changes has largely been ignored from analyses, though it may contribute to population persistence (Strand and Weisner 2004; Stanton et al. 2000). Attempts to understand linkages, trade-offs and dependency among traits based on basic ecophysiological and evolutionary mechanisms, as reviewed in Sect. 13.2, are the way forward to address these complex responses (Ackerly et al. 2000; Westoby et al. 2002). In the context of global change, our ability to generate reliable projections of future vegetation is further limited by the fact that different combinations of climatic factors could occur in the future, as they have in the past (Jackson and Williams 2004), as will novel combinations of atmospheric CO_2 concentration, climate and disturbance regimes. Our ability to apply plant functional responses to generate future vegetation projections must therefore rely on more experimental and modeling work. One remaining challenge for modeling, however, lies in the construction of PFTs from analyses of continuous plant traits. This methodological challenge can be solved with statistical approaches (Pillar and Sosinsky 2003; Nygaard and Erjnaes 2004), but is also a more fundamental issue because of the assumption that future responses to multiple factors will be stable within groups.

13.4 Scaling from Individual Plants to Communities: from Response Traits to Community Assembly

Having learned how populations of individual species respond to environmental variation across landscapes, understanding how communities assemble remains a significant challenge (Weiher and Keddy 1999; Ackerly 2003; Suding et al. 2003). This challenge is particularly significant when novel environmental conditions and landscape fragmentation by land use may lead to entirely new assemblages, as have different environmental conditions in the past (Jackson and Williams 2004). Effects of changes in climate or land use might be modeled as changes in the strength of different abiotic (climatic, atmospheric CO_2 concentration, resource availability, disturbance) and biotic (competition, predation, mutualisms) filters that successively constrain which species and traits, from a regionally available pool, can persist at a site (Woodward and Diament 1991; Díaz et al. 1999; Naeem and Wright 2003; see also Díaz et al. 2007, Chap. 7 of this volume). We should then be able to predict the trait composition of communities by combining knowledge of (1) the regional species pool, (2) the nature and strength of different filters, (3) the response traits associated with each filter and (4) the rules that shape assembly (Campbell et al. 1999).

Attempts to predict interspecific competition from plant traits have had mixed success (Keddy et al. 1998; Wardle et al. 1998), in particular because species competitive rankings are sensitive to nutrient availability (Keddy et al. 2000), disturbance (Suding and Goldberg 2001), and to mycorrhizal associations (van der Heijden et al. 1998; Wardle et al. 1998). A reasonable consensus has been reached regarding tolerance of competition by neighbours (competitive response) where plant height and seed mass are positively associated with greater tolerance (Goldberg 1991). However, the attributes that determine competitive effects of plants upon their neighbours, and how these may vary with resources and disturbance, remain to be elucidated. Grime's competitive syndrome (1977, 2001) includes attributes such as tall stature, wide spread, nutrient monopolization and abundant litter production. Tilman (1988) also emphasised the importance of height in productive conditions, but in nutrient-poor environments leaf and root attributes associated with nutrient uptake are those expected to confer competitive effects (Craine et al. 2001, 2005). Further, Goldberg and Novoplansky (1997) proposed that competitive effects of species may depend on whether nutrients or water is most limiting. Relating this idea to the strategy model by Ackerly (2004b) in the case of nutrient limitation, a 'conservative competitor' strategy, with leaf traits promoting resource conservation, such as a low SLA, high tissue density and long life span, is expected. Otherwise an 'exploitative competitor' strategy, with opposite leaf traits, is expected (Michalet 2001; Liancourt et al. 2005). In addition, other types of plant-plant interactions such as facilitation and allelopathy may gain importance in either resource-poor and physically stressful, or resource-rich and physically benign environments (Bertness and Callaway 1994; Pellissier 1998; Bruno et al. 2003). Which plant traits are conducive to these other mechanisms remains to be elucidated, but are most likely related to the nutrient and water acquisition vs. conservation syndromes (Liancourt et al. 2005), including their effects on herbivory.

Another fundamental interaction structuring communities is herbivory (Crawley 1992). There is good evidence that structural and chemical traits known to be associated with nutrient or climatic gradients influence patterns of herbivory by generalist invertebrates (Grime et al. 1996; Wardle et al. 1998; Cornelissen et al. 1999; Pérez-Harguindeguy et al. 2003) and vertebrates (McKey et al. 1978; Bryant et al. 1991). Nutrient and/or water limitation tends to select for conservative strategies which result in low attractiveness to these herbivores due for example, to leaf high tensile strength (toughness) and low nutritive value (e.g., high C/N ratio) (Bryant et al. 1983; Coley et al. 1985; Cebrían 1998; Díaz et al. 2004). The opposite applies to resource-rich environments. How antiherbivore defences may then feedback to ecosystem productivity *via* the soil is discussed in Sect. 13.5.

Finally, the strength of interactions among plants is also expected to co-vary with other key traits along environmental gradients. This is because the nature and the quantity of the production of secondary biochemical compounds involved in anti-herbivore defense, litter decomposition, or allelopathy (Pellissier and Souto 1999) can also be affected by microclimate and resource availability (Herms and Mattson 1992; Hartley and Jones 1997).

Other types of trophic interactions that influence community structure and ecosystem processes are associations with soil microbes, for instance mycorrhizae (van der Heijden et al. 1998; Klironomos et al. 2000; Langley and Hungate 2003; Read et al. 2004; Rillig 2004). Cornelissen et al. (2001) revealed consistent large and significant differences in inherent relative growth rate (RGR), foliar chemistry and leaf litter decomposability among plants with mycorrhizal association strategies. This results in slow carbon cycling in ericoid and ectomycorrhizal plant species from temperate ecosystems with low pH, vs. low nitrogen availability and fast carbon cycling in arbuscular and non-mycorrhizal species, found in more nitrogen-rich ecosystems with higher pH. The relative abundance of dependent and non-dependent species in a community will determine the importance of this plant-fungus interaction (Urcelay and Díaz 2003). All together, these findings support Read's (1991) hypothesis that mycorrhizal type is an important component of a plant's strategy in the context of nutrient availability. However, at a global scale we still know little about links between plant-associated microbes and plant traits, or about belowground plant traits in general. Recent efforts in this field are promising (Jackson et al. 1996; Ryser 1996; Craine et al. 2003; Craine and Lee 2003; Wardle 2002).

In order to better capture the complexities of community assembly, and how these may link to individual plant traits, Suding et al. (2003) proposed that trade-offs among species traits (e.g., ability to capture and cycle resources quickly vs. leaf toughness) determine community structure through the nature and intensity of competition and other interspecific interactions depending on environmental conditions. Our current knowledge, as summarised above, highlights a number of these linkages. For instance, we expect that nutrient-poor environments will select for species with leaf traits promoting resource conservation, such as low SLA, high tissue density and long life span. As a consequence of these primary traits, predominant plants in such environments will compete with their neighbours by sequestering nutrients – possibly with the help of mycorrhizal associations, by accumulating poorly degradable litter (Berendse 1994), and sometimes through allelopathy or nutrient immobilization (Michelsen et al. 1995; Hättenschwiller and Vitousek 2000); while also facilitating subordinates by herbivore protection. The converse would be expected in nutrient-rich environments (Table 13.2).

13.5 Scaling from Communities to Ecosystems: from Response Traits to Effect Traits

The 'Holy Grail' hypothesis states that environmental changes will lead to changes in community composition and thus in plant traits, and these in turn will affect ecosystem functioning. This hypothesis was first approached by matching lists of response attributes with known effects of some of these attributes (or their correlates) on ecosystem processes (Díaz et al. 1999; Walker et al. 1999; Eviner and Chapin 2003; see also Díaz et al. 2007, Chap. 7 of this volume; see Tables 13.1 and 13.2 and Table 1 *in* Lavorel and Garnier 2002). Inspections of these lists have revealed that the resource axis has maximum overlap between response and effect traits, whereas overlaps are few in the case of disturbance. One essential step to understanding the causes of these differing degrees of overlap has been the analysis of the specific functions of the traits involved in either response or effect (Lavorel and Garnier 2002; see Table 13.1). For the resource axis it showed that responses to resource availability and effects on biogeochemistry are jointly constrained by the trade-off between acquisition and conservation strategies, and their characteristic traits (Chapin et al. 1993; Grime 2001). For example, plants growing in adverse environments have low specific leaf area, high C/N ratio, and high tensile strength. These traits make them less palatable to generalist herbivores (see above), and persist in litter, thereby strongly influencing decomposition (Wardle et al. 1998; Cornelissen et al. 1999; Pérez Harguindeguy et al. 2000). This way, herbivore-induced changes in the balance of palatable and unpalatable species lead to changes in the net litter quality and therefore in decomposer activity (Wardle et al. 1998; Cebrían et al. 1998; Wardle 2002). Association with N_2 fixing bacteria is another trait that provides feedback on ecosystem productivity *via* N-rich litter. This mechanism is in particular a recurrent one underlying the impacts of invasive species on nutrient cycling (D'Antonio and Corbin 2003). On the other hand, regeneration and demographic traits associated with response to disturbance (e.g., fire, grazing) are known to have little direct relation with adult ecophysiological traits, and would therefore be of little relevance to biogeochemistry.

The ultimate goal of response-effect analyses should be the formulation of parsimonious quantitative relationships expressing the different components of each ecosystem function in relation to particular traits (Lavorel and Garnier 2002; Eviner and Chapin 2003). These relationships would make it possible to use traits to scale from individual plants and the communities they form to the ecosystem level (Dawson and Chapin 1993). Such formulations have been proposed for aboveground primary productivity (Chapin 1993 and further modifications by Lavorel and Garnier 2002 and Garnier et al. 2004). Specific annual net primary productivity (SANPP; "ecosystem efficiency", Reich et al. 1997) expresses ANPP per gram of green biomass, and can be written as:

$$\mathrm{SANPP} = \frac{\log_e\left[\sum_{i=1}^{n\,\mathrm{species}} p_i x e^{\mathrm{RGR}_i x (tf-to)_i}\right]}{\Delta T}$$

where p_i is the relative contribution of species i to the biomass of the community, RGR_i and $(tf\text{–}to)_i$ are the aboveground relative growth rate and period of active growth of species i, respectively, and ΔT is the period over which SANPP is assessed. Garnier et al. (2004)

tested this relationship against independent measurements of leaf traits and productivity and showed that specific leaf area, LDMC, and leaf nitrogen concentration are indeed correlated with SANPP due to the well-established links between these traits and RGR (Reich et al. 1992; Poorter and Garnier 1999). In this equation, contributions of individual species to ecosystem function are proportional to their abundance in the community. Díaz et al. (this volume) further discuss the role of dominant species in functional diversity – ecosystem function relationships.

Correlations have also been established between rates of litter decomposition and leaf traits (SLA, LDMC and leaf tensile strength) of individual species (Cornelissen et al. 1999) and over communities (Garnier et al. 2004). However, in contrast to the case of ANPP there is no mechanistic model available. Empirical relationships between response and effects have been proposed for several other environmental factors and ecosystem functions (Chapin 2003; Eviner and Chapin 2003; Diaz et al. 2007, Chap. 7 of this volume), but developing formal models must be the next step.

Our understanding remains even more limited when attempting to link disturbance response and effect traits. Lavorel and Garnier (2002) showed that the list of traits relevant to ecosystem flammability has in fact minimal *direct* overlap with traits relating to fire response. When functional linkages between traits promoting fire tolerance and those involved in ecosystem flammability exist (Bond and Midgley 1995), even once phylogeny has been accounted for (Schwilk and Ackerly 2001), they result from associations or trade-offs between fire response traits and the actual traits that determine flammability, and are therefore *indirect*. For instance, a high growth rate is required to increase the success of seed regeneration after fire, and is also often associated with canopy architectures with many thin stems and high surface/volume ratios, which promote fire. Large underground structures allow resprouting, which increases fire survival, and drought tolerance, which allows low water potential and hence increases flammability. Closer investigations using phylogenetically independent analyses across floras evolved in high vs. low fire regimes, or sites with high vs. low resources, are needed to explore this issue further. Further knowledge will also be gained by analysing trait and ecosystem processes for cases of invasions that trigger positive fire feedback loops (D'Antonio 2000; Grigulis et al. 2005). Likewise, formal analyses and models linking grazing response strategies and palatability along resource gradients are still needed to build on the abundant but dispersed grazing literature (Landsberg et al. 1999; Adler et al. 2004). Pasture agronomists have shown that patterns of pastoral value (i.e., biomass quantity and quality over the growing season) along gradients of nutrient availability can be related to response traits such as LDMC (Cruz et al. 2002; Duru et al. 2004).

13.6 So, Are We Getting Closer to the Holy Grail? Scaling beyond Ecosystems

13.6.1 Plant Functional Traits and Landscape Dynamics

Plant functional types have been for a long time 'building blocks' of models of patch and landscape dynamics. At the landscape scale their most widespread use has been in models that couple successional dynamics as represented by applications of the Vital Attributes (VA) model (Noble and Slatyer 1980) with sub-models of lateral processes such as seed dispersal and disturbance propagation. These applications have been particularly successful in the case of 'Landscape Fire Succession Models' (*sensu* Keane et al. 2007, Chap. 12 of this volume), probably because the VA scheme was first designed to capture plant response to fire, and represents an intermediate level of complexity that is amenable to sophisitication by addition of new processes. Examples include applications to Australian wet sclerophyllous forest (Noble and Gitay 1996), Mediterranean shrublands (Pausas 2003) and of coniferous-dominated forests of northwestern America (Roberts and Betz 1997).

More complex versions of VA, such as the FATE model (Moore and Noble 1990) have been adapted to model landscape-fire interactions (LAMOS, Grigulis et al. 2005; FATELAND, Pausas and Ramos 2005) and responses to other disturbances such as grazing (Cousins et al. 2003) by including a series of semi-quantitative traits (e.g., for shade tolerance, recruitment). The latest developments of VA-based landscape models can take into account continuous traits and processes e.g., for biomass production and the dispersal phase (Grigulis et al. 2005). Current challenges lie in including biogeochemical processes, as captured by plant effect traits into the current models that simulate responses to changing soil resources, disturbances and their modifications by climate. Such models will make it possible to better capture important non-linearities associated with landscape dynamics (Reynolds et al. 1997; Boer and Stafford Smith 2003).

13.6.2 Regional to Global Models – Revisiting the Early Functional Classifications

Dynamic Global Vegetation Models (DGVMs: Foley et al. 1996; Friend et al. 1997; Woodward et al. 1998; Potter and Klooster 1999; Sitch et al. 2003; Gerten et al. 2004) simulate natural vegetation distribution and terrestrial carbon cycling in response to atmospheric and soil environment, disturbance and their interactions. The properties of the vegetation system arise out of competition between a limited number of PFTs whose behavior is, in turn, determined by basic physiological constraints.

DGVMs can be used with some confidence to predict the broad-scale behavior of terrestrial vegetation in response to observed climate changes in the recent past, and have been used to explore the consequences of past climate changes and future climate scenarios for the functioning of terrestrial ecosystems (Cramer et al. 2001; Prentice et al. 2007, Chap. 15 of this volume). Plant functional classification is central to all current approaches to modeling the response of vegetation to a changing environment at regional to global scales. However, even state-of-the-art DGVMs only use a relatively small number (<10) of PFTs. While the bioclimatic limits of these PFTs are explicit, their characterization in terms of observable traits are sketchy, or at best defined from a small set of postulated characteristics (based on life form or leaf form) and descriptions of function (phenology, photosynthetic pathway, life cycle, bioclimatic tolerance).

Two approaches to improving the representation of biospheric complexity in DGVMs have been advocated. The first approach is simply to increase the number of PFTs, perhaps by incorporating functional types that have been identified as important for some specific ecological function or are responsive to specific aspects of climate. There are more complex PFT classification schemes (Box 1981) that would be candidates for such a model expansion. Increasing the number of PFTs could improve modeling of the response to both disturbance and of migration. The IPCD approach (see Sect. 13.3) could provide a generic framework for modeling vegetation dynamics in chronically disturbed systems. Ongoing analyses of how long distance dispersal is distributed across life forms and in relation to other traits may inform the development of new classifications (Higgins et al. unpublished, Midgley et al. 2007, Chap. 11 of this volume). Increasingly detailed classifications (recognising up to 100 different PFTs) have been devised. However, it remains to be examined whether and how these 'top-down' schemes can be matched with 'bottom-up' classifications obtained from empirical work, and the degree to which they are useful for predicting changes in community composition and ecosystem functioning in response to scenarios of changes in multiple environmental drivers. In addition, to be able to simulate the behavior of a given PFT, it is necessary to provide quantitative values for a number of parameters relating to plant physiology, phenology, allocation strategy and response to disturbance (Prentice et al. 2007, Chap. 15 of this volume). Thus, data availability is a key limitation on the number of PFTs that could usefully be included in DGVMs. The statistical analysis of field measurements of trait abundance along climatic, nutrient and/or disturbance gradients (see Sect. 13.3), and resulting data bases, may go some way to providing these quantitative estimates but does not provide information on absolute physiological limits. Additional work in comparative ecophysiology and modeling is required to establish robust relationships between 'soft' traits that are routinely measured over a diversity of ecosystems, and the 'hard' traits used by models (see e.g., Arora and Boer 2005).

An alternative approach to increasing biotic complexity in models is to simulate traits explicitly. This avoids the classification problems inherent in defining discrete plant functional types from trait assemblages, but still raises the need for explicit, quantitative information for each trait. It also requires a fundamental rearrangement in the structure of current models. Some continental-scale models are using continuous traits rather than a discrete classification. For example, Berry and Roderick (2002a,b) used two fundamental leaf traits, leaf surface area to volume ratio and leaf thickness, to capture the combined response to water and mineral resource availability and CO_2. This classification was sufficient to describe current distribution of vegetation types on the Australian continent and to investigate historical and palaeoenvironmental changes. This plant functional scheme is also a functional effects scheme, and can be applied to modeling the carbon cycle at continental scale (Berry and Roderick 2004). Continuous response traits may also be used to capture other land-atmosphere feedbacks, such as effects on climate (Chapin 2003; Díaz et al. 2007, Chap. 7 of this volume).

13.6.3 Validation: the Contribution of Paleo-Data

Palaeoecology provides insights into how vegetation has responded to global changes in the past (Overpeck et al. 2003). Although the causes of these changes are not identical to the causes of expected future changes, our confidence in the ability of models (of climate and/or ecosystems) to make future projections can only be assured by demonstrating that these models are capable of reproducing the range of conditions that are documented from different periods during the recent geological period (Harrison and Foley 1995; Grassl 2000; Joussaume and Taylor 2000). The ability to test models under past conditions depends, in part, on palaeodata being represented in a form compatible with global model outputs (Prentice and Webb 1998; Kohfeld and Harrison 2000; Prentice et al. 2000). The desire for such a representation motivated the GAIM/GCTE-sponsored Palaeovegetation Mapping Project (BIOME 6000: Prentice and Webb, 1998 ; Prentice et al. 2000), which used pollen and plant macrofossil data to produce vegetation maps for the last glacial maximum and the mid-Holocene. To reduce the taxonomic diversity of the fossil data to a manageable level, BIOME 6000 adopted a method that relied on the allocation of pollen and plant macrofossil taxa from different floras to a common global suite of PFTs. Recent regional reconstructions (Harrison et al. 2001; Bigelow et al. 2003) have converged on a scheme which recognises a suite of 99 climatically-diagnostic PFTs based on combination of traits describing life form, leaf morphology, phenology and bioclimatic tolerances (principally related to cold tolerance mechanisms in woody plants). Together, the BIOME 6000 data set (Prentice et al. 2000) along with more recent updates (Harrison et al. 2001 ; Harrison and Prentice 2003 ; Bigelow et al. 2003; Pickett et al. 2004), and the global PFT-scheme which underlies it suggest one route for continuing improvement of the representation of PFTs in DGVMs.

13.7 Summary and Conclusions

Plant functional type research has soared for over ten years under the impetus of GCTE. The requirement from large scale ecosystem models to group plants according to similarity in response to changes in their environment *and* effects on ecosystem structure and processes has proved to be the 'Holy Grail' of plant functional type research.

One first achievement has been the production of standardised lists of the most significant and easily measurable and well understood traits. Based on these and large data bases, and on large efforts to synthesise the literature, it has been possible to identify and explain plant functional response traits associated with response to resource gradients (esp. nutrients) and widespread disturbances such as grazing and fire. Current research is focusing on the links between these and effects on biogeochemistry, confirming the relevance of fundamental trade-offs that constrain the way plants manage their resources (Grime 2001). This progress and the remaining challenges for ecosystem level plant functional research can be summarised in a series of confirmed or hypothetical linkages between individual plant traits and processes at different levels of organisation (Table 13.2). Significant remaining challenges not only concern further understanding the significance of particular traits, fundamental trade-offs among them, or how short a minimal trait list can be. First, understanding the mechanisms through which species traits, as determined by environmental factors, determine community structure is a priority that will require theoretical, experimental and modeling approaches. Second, our understanding of how these response traits also determine (or not) effects on ecosystems, remains very preliminary. Significant challenges to be addressed regard effects of plant disturbance response on biogeochemical cycles and on disturbance regimes. For this, and also to further resolve the effects of plant resource response on biogeochemistry, it is essential to recognize that simultaneous effects on multiple, linked ecosystem processes are involved (Chapin 2003). Progress in this area will call upon multi-factorial manipulations (see Norby et al. 2007, Chap. 3 of this volume), biodiversity experiments (Hooper et al. 2005; Naeem et al. 2003 and the further development of ecosystem models that directly use those plant traits that can be easily measured for large numbers of species.

Current approaches to defining PFTs that emphasize the importance of classifying plants according to well-defined, readily observable and usually continuous plant traits with known responses to particular environmental factors (CO_2 concentration, soil resources, climate, and different types of disturbances) should encourage the development of a new generation of DGVMs that explicitly represent key features of this global classification. Model development, however, needs to be paralleled by the global collection of trait data following unified protocols, and by the development of an internally-consistent modern (actual) vegetation map explicitly based on plant functional properties (Nemani and Running 1996).

"The same happens to all of us. One hears about the Grail and one thinks one is the only one who will find it" (U. Eco, Baudolino). Rather, the last decade of plant functional research has taught us that, if "There is much to be done. There is also a real hope that we may be getting somewhere" (Westoby et al. 2002), getting somewhere will require continued collaboration across those multiple fields that span from ecophysiology to global modeling.

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Chapter 14

Spatial Nonlinearities: Cascading Effects in the Earth System

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14.1 Introduction

Nonlinear behavior is prevalent in all aspects of the Earth System, including ecological responses to global change (Gallagher and Appenzeller 1999; Steffen et al. 2004). Nonlinear behavior refers to a large, discontinuous change in response to a small change in a driving variable (Rial et al. 2004). In contrast to linear systems where responses are smooth, well-behaved, continuous functions, nonlinear systems often undergo sharp or discontinuous transitions resulting from the crossing of thresholds. These nonlinear responses can result in surprising behavior that makes forecasting difficult (Kaplan and Glass 1995). Given that many system dynamics are nonlinear, it is imperative that conceptual and quantitative tools be developed to increase our understanding of the processes leading to nonlinear behavior in order to determine if forecasting can be improved under future environmental changes (Clark et al. 2001).

Although most global change studies have examined nonlinear behavior through time (e.g., Pascual and Ellner 2000; Gill et al. 2002; Gerber et al. 2004), it is increasingly recognized that spatial interactions, transport processes, and landscape complexity are important in generating nonlinear behavior through time *and* across space (Aber et al. 1999; Reiners and Driese 2001, 2004). In particular, contagious processes that propagate nonlinearly through time from small to broad spatial extents (i.e., spatial nonlinearities) often generate surprising behavior where dynamics at one scale cannot be easily predicted based on information obtained at finer or broader scales (Holling 1992, 1996; Nieminen 2003). These cascading effects often result in severe consequences for the environment and human welfare (i.e., catastrophes) that are expected to be particularly important under conditions of changes in climate and land use (NRC 2001; Steffen et al. 2004). A key challenge to Earth System science in the face of global change is to understand and predict these cascading effects and their catastrophic consequences (Steffen et al. 2004).

Earlier frameworks have described nonlinear, catastrophic behavior in terms of spatial propagation, positive feedbacks, and thresholds. Holling's (1973) seminal work linked disturbances to alternative stable states and thresholds between them through feedback mechanisms. The concept of self organized criticality introduced the notion that perturbations at critical thresholds may involve self-propagating changes at a variety of spatial and temporal scales (Bak et al. 1988; Chen et al. 1991). Together, these ideas linked spatial and temporal pattern to describe how dynamics may be self-organized. This linkage illustrated the value of recognizing coupled spatial and temporal patterns in ecosystems at multiple scales, and underlies the search for feedback mechanisms (Folke et al. 2004), critical thresholds of connectivity in applications of percolation theory (Davenport et al.1998) and the recognition of patch- to landscape pattern to explain catastrophic shifts in the pattern of vegetation (Rietkerk et al. 2004).

Despite these advances, our understanding of and ability to predict events that propagate across scales (i.e., cascade) and produce catastrophic changes remains limited. For example, this class of ecological problems includes insect outbreaks that spread nonlinearly from fine to broad scales (Swetnam and Lynch 1993). Because the rate and extent of an insect outbreak may be related to climatic patterns (Speer et al. 2001) and interactions with disturbance (Scheller and Mladenoff 2005), changes in climate and land use are expected to have large effects on these dynamics. Similarly, single lightning strikes can initiate broad-scale wildfires as a result of positive feedbacks among weather, fire behavior, land-use patterns, and vegetation interacting across multiple scales. Nonlinear patterns in connectivity of fires are often related to spatial variation in fuel loads (Miller and Urban 2000). Extensive and rapidly expanding fires may be driven by feedbacks with the atmosphere. Although fire (and other) behaviors have been described with respect to the internal forces of self-organized criticality (Drossel and Schwabl 1992), they have not been considered with reference to the role of feedbacks involving a variety of external drivers.

In this chapter, we *first* briefly describe a general conceptual and mathematical framework for understanding and forecasting spatially nonlinear responses to global change in driving variables. The *second* goal of this chapter is to illustrate the utility of our framework in describing the spread of catastrophic events using one historical example (the Dust Bowl) and two current examples (wildfires, invasive species and desertification). *Finally*, we discuss the consequences of applying these ideas to forecasting future dynamics under a changing global environment. Given the continuing challenges associated with global change, our synthetic approach that crosses disciplinary boundaries to include interactions and feedbacks across multiple scales shows great potential to increase our ability to forecast catastrophic events and to develop strategies for minimizing their occurrence and impacts.

14.2 Conceptual Framework

In our framework, we focus on catastrophic events that start small, and propagate nonlinearly to influence broad spatial extents (described in detail in Peters et al. 2004). Mathematically, spatial nonlinearities can be illustrated as:

$$\mathrm{d}Y/\mathrm{d}t = g(I_g, E_g) + f(Y, E_f) + D(Y, E_D) + c(Y, E_c)$$

where each term is associated with one of the four stages in the general model, and is a function of different parameters. All terms except g depend, at least in part, on properties of Y. As the rate of change in Y increases (decreases) through time, it is increasingly governed by terms towards the right (left) [from $g(I_g, E_g)$ to $c(Y, E_c)$] as the amount, connectivity, and spatial extent of Y increases (decreases). Three thresholds occur between the various stages. Stage 14.1 (initiation of Y) is defined by $g(I_g, E_g)$ where (I_g) is internal factors and (E_g) is external factors (e.g., weather) that influence initiation. Stage 14.2 (within patch spread of Y) is defined by $f(Y, E_f)$ where Y is within patch properties and (E_f) is external factors that influence patch heterogeneity (e.g., local weather). Stage 14.3 (spread of Y among patches) is defined by $D(Y, E_D)$ where Y is among patch heterogeneity in Y and E_D is external factors that influence among patch spread (e.g., template heterogeneity). Stage 14.4 (land-atmosphere feedbacks that influence the spread of Y) is defined by $c(Y, E_c)$ where Y is broad scale properties of Y and E_c is broad scale processes or forcing functions.

Our framework includes cross scale interactions, threshold behavior, and feedback mechanisms that generate spatial nonlinearities. There are four key characteristics of our framework: (1) feedback mechanisms are prevalent at a number of scales, (2) thresholds in the dynamic behavior of the system are crossed through time with broader scale consequences, (3) the dominant process controlling system dynamics changes through time and across space, and (4) connectivity along spatial units is important to the generation of cascading dynamics. Although the significance of feedbacks and thresholds is recognized in many disciplines (Elsner and Tsonis 1992; Zeng et al. 1993; Hethcote 2000; Scheffer et al. 2001; Tsonis 2001), the incorporation of processes across spatial scales that cross traditional disciplinary boundaries is required to understand and forecast these events.

14.3 Insights to Global Change Issues

14.3.1 Historical Example: the Dust Bowl of the 1930s

Extreme climatic events have played important roles in ecosystem dynamics historically (Swetnam and Betancourt 1998), and are expected to become increasingly important if the frequency, intensity, and magnitude of extreme events increase with time (Easterling et al. 2000). One historical event that was related to extreme climate interacting with land use was the Dust Bowl that occurred in the 1930s in the United States. This catastrophic event involved localized wind erosion from individual agricultural fields that propagated nonlinearly to generate massive dust storms that were accompanied by mass migrations and economic hardship felt throughout the U.S. Insights gained by examining this historical event within the context of our new cross scale framework can improve our ability to understand, mitigate, and forecast similar catastrophic events.

The Dust Bowl or the "Dirty Thirties" was characterized by a series of years with very low rainfall and high temperatures that generated intense drought conditions throughout the central Great Plains (Worster 1979). Recent analyses indicate that these atmospheric conditions were likely caused by anomalous tropical sea surface temperatures (Schubert et al. 2004). Although these atmospheric conditions were unusual for the 20th century, major droughts have occurred in this region once or twice a century for the past 400 years (Woodhouse and Overpeck 1998). Thus, it is unlikely that extreme climatic conditions alone were sufficient to result in the Dust Bowl, but rather that land-atmosphere interactions increased its severity (Schubert et al. 2004).

Importantly, the Dust Bowl was preceded in the 1920s with government policies that favored cultivation of drought sensitive crops on increasingly marginal land (Hurt 1981). Thus, the landscape consisted of a mosaic of cultivated, drought-susceptible land interspersed with small areas of native grassland. Hot, dry weather combined with strong winds in the 1930s resulted in decreased plant cover and high plant mortality on these cultivated fields (Fig. 14.1a); similar patterns were observed on native grassland, but the effects were not as severe (Weaver and Albertson 1936, 1940; Albertson and Weaver 1942). Low plant cover and strong winds resulted in localized wind erosion and blowing dust at the scale of individual fields (Fig. 14.1b). At the landscape scale, these small dust storms became aggregated among fields (Fig. 14.1c) to generate massive dust storms ("black blizzards") that

Fig. 14.1. a Drought in the 1930s resulted in decreased plant cover and high plant mortality at the scale of individual fields (Morton County, Kansas, 1938. Photo courtesy of USDA-ARS-Wind Erosion Research Unit and Kansas State University, http://www.weru.ksu.edu/), **b** wind erosion from within a field in South Dakota, (R. Lord, 1938. Miscellaneous Publication No. 321, U.S. Department of Agriculture. Photos courtesy of the National Oceanic and Atmospheric Administration, http://www.photolib.noaa.gov), **c** dust rising from a landscape of agricultural fields (photo courtesy of USDA-ARS-Wind Erosion Research Unit and Kansas State University, http://www.weru.ksu.edu/), and **d** aggregation of dust storms resulted in Black Sunday April 14, 1935 (photo courtesy of USDA-ARS-Wind Erosion Research Unit and Kansas State University, http://www.weru.ksu.edu/)

spread to the regional and continental scales (Fig. 14.1d). Blowing soil from the Great Plains was documented as far as the East coast, over 1500 km away (Miller 1934). Although it was not documented at the time, it is likely that these large dust storms had important feedbacks to the weather through high atmospheric dust loading and high albedo (Fig. 14.2). These changes would have reduced rainfall (Rosenfeld et al. 2001) and increased temperatures, similar to land-atmosphere feedbacks documented in Saharan Africa (Clausen et al. 1999).

Mass migrations, reduced quality of life, and agricultural depression as a result of these dust storms had economic and social ripples to other parts of the country (Lockeritz 1978). Approximately 35 million acres of formerly cultivated land was destroyed with >200 million acres of cropland with reduced topsoil (Yearbook of Agriculture 1934). In April 1935, the U.S. Congress declared soil erosion "a national menace". Federal drought assistance to farmers has been estimated at $1 billion (in 1930s dollars) (Warrick 1980). In addition, migration of people from the Dust Bowl region created economic strain in other parts of the U.S.

We can understand the sequence of processes leading to the Dust Bowl using our conceptual framework that includes multiple stages, thresholds, and a change in dominant process through time and across space. The Dust Bowl was initiated (Stage 14.1) by two interacting conditions: consecutive years with extreme weather com-

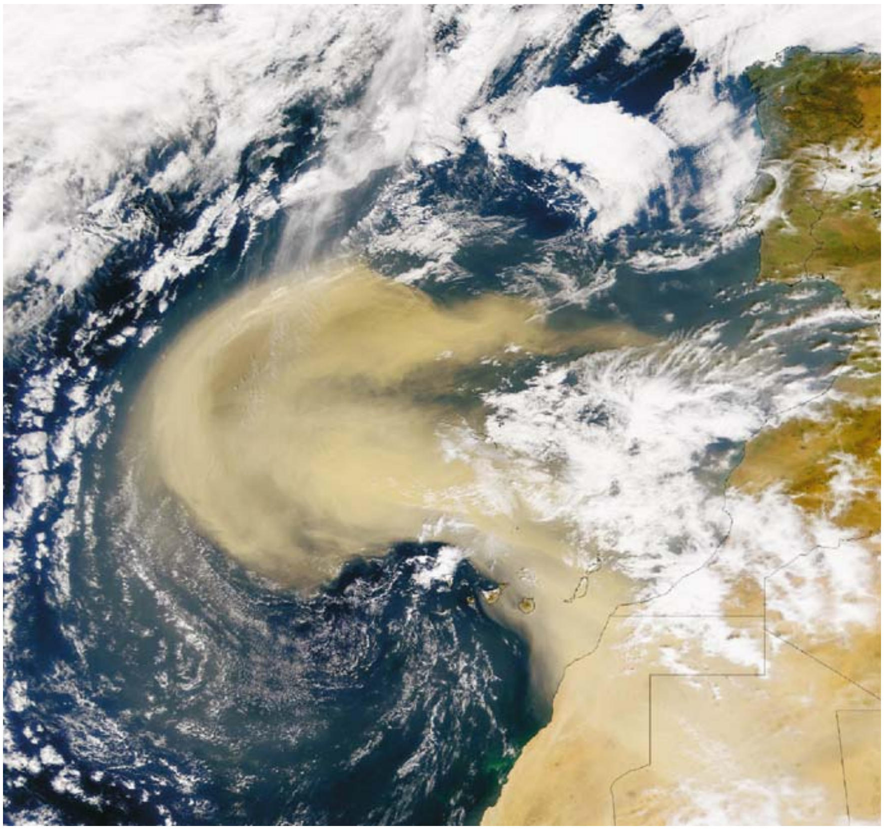

Fig. 14.2. Land-atmosphere interactions can result in regional- to continental-scale dust storms, such as this one from the African Sahara, February 26, 2000 (photo courtesy of SeaWiFS and NASA Goddard Space Flight Center, http://visibleearth.nasa.gov)

bined with individual farmer decisions to cultivate increasingly marginal farmland. Onset of the drought would have resulted in high mortality of plants and an increase in the amount of bare soil on individual fields. Strong winds would have generated soil erosion from individual fields after thresholds in wind velocity and plant cover were crossed (Stage 14.2). Because a number of farmers made the same decisions about crop and field selection, and the drought conditions were widespread, a second threshold would have been crossed related to connectivity among fields such that dust storms developed and spread across the landscape (Stage 14.3). At this stage, the rate and spatial extent of wind erosion would have been determined by the number, size, and spatial arrangement of fields interacting with regional scale weather conditions (Fig. 14.3). As the spatial extent of wind erosion continued to increase, another threshold would have been crossed where land-atmosphere interactions would have become operative to generate positive feedbacks and the creation of massive dust storms at the regional to continental scale (Stage 14.4).

It was recognized during the Dust Bowl period that a complex set of interactions were involved that included weather, vegetation, soils, and human activity (Great Plains Committee 1937). Although the committee stated that "all too frequently what appears to be good to the individual in the long run is not good for the people of the region" (Great Plains Committee 1937), our understanding about how these individual decisions interact with climate and ecological systems has remained limited. For example, conservation practices remain focused on the protection of individual fields or a small collection of fields rather than reducing connectivity among a large number of fields. Our framework suggests that limiting connectivity among fields is key to reducing the severity of these kinds of events.

Drought and other extreme climatic events (e.g., floods, hurricanes) will continue to occur in the Earth System (Easterling et al. 2000). Nonlinear interactions and positive feedbacks among climate, land use, and land cover can result in the propagation of impacts across broad spatial scales in relatively short time periods. However, the spatial extent and impact of these events can be mitigated, and possibly forecast, by understanding how these spatial nonlinearities develop and spread. In some cases, limiting landscape scale connectivity can reduce these impacts.

14.3.2 Wildfire

Wildfires are dominant forces shaping the structure and dynamics of forests, savannas, and grasslands as well as their neighboring or imbedded urban areas worldwide (Scholes et al. 2003). Policies associated with natural areas, particularly in developed countries, have often promoted the development of nearly continuously distrib-

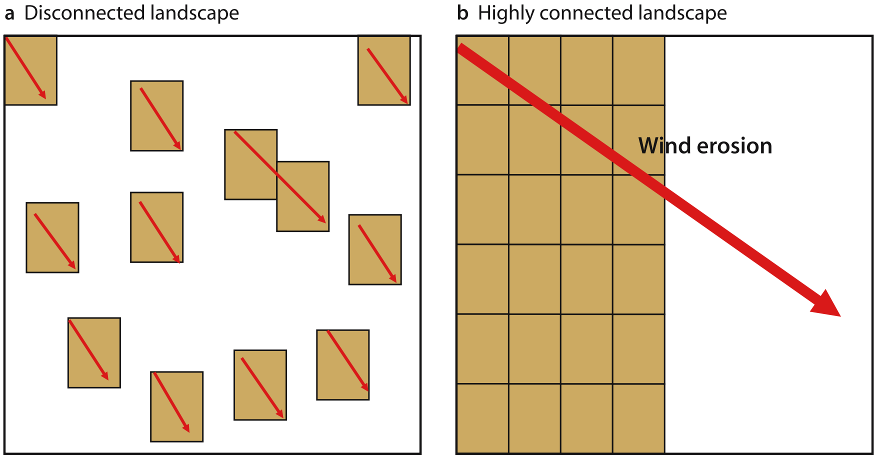

Fig. 14.3. Potential for wind erosion is less for landscapes consisting of a few, widely distributed bare fields (**a**) compared with a landscape that is mostly bare fields (**b**). Farming practices in the 1920s and 1930s in the U.S. predisposed these landscapes to high connectivity resulting from interactions between drought and strong winds, thus leading to the Dust Bowl

uted fuel loads that increasingly allow large, rapidly spreading fires to emerge (USDA 1978). The costs of wildfires are substantial: annual wildfire suppression costs in the U.S. now routinely exceed US$1 billion yr^{-1}. In addition, wildfires can have substantial impacts on atmospheric carbon monoxide (CO) and fine particulates (Scholes et al. 2003). For example, fires in Southeast Asia (2001) resulted in plumes of CO that extended across the Pacific Ocean to the west coast of North America (Steffen et al. 2004). Regional effects are also important: CO emitted by the Hayman fire in Colorado, USA (2003) was at least five times the annual amount produced by industrial sources in that state (Graham 2003). These pulse emissions occurred over a period of days with longer-term impacts on rainfall from the fine particles that extended hundreds of kilometers downwind.

Although it is recognized that short- and long-term weather conditions interacting with the amount, moisture content, and spatial distribution of fuels affect the extent, rate of spread, and severity of wildfires (Graham 2003), the factors that determine if a wildfire can be contained or if it will "blow up" and create catastrophic conditions have not been quantified. For example, 14 firefighters were killed during the Storm King Mountain fire in western Colorado USA (1994) following a sudden wind shift that created surface winds exceeding 55 km h^{-1} and flames 60–90 m high (Butler et al. 1998). Highly connected fuels interacted nonlinearly with the heat of the fire and with a larger scale wind shift to create this rapid change in wind direction and speed. In addition, positive feedbacks among landscape structure, fire, and weather can occur if the climate in the region warms (Laurance and Williamson 2001; McKenzie et al. 2004). Thus, the explosive spread of wildfires across landscapes is not easily forecast based either on fine scale fire behavior or broad scale atmospheric conditions. Our framework that focuses on spatial nonlinearities resulting from connectivity within and among patches of vegetation, and feedbacks to the atmosphere provides new insights into these complex fire dynamics.

We distinguish four major stages of wildfire behavior that are associated with three thresholds or nonlinear changes in the rate of fire spread through time and across space (Peters et al. 2004). This model is supported by published data from two fires in Colorado, USA with similar behavior, yet very different spatial extents (Peters et al. 2004). Similar patterns of fire spread have been documented for other major fires.

In Stage 14.1, fire that is ignited naturally or started by human activities can either spread or stop (Fig. 14.4a). The fire can cross a threshold (T1) to Stage 14.2 by spreading within a patch if local weather conditions, fuel load, and connectivity are sufficient (Fig. 14.4b) (Whelan 1995). For canopy fires to spread, the trees must be sufficiently close for flames to move from one tree to another within a patch. For surface fires to spread, threshold amounts and spatial connectivity of herbaceous fuels must be present. In addition, surface fires can move upward into tree canopies when vertically continuous "ladder" fuels (e.g., small subcanopy trees) connect the burning surface fuels with canopy fuels, generating localized torching.

A second threshold (T2) is crossed when the fire enters Stage 14.3 and burns from one patch to another at varying rates that depend on connectivity and spatial distribution of fuel load as well as interactions with local weather conditions (Fig. 14.4c). Patches that are poorly connected to other patches have low probabilities of the fire spreading whereas fire frequently spreads among patches that are highly connected. Parts of the landscape with low fuel connectivity often burn more slowly and less completely than highly connected parts of the landscape (Turner et al. 2003). As the fire continues to increase in extent and intensity, a third threshold can be crossed (T3) to move the fire into Stage 14.4 that depends on interactions and feedbacks between the fire and the atmosphere. As heated gases from the fire rise into the atmosphere, low air pressure pulls air into the fire, thus creating strong winds. These surface winds drive fire behavior by accelerating fire

Fig. 14.4. The four stages and three thresholds involved in wildfires: **a** a lightning strike can initiate a fire that either goes out or **b** spreads within a patch. Through time, the fire can **c** spread among patches across a landscape and **d** blow up when the heat and intensity of the fire interact with atmospheric conditions to provide a positive feedback to the fire

intensity and rate of spread. These positive feedbacks between fire activity and wind circulation develop rapidly resulting in a "blowup" of the fire with preheating of fuel and "spotting" ahead of the fire front (Fig. 14.4d). Explosive fire activity of this sort can generate large pyrocumulus clouds, particularly when atmospheric conditions are unstable and susceptible to convectional cloud formation (Byram 1954). Under these "blowup" conditions, all parts of the landscape burn, often at higher temperatures, regardless of fuel load or connectivity.

Although general stages of fire behavior have been documented previously and wildfires have been extensively studied at individual scales, we are still missing a clear understanding of the key processes and conditions that lead to catastrophic fire behavior (Steffen et al. 2004). Our approach provides a framework for linking these extensive datasets and models that were developed for specific applications and scales. Understanding cross-scale interactions and feedbacks will improve our ability to identify the key processes generating fire behavior across scales, and to forecast the conditions under which fine scale processes cascade nonlinearly to impact broad spatial extents with consequences for land-atmosphere interactions. Understanding these cross scale interactions will improve our ability to forecast fire behavior under changing weather and land-use regimes that include the continued use of fire as a management tool for many regions of the world (Scholes et al. 2003).

14.3.3 Invasive Species and Desertification

We illustrate the spread of invasive species using woody plant encroachment into perennial grasslands and associated land degradation (i.e., desertification). A wide range of native and exotic species exhibit similar patterns and dynamics (e.g., Hobbs and Humphries 1995; Mack et al. 2000). Desertification is a major problem globally: ca. 40% of the Earth's land surface consists of drylands that are susceptible to desertification and support ca. 20% of the world's human population (Reynolds and Stafford Smith 2002). Conversion of grasslands with homogeneous plant cover to shrublands or woodlands with discontinuous cover interspersed with bare areas often results in local to global consequences, such as increased soil erosion by wind with dust generation to the atmosphere (Schlesinger et al. 1990; Tegen and Fung 1995; Husar et al. 2001). The problem of desertification is complicated by the presence of multiple interacting processes, threshold behavior, and feedbacks with meteorological, hydrological, ecological, and human dimensions (e.g., Rietkerk and van de Koppel 1997; Zeng et al. 1999; Ludwig and Tongway 2000; Reynolds and Stafford Smith 2002; Wilcox et al. 2003). Although numerous studies have been conducted on desertification, a clear consensus is missing regarding the key processes involved and how they produce a variety of responses under apparently similar conditions as well as similar ecological consequences under different conditions (Peters et al. 2006). We propose that cross-scale linkages among three system elements are key determinants of desertification dynamics: (1) local soil and grass degradation associated with large herbivore grazing and other factors, (2) connectivity of erosion processes at multiple scales, and (3) land-atmosphere feedbacks.

Desertification is initiated by the introduction of woody plant seeds into a grass-dominated system (Stage 14.1) as a result of vectors, such as wind, water, and cattle, which transport seeds from woody plant-dominated areas to grasslands (Brown and Archer 1987). In some cases, initiation events fail because microenvironmental conditions are insufficient for establishment. In other cases, particularly when excessive grazing by large herbivores reduces grass cover and competitiveness with a resulting decrease in fire frequency, shrub establishment events succeed and a threshold is crossed (T1) where shrub invasion proceeds (Fig. 14.5). Local spread of a patch of established woody plants within a grassland then occurs (Stage 14.2), either through vegetative expansion or local seed dispersal followed by establishment (Archer 1990). Feedback mechanisms among woody plants and soil properties influence the rate of within-patch expansion. As woody plant size or density increase within a patch, the spatial extent of bare area between woody plants increases, such

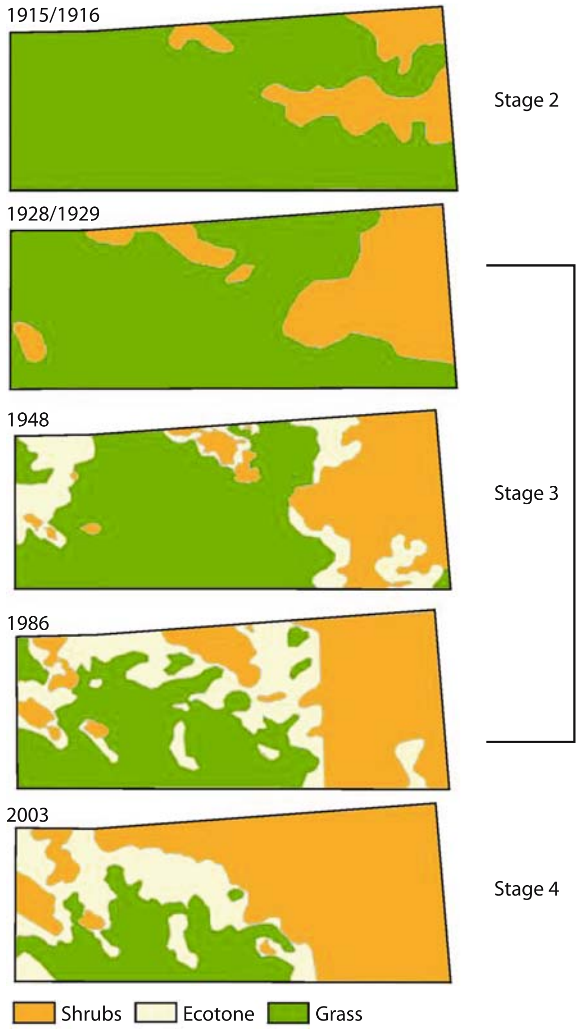

Fig. 14.5. The four stages and three thresholds in desertification. The five panels (942 ha total area) show three classes of vegetation: grasslands, ecotones containing grasses and shrubs, and shrublands through time in the Chihuahuan Desert of southern New Mexico. Field surveys (1915, 1928–1929; Gibbens et al. 2004), black and white (1948) and color infrared photos (1986) and Quickbird satellite images (2003) were scanned at 1200 dpi and geometrically corrected to the satellite image. Boundaries of three classes were manually digitized and areas were calculated in ArcGIS (data shown in Peters et al. 2004). *Stage 14.1:* Desertification begins with the introduction of shrub seeds into a grass-dominated system. In some cases, initiation events fail, and in other cases, they succeed and a threshold is crossed (*T1*) where shrub proliferation (Stage 14.2) proceeds. At this site in NM, this initiation occurred prior to 1915. *Stage 14.2:* Established shrubs proliferate around initial colonizers to form expanding patches (shown in 1915 map). *Stage 14.3:* As the size and density of woody plants continue to increase through time, a second threshold is crossed (*T2*) where contagious processes among patches, in particular wind erosion of bare soil patches, become the dominant factors governing the rate of desertification. *Stage 14.4:* Eventually sufficient land area is converted from grassland (low bare area, low albedo) to a shrubland (high cover of bare area, high albedo) that atmospheric conditions are affected, in particular wind speed, temperature, and precipitation, and a third threshold in crossed (*T3*). Because 92% of the land area of the surrounding research site was shrub dominated in 1998 (Gibbens et al. 2004), we hypothesize that *T3* occurred after 1986

that wind and water can redistribute resources in bare interspaces to areas beneath shrubs, thus forming resource islands (Schlesinger et al. 1990). Seed availability within shrub patches also increases the probability of new initiation events that result in isolated woody plants within the neighboring grassland matrix.

As the size and density of woody plants continue to increase through time, a second threshold is crossed (T2) where contagious processes among patches become the dominant factor governing the rate of desertification (Stage 14.3). This dispersion of woody plants often depends on the connectivity and spatial extent of bare areas that are influenced by wind or water erosion or their combination (Breshears et al. 2003). Bare areas influence woody plant establishment and survival as well as grass mortality with effects on vegetation patterns and dynamics.

Through time, erosion continues to increase the size and connectivity of bare soil patches, grass mortality, and hence woody plant dominance, such that adjoining areas of the landscape can be affected by wind-deposited soil (Youlin et al. 2001). Sufficient land surface area is converted from grasslands with low bare area and low albedo to woodlands with high percentage cover of bare area and high albedo. This broad-scale change in land-cover type can affect regional atmospheric conditions, in particular temperature and precipitation (e.g., Charney et al. 1977; Balling et al. 1998; Xue and Fennessy 2002) such that a third threshold is crossed (T3) in which land-atmosphere interactions with feedbacks to plants strongly influence vegetation dynamics (Stage 14.4) (Pielke 2001; Kabat et al. 2004). These climatic feedbacks to broad-scale vegetation patterns as a result of desertification have been documented: biophysical feedbacks may have resulted in a drier climate and a shift to desert vegetation ca. 5 500 years ago in the Sahara region of Africa (Claussen et al. 1999; deMenocal et al. 2000). Increased wind erosion and deposition of sand off the coast of West Africa may have resulted from this change in climate and shift in vegetation (deMenocal et al. 2000). Dust and other airborne particles can reduce water droplet sizes in clouds to result in reduced rainfall (Rosenfeld et al. 2001) that would then generate feedbacks to the vegetation.

Interactions among climate, land use, and land management will continue to be important drivers in future desertification dynamics. In these water-stressed environments, directional changes in climate or increases in its variability could increase aridity and push these systems to states and dynamics that go beyond current and past experience. For example, an increase in the frequency or severity of drought will likely interact nonlinearly with land management decisions to result in nonlinear increases in the rate and extent of desertification (Squires 2001). By accounting for cross-scale interactions, our approach provides new directions for combating desertification that are currently constrained by observations and models based on particular scales (Peters et al. 2004). Developing site-specific remedies requires quantification of cross-scale interactions among human activities, livestock grazing, drought, and other factors that are coupled by spatial patterns of vegetation at multiple scales. Data collected according to our interdisciplinary framework can be used to identify the key processes governing patterns and rates of desertification as well as thresholds. These data will indicate optimal strategies for manipulating connectivity across scales in order to minimize negative impacts and to capitalize on opportunities for remediation.

14.4 Forecasting Spatial Nonlinearities and Catastrophic Events

Catastrophic events resulting from spatial nonlinearities often result in major changes in ecosystem properties and services as well as loss of life or quality of life, and economic hardship. Our ability to forecast these events, particularly in the presence of environmental and societal changes, is constrained by our limited understanding of the processes, feedbacks, and nonlinear interactions that result in these spatially complex dynamics (Sarewitz et al. 2000). Most of our ecological understanding is based on experiments, observations, and simulation modeling from individual spatial or temporal scales. Experiments are most often conducted at fine scales whereas observations and simulation modeling can include multiple scales from fine to broad. Results from these single or multiple scale studies are often unable to detect cross scale interactions and dynamics that propagate across space (Peters et al. 2004).

We advocate experimental, observation, and modeling networks of studies that explicitly address cross scale interactions as the most fruitful approach to forecasting catastrophic events resulting from spatial nonlinearities. Existing networks of research sites, such as the U.S. National Science Foundation supported Long Term Ecological Research program, provide invaluable site-based information, often with historical and spatial context (Hobbie et al. 2003). However, there is currently insufficient spatial coverage by existing sites as well as insufficient integration, infrastructure, and measures of connectivity across scales, both within and among sites, to assess whether skillful forecasting is possible of how, when, and why small events cascade nonlinearly to result in broad-scale catastrophic impacts. Networks that attempt to address these types of national level, continental scale problems are on the horizon (e.g., National Ecological Observatory Network; http://www.neoninc.org/) that will provide the necessary information to improve our understanding and ability to forecast and mitigate these events.

14.5 Summary and Conclusions

Given the complexity of the issues in Earth System science, future research will need to adopt approaches that cross traditional disciplinary boundaries in order to address cross scale interactions, threshold behavior, and feedback mechanisms leading to catastrophic events (Steffen et al. 2004). Our understanding of broad-scale patterns and dynamics has improved through collaborative efforts among ecosystem ecologists and atmospheric scientists (e.g., Rial et al. 2004). In addition, human dimensions are increasingly recognized by ecologists as integral to explaining system dynamics (e.g., Reynolds and Stafford Smith 2002). However, cross-disciplinary studies are needed to understand and forecast nonlinear dynamics and threshold behavior through time and across space (Peters et al. 2004). The blending of ideas and terms across scientific disciplines by our framework is an important step in this new level of cross-disciplinary research. Future steps include integrated experiments and modeling studies that synthesize technologies and expertise from diverse disciplines. Our ability to show similarities in system dynamics from seemingly disparate disciplines indicates that much is to be gained by cross disciplinary efforts that capitalize on the strengths of each discipline.

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Chapter 15

Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change

I. Colin Prentice · Alberte Bondeau · Wolfgang Cramer · Sandy P. Harrison · Thomas Hickler · Wolfgang Lucht
Stephen Sitch · Ben Smith · Martin T. Sykes

15.1 Introduction

The annual exchange of carbon between the atmosphere and the land biota amounts to one-sixth of the atmospheric content of carbon dioxide (CO_2), and the average turnover time of terrestrial organic carbon (including the biota and soils, but excluding geological storages) is only about 20 years. The land biosphere therefore plays a dynamic role in the global carbon cycle on time scales relevant to human activities (Prentice et al. 2001; Schimel et al. 2001; Field et al. 2004). The land biosphere's variations in space and time also influence the fluxes of energy, momentum, water vapor, and many climatically important or reactive trace gases and aerosol precursors across the lower boundary of the troposphere. The land biota respond individualistically to local environmental factors such as photosynthetically active radiation (PAR), temperature, atmospheric humidity, soil moisture, CO_2 concentration and land management. These responses of organisms to their environment are fundamental for the continuing provision of ecosystem goods and services on which all human activities ultimately depend (MA 2003).

Among the many methods for observing the dynamics of terrestrial ecosystems, each method has a restricted window of applicability in space and time. Ground-based measurements (biomass inventories, community descriptions, productivity measurements, flux measurements) are made at single sites or across networks, but are not readily scaled up. Satellite-based measurements provide up to 20 years of global coverage with spatial resolution on the order of a few kilometres, and temporal sampling intervals of days to weeks. Satellite observations have special importance for understanding large-scale processes because they can provide comprehensive coverage, averaged over landscapes. New sensors and satellites are expanding the scope of such observations. But there are limitations on what can be observed from space, particularly with regard to biodiversity and belowground processes. For the foreseeable future, it will be important to use multiple sources of information on terrestrial ecosystem structure and dynamics, and to use modeling techniques to link them.

The identification of mechanisms in the functioning of the land biosphere has meanwhile become a high scientific priority. On a fundamental level, many nonlinearities and feedbacks in the Earth System, including processes determining changes in atmospheric composition on glacial-interglacial and longer time scales and rapid changes in ecosystems and the atmosphere during the recent geological past, originate in the incompletely understood coupling between global biogoechemical cycles and the physical climate (Prentice and Raynaud 2001; Overpeck et al. 2003). On a more practical level, anthropogenic alterations of the global environment have accelerated massively, through land-use change (Foley et al. 2005) as well as changes in atmospheric composition and climate (Houghton et al. 2001); this situation has created an urgent demand by society for tools to predict the risks of continued environmental changes for ecosystem services, and indeed for the future of climate and sustainable land management. The development of Dynamic Global Vegetation Models (DGVMs) by several research groups during the past 10–15 years has been largely a response to these dual "drivers" of interdisciplinary Earth System science.

15.2 Historical Antecedents and Development of DGVMs

The conceptual development of a DGVM dominated the activities of the Biosphere Dynamics Project, led by Allen M. Solomon, at the International Institute for Applied Systems Analysis (IIASA) during 1988–1990. GCTE subsequently adopted DGVM development as a near-term goal, and provided an umbrella for further work by several groups. DGVMs fuse research on four broad groups of processes: *plant geography*, *plant physiology and biogeochemistry*, *vegetation dynamics*, and *biophysics*, each historically pursued by a separate research community (Fig. 15.1). The early development of DGVMs concentrated on representing these processes and their interactions as they would have occurred without human influence. Lately DGVM development has expanded to include the representation of *human intervention* (agriculture, urbanization and forest management).

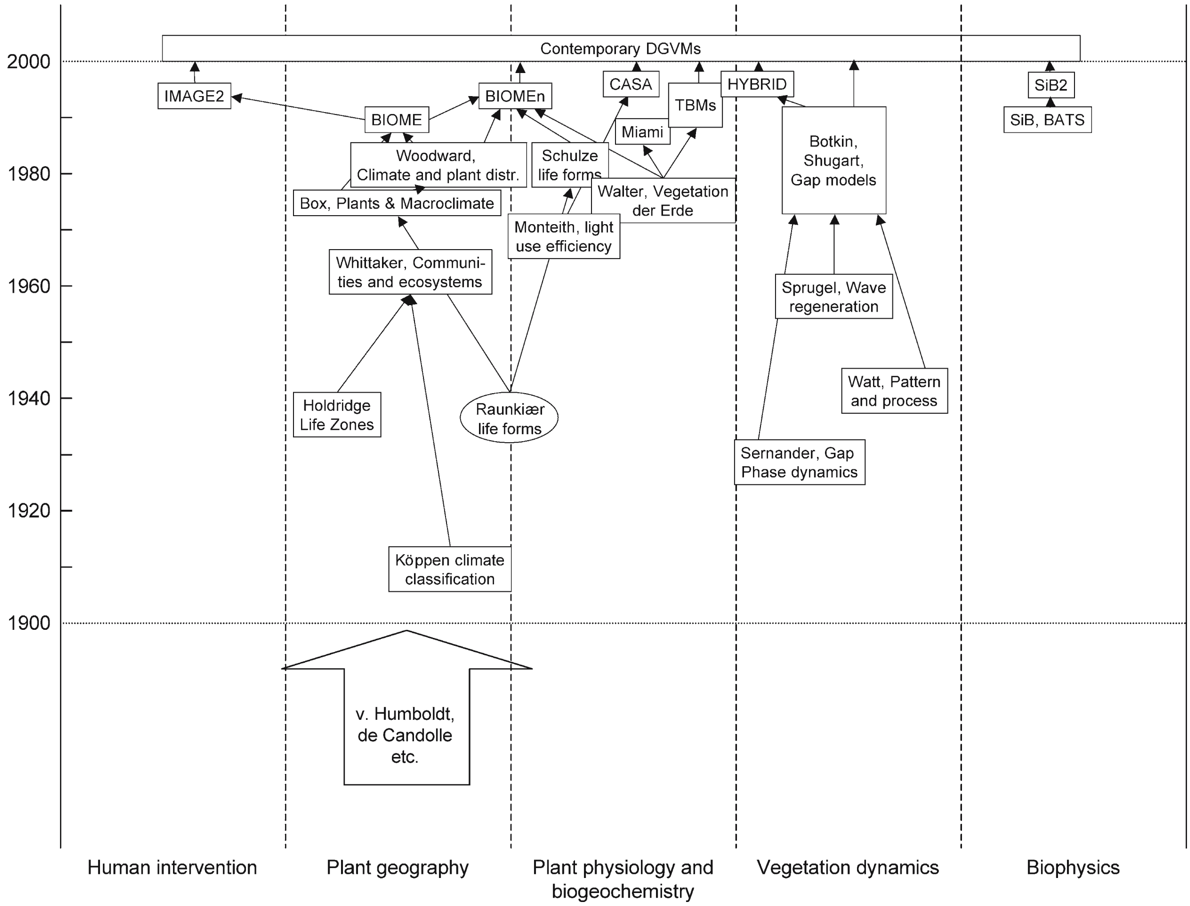

Fig. 15.1. A summary of the historical antecedents and recent development of DGVMs

15.2.1 Plant Geography

The beginnings of predictive modeling in plant geography can be traced to Köppen's (1931) world climate zones. Köppen tried to match the distribution of biomes, and included relevant seasonal aspects of climate in his classification scheme. A later (but more artificial) classification scheme based on annual climate statistics by Holdridge (1947) was used by Emanuel et al. (1985) to produce the first climate-derived map of global potential natural vegetation, and the first global projection of vegetation for a "greenhouse world" as simulated by a general circulation model (GCM). Further climate classifications designed to match biome distributions have been proposed by Whittaker (1975) and several others.

None of these schemes was based explicitly on an underlying theory of the controls on vegetation distribution, although the rudiments of a theory had been put forward by Raunkiær (1909, 1913, 1934). Raunkiær emphasized the role of mechanisms for surviving the unfavourable season in determining the distribution of different types of plants, which we would now call "plant functional types" (PFTs). Building on Raunkiær's ideas, Box (1981) created the first numerical model of global PFT distributions driven by climate. Woodward (1987) created the first explicitly process-based model of global biome distribution. The model included limits to woody PFT survival associated with cold tolerance, based on a review of experimental data. It included the dependence of leaf area index (LAI) on water availability, using an optimization principle introduced by Specht (1972). Woodward's approach was further developed in the "equilibrium biogeography models" BIOME (Prentice et al. 1992) and MAPSS (Neilson et al. 1992; Neilson and Marks 1994; Neilson 1995).

15.2.2 Plant Physiology and Biogeochemistry

General quantitative relationships between plant growth and resource availability became available during the 1960s through the International Biological Programme (IBP). Walter's *Vegetation der Erde* (Walter 1962, 1968) combined the older principles of plant geography with the new understanding of plant production. Lieth (1975) analysed IBP data statistically to create the so-called Miami model for net primary production (NPP) as a function of climate. Schulze (1982) reviewed the role of carbon, water and nutrient constraints in determining the distribution of PFTs, emphasizing the importance of competitive success as well as survival limits.

"Terrestrial biogeochemistry models" (TBMs), as they are now known, were originally developed with the main goal of simulating NPP. The first to be applied globally was the Terrestrial Ecosystem Model (TEM) (Melillo et al. 1993). Other TBMs include Century (Parton et al. 1993), Forest-BGC (Running and Gower 1991: later BIOME-BGC; Running and Hunt 1993), CASA (Field et al. 1995), G'DAY (Comins and McMurtrie 1993), CARAIB (Warnant et al. 1994), DOLY (Woodward et al. 1995) and BETHY (Knorr 2000; Knorr and Heimann 2001). The more recent TBMs use the biochemical model of Farquhar et al. (1980) for the dependence of photosythesis on external variables. This model makes explicit the dependence of photosynthesis on the leaf-internal partial pressure of CO_2, providing a key component for process-based simulation of CO_2 effects.

Several of the original TBMs are still used widely. In addition, the BIOME*n* models (Haxeltine and Prentice 1996a,b; Kaplan et al. 2003) are a hybrid of the equilibrium biogeography and TBM approaches. They predict geographic distributions of biomes by comparing the modeled NPP of different PFTs within each PFT's survival limits. They can therefore make competition-based distinctions among biomes that the earlier equilibrium biogeography models could not, and they can incorporate CO_2 effects mechanistically (Cowling 1999; Harrison and Prentice 2003).

15.2.3 Vegetation Dynamics

All of the models discussed above are restricted in their application because they cannot represent dynamic transitions between biomes (Prentice and Solomon 1991; VEMAP Members 1995; Neilson and Running 1996; Woodward and Lomas 2004). To provide this capability, DGVMs have drawn on a very different scientific tradition. Classic ecological studies of vegetation dynamics, including Sernander (1936), Watt (1947) and Sprugel (1976), laid the foundations for the modern understanding of vegetation dynamics and prepared the way for the formal description of forest dynamics in terms of individual tree establishment, growth and mortality in JABOWA (Botkin et al. 1972), FORET (Shugart and West 1977), LINKAGES (Pastor and Post 1985) and a host of descendants (Shugart 1984), including extensions to non-forest vegetation types (e.g., Prentice et al. 1987). Newer incarnations of this "gap model" concept include FORSKA (Prentice and Leemans 1990; Prentice et al. 1993) and SORTIE (Pacala et al. 1993, 1996). These models typically are applied in a small region with parameter sets based on observations for individual species. They are computationally intensive because they simulate the stochastic behavior of many individual plants on multiple replicate plots.

DGVMs struggle to represent vegetation dynamics in a computationally efficient way without losing essential features that depend on interactions between plant individuals. Friend et al. (1997) used a simplified gap model approach, representing grid cell dynamics by a sample of patches. More efficient layer- (Fulton and Prentice 1997) and cohort-based (Bugmann 1996; Bugmann and Solomon 2000) approximations for vegetation dynamics exist, but have not been widely adopted. Most DGVMs rely instead on various *ad hoc* large-area parameterizations. Smith et al. (2001) however showed that the gap model formalism continues to give more realistic estimates of PFT dynamics, at least when compared to the large-area parameterization in the Lund-Potsdam-Jena (LPJ) DGVM (Sitch et al. 2003; see also Hickler et al. 2004a). A possible route to a more rigorously "traceable" representation of individual-based processes over large areas is suggested by the work of Moorcroft et al. (2001).

15.2.4 Biophysics

GCMs include representations of the controls on the exchange of energy, water vapor and momentum between the atmosphere and the land surface. Biophysical models developed for this purpose are called "land surface schemes" or "soil-vegetation atmosphere transfer models" (SVATs). Vegetation properties needed by the GCM include rooting depth, soil porosity, surface albedo, surface roughness, fractional vegetation cover, and surface conductance. Surface albedo depends on leaf reflectance, canopy structure and vegetation structural properties (including height) that determine the "masking" of snow. Changes in vegetation that affect surface albedo can profoundly affect climate (Bonan et al. 1992). Surface conductance depends on leaf area index and stomatal conductance, and is one of the controls on evapotranspiration. Accurate simulation of exchanges between the land and the free troposphere also depends on having an adequate representation of the planetary boundary layer (PBL). PBL dynamics depend on properties of the land surface, including the latent heat flux from the canopy (Finnegan and Raupach 1987; Monteith 1995; Prentice et al. 2004).

The first GCM land-surface schemes to represent vegetation explicitly were SiB (Sellers et al. 1986) and BATS (Dickinson et al. 1993). These models represented variations in stomatal conductance by empirical functions of PAR, temperature, humidity and soil moisture (Jarvis 1976). Later models have exploited the tight coupling of CO_2 and water exchange through stomatal conductance (Collatz et al. 1991). The current trend is to replace GCM land-surface schemes with full DGVMs. For this purpose, exchanges of energy, water vapor and momentum must be modeled at a time step similar to the shortest atmospheric time step of the GCM (typically about 30 minutes). The DGVMs IBIS (Foley et al. 1996) and TRIFFID (Cox 2001) were developed for GCM coupling. Full coupling to an atmospheric GCM was first achieved by Foley et al. (1998) and Delire et al. (2002). Full physical coupling to an ocean-atmosphere GCM has been achieved by Robert J. Gallimore and others (e.g., Notaro et al. 2004) using LPJ (Sitch et al. 2003). LPJ also provided the basis for a generic vegetation dynamics component in Orchidée (Krinner et al. 2005) and several other DGVMs that are being developed for GCM coupling. All of the major climate modeling groups are now working towards full physical and carbon-cycle coupling of atmosphere, ocean and land, as first implemented by Cox et al. (2000).

15.2.5 Human Intervention

A final strand of model development addresses the changing suitability of the land for human land use and the reciprocal influence of human land use on the state of the biosphere. The most widely known example, and the most explicit in terms of representing land cover, is IMAGE2 (Alcamo 1994). IMAGE2 is widely cited and used for integrated assessment and scenario development. The land surface component of IMAGE2 was derived from BIOME (Prentice et al. 1992). However, several groups are now developing more advanced large-area representations of managed ecosystems, including explicit simulations of agricultural and forest management, as components of DGVMs (Bondeau et al. in press).

15.3 Principles and Construction of DGVMs

15.3.1 Model Architecture

The modular organization of DGVMs is rather uniform (Cramer et al. 2001; Sykes et al. 2001; Beerling and Woodward 2001; Woodward and Lomas 2004; Fig. 15.2). The design and process formulations of DGVMs are not fundamentally different from those in TBMs, which have been used to investigate some of the same questions (Heimann et al. 1998; McGuire et al. 2001). The most important unique feature of DGVMs is their ability to simulate vegetation dynamics. Within a grid cell, vegetation may be represented by fractions or strata occupied by different PFTs. Age or size classes may be distinguished, but more typically the modeled properties represent averages among the entire grid cell population of a given PFT (e.g., Sitch et al. 2003; Fig. 15.3). PFT-specific state variables, i.e., physical properties that change dynamically in the course of the model simulation, may include a description of the average geometry of individual plants, the carbon content of one or more plant biomass compartments (leaves, roots, wood), nitrogen (N) status, factors affecting resource uptake capacity (leaf area index, root density) and population density.

DGVMs implement two or three nested timing loops, calling different processes on different operational time steps (Fig. 15.2) corresponding loosely to the fastest characteristic time scale of the process. "Fast" processes varying on a diurnal cycle include energy and gas exchange

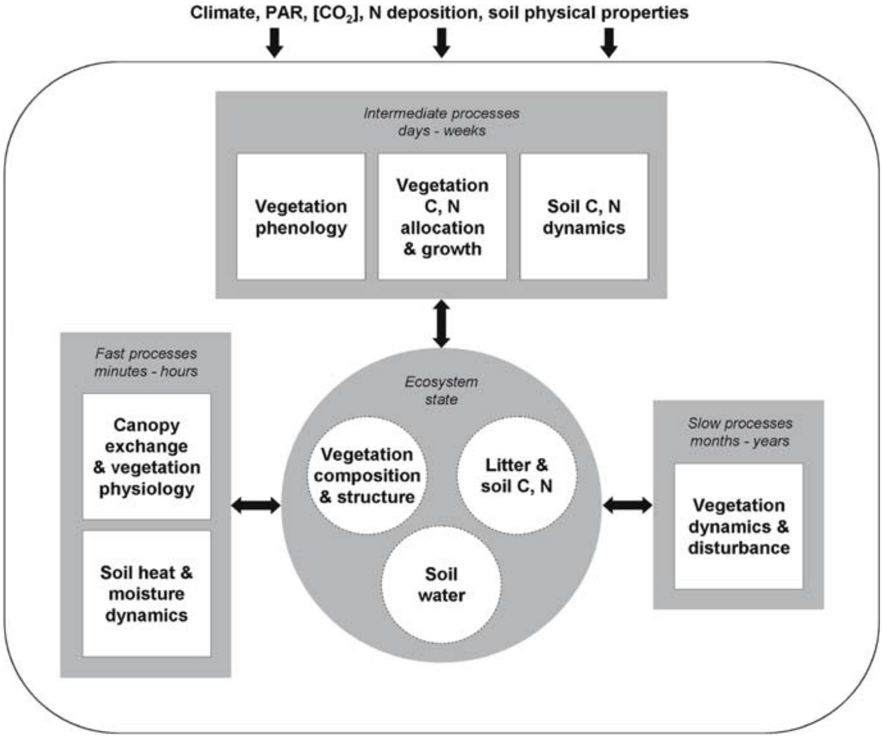

Fig. 15.2.
DGVMs are structurally rather similar. This figure illustrates a typical structure, showing driving variables, main process modules (organized by operational timestep) and state variables

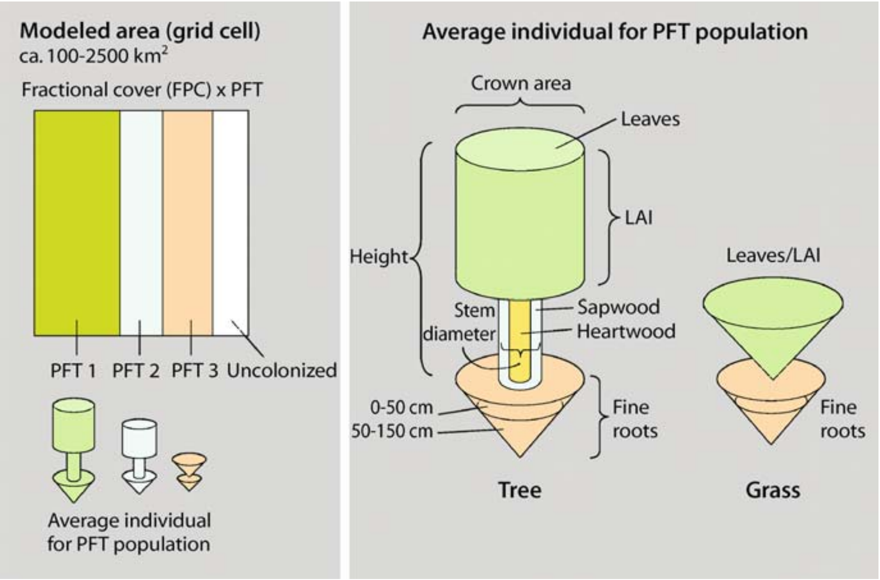

Fig. 15.3.
Each DGVM has adopted a different large-area parameterization for vegetation dynamics. This figure depicts one example (Sitch et al. 2003). Here, each PFT occupies a fraction of the modeled area (grid cell). Structural properties for one *average individual* for each PFT vary dynamically depending on carbon allocation, tissue turnover and allometric relationships. Population density scales PFT properties from the average individual to the grid cell

at the canopy-atmosphere interface, photosynthesis and plant-soil water exchange. These processes are invoked either on a time step of one day, using daily integrals of driving variables such as PAR, or (more accurately, in principle) at shorter time steps of one hour or less, in models that explicitly simulate the diurnal cycle. Processes with seasonal dynamics include plant phenology, growth and soil organic matter dynamics; the typical time step used for these processes is one month. Vegetation dynamics are generally the slowest process modeled, and are typically represented with a time step of one year.

15.3.2 Net Primary Production

The currency of growth in DGVMs is NPP, the balance of carbon uptake by photosynthesis and release by autotrophic respiration. Most DGVMs use the Farquhar et al. (1980) model, or derivatives thereof (Collatz et al. 1991, 1992; Haxeltine and Prentice 1996a,b), to model photosynthesis at the leaf level. Environmental and leaf parameters are either available from the input data (e.g., air temperature and CO_2 concentration), calculated based on the current vegetation or system state (stomatal conductance, leaf nitrogen content), or prescribed (specific leaf area). DGVMs explicitly or implicitly take into account shading of leaves at lower levels in the vegetation canopy by the levels above. Nitrogen invested in leaf functional proteins is commonly assumed to distribute among canopy layers in a fashion that maximises net assimilation, i.e., photosynthesis minus leaf respiration (Haxeltine and Prentice 1996a,b; Foley et al. 1996; Friend et al. 1997; Sitch et al. 2003), at each canopy level (see Dewar 1996 and Prentice 2001 for further discussion of this hypothesis and its variants).

The rate of diffusion of CO_2 from the ambient air via the boundary layer adjacent to leaf surfaces and the stomata is controlled by aggregate stomatal conductance, and limits photosynthesis. Plants are considered to regulate stomatal conductance, within limits, to optimise CO_2 uptake in relation to water loss through transpiration (Cowan 1977; Collatz et al. 1991). Thus, DGVMs typically couple photosynthesis, canopy biophysics and soil hydrology submodels via canopy conductance, although the detailed formulations vary.

Respiration is usually separated into maintenance and growth components. Maintenance respiration is sensitive to temperature and differs among tissues (Ryan 1991). Models may adopt a tissue-specific scaling factor combined with a common temperature response function, generally a Q_{10} or Arrhenius relationship. Alternatively, a function based on tissue C/N ratio may replace the tissue-specific multiplier. Growth respiration is usually defined as a fixed fraction of NPP. Some DGVMs alternatively use more empirical approaches to estimate NPP, with a potential rate moderated by scalars standing for environmental stresses (e.g., soil water, low temperatures, shading of grasses by trees: Daly et al. 2000) and/or resource availability and uptake capacity (Pan et al. 2002; Potter and Klooster 1999).

15.3.3 Plant Growth and Vegetation Dynamics

In all DGVMs, multiple PFTs are allowed to co-occur and compete. Tolerance limits for bioclimatic variables, such as coldest-month mean temperatures and growing-season heat sums, define the climatic space each PFT can occupy (Woodward 1987; Harrison et al. submitted). PFTs may be switched "on" or "off" in a particular grid cell, through PFT-specific establishment and mortality functions, as the favourability of the climate varies. The driving force for vegetation dynamics is then the NPP of competing PFTs. In the simplest formulations of vegetation dynamics (e.g., Foley et al. 1996; Potter and Klooster 1999), individual and population growth are combined in an overall parameterization of the effects of resource competition on PFT abundances. Carbon assimilated by each PFT is partitioned among its biomass compartments (leaves, roots, stems) according to fixed allocation coefficients. Each compartment has a residence time, which determines the rate of transfer of carbon to litter pool due to tissue turnover and mortality. More mechanistic approaches distinguish individual- and population-level growth. In the LPJ implementation, the NPP accumulated by a tree PFT population during a year is first partitioned among "average individuals" based on the current population density (Sitch et al. 2003). Allocation and tissue turnover are calculated for the average individual, and are constrained to satisfy allometric relationships (Fig. 15.3). Population growth is the balance of an annual rate of establishment of new saplings, influenced by current density, and mortality, which may increase under conditions of resource limitation, crowding or disturbance.

The ability to adjust allocation patterns to maintain a balance between resource uptake and utilization is a key feature of plant competitive strategies (Field et al. 1992). Modeled allocation patterns in DGVMs can therefore be influenced by the relative supply of above- and below-ground resources. Soil water deficits in the current growing season, for example, may lead to increased investment in roots at the expense of leaves the following growing season.

15.3.4 Hydrology

DGVMs typically include some multi-layer scheme for soil water, with percolation and/or saturated flow between layers. Evaporation from the upper soil layer and the vegetation canopy (i.e., interception loss) may supplement plant transpiration. Water content in excess of field capacity is lost as runoff. Some models take account of the effects of snow and ground frost on seasonal water cycles. DGVMs have also been coupled to large-scale models for lateral water transport, in order to examine e.g., impacts of land-use change on river flow.

15.3.5 Soil Organic Matter Transformations

Carbon enters the soil as litter associated with tissue turnover and mortality. Litter and soil carbon provide the substrate for soil heterotrophs, whose respiration releases CO_2. "Pools" with different degrees of decomposability are usually distinguished. As the labile fractions are consumed, residues are transferred to pools with longer average residence times. The number of pools represented ranges from two or three to eight or more in models that implement the soil module from Century. Decomposition rates for a given pool are influenced by temperature, soil moisture status and, in some models, properties such as the C/N ratio of the decomposing material, soil texture and clay content.

15.3.6 Nitrogen (N) Cycling

After light and water availability, plant-available N is the most important limiting factor in many terrestrial ecosystems (e.g., Townsend et al. 1996). Nevertheless, only some of the current DGVMs include a full interactive terrestrial N cycle, taking into account below-ground controls on N mineralization as well as N limitations on NPP. DGVMs that incorporate the Century approach to soil processes inherit its coupled soil C and N scheme (Friend et al. 1997; Potter and Klooster 1999; Daly et al. 2000; Woodward et al. 2001; Bachelet et al. 2001). Here litter quality influences net N mineralization and decomposition rates; labile "metabolic" inputs, such as litter derived from leaves and fine roots, tend to increase net N mineralization, whereas lignin-rich "structural" material causes N immobilization and may limit N availability to plants. N limitation of production may be modeled by scaling net assimilation to plant uptake of N from the soil mineral N pool. In the Hybrid DGVM, N limitation implicitly reduces investment in Rubisco and chlorophyll, resulting in a lower maximum carboxylation rate and reduced photosynthesis (Friend et al. 1997).

15.3.7 Disturbance

The term "disturbance" is widely used to refer to processes such as fires, windstorms and floods, which rapidly destroy biomass, alter vegetation structure and alter the conditions for the growth of remaining plants and/or the establishment of new plants. This usage is illogical because "disturbances" by this definition are intrinsic to ecosystems and part of the mechanism that maintains their typical composition and character (Allen and Hoekstra 1990); however, it is entrenched in the literature. The stochastic nature of disturbance regimes makes them difficult to represent in models. Some DGVMs do not explicitly model disturbances; instead, they incorporate their effects implicitly in turnover constants for vegetation carbon (Foley et al. 1996; Friend et al. 1997).

Fire is the most important type of natural disturbance type worldwide, affecting all biomes except rainforests and deserts, at frequencies ranging from every year to once every few centuries. The most important controls on fire regimes are the frequency of ignition (whether natural or human-caused) and the amount, moisture content and flammability of biomass fuels. These controls depend on both climate and vegetation state, allowing for a variety of feedbacks in vegetation dynamics involving fire. Thonicke et al. (2001) introduced a semi-empirical fire module for use in DGVMs (Pan et al. 2002; Sitch et al. 2003). The modeled area (grid cell) is considered to be large enough that ignition sources are available, and that the *fraction* of the grid cell affected by fire in a given year is equal to the *probability* of fire affecting a randomly chosen point. This probability is estimated using empirical equations based on fuel load and moisture content (estimated from the moisture of the top soil layer). PFTs differ in their resistance to fire, so that the degree of damage caused to standing biomass depends on the vegetation composition. Fires result in vegetation mortality and volatilization of a fraction of litter and biomass over the affected area.

A more advanced approach to modeling fire dynamics has been adopted in the MC1 DGVM. This model distinguishes surface and crown fires, and fire effects are sensitive to stand structure as well as fuel load (Lenihan et al. 1998; Daly et al. 2000; Bachelet et al. 2001, 2003). Venevsky et al. (2002) and Arora and Boer (in press) have developed fire models of intermediate complexity that allow for variations in ignition rates associated with human activities.

15.4 Evaluating DGVMS

DGVMs simulate processes at a wide range of space and time scales and, accordingly, many different types of contemporary observations can be used to test their performance. The following is a non-exhaustive summary of observational "benchmarks" for DGVMs. For further examples see e.g., Kucharik et al. (2000), Beerling and Woodward (2001) and Woodward and Lomas (2004).

15.4.1 Net Primary Production

Following the Potsdam NPP Intercomparison Project (Cramer et al. 1999), which engaged mainly TBMs in a first large-scale comparison of terrestrial models driven by a common set of input variables, the Ecosystem Model-Data Intercomparison project (http://gaim.unh.edu/Structure/Intercomparison/EMDI/) ran site-specific simulations of NPP and compared them to measurements of NPP from sites in each of the major biomes. A large data synthesis effort yielded NPP values at 162 Class A sites ("well documented and intensively studied") and 2363 Class B sites ("globally extensive but less well documented and with less site-specific information"). A tendency was found for models to over-estimate low- to mid-range production at boreal and temperate sites, and to underestimate NPP in highly productive tropical sites. Modeled NPP tended towards an asymptote ~1000 g C m^{-2} while measurements showed some higher values. The reasons for these discrepancies remain to be established.

15.4.2 Remotely Sensed "Greenness" and Vegetation Composition

The fraction of Absorbed Photosynthetically Active Radiation (fAPAR) is the ratio of vegetation-absorbed to incident PAR. It can derived from satellite spectral reflectance data and is a measure of vegetation "greenness". The seasonal course of fAPAR provides a way to test modeled phenology (Bondeau et al. 1999). Some TBMs, known as light-use efficiency models, use remotely sensed fAPAR as input (e.g., Potter et al. 1993; Knorr and Heimann 1995; Ruimy et al. 1996). Alternatively, fAPAR observations can also be used to calibrate phenology in models (Kaduk and Heimann 1996; Botta and Foley 2002; Arora and Boer 2005). Seasonal cycles of fAPAR have also been used together with ancillary information to construct global maps of vegetation composition in terms of a few broadly defined PFTs. For example, Sitch et al. (2003) used the DeFries et al. (2000) global data set of estimated fractional PFT cover as a benchmark for vegetation composition, while Woodward and Lomas (2004) used the HYDE land-cover type data set of Klein Goldewijk (2001).

15.4.3 Atmospheric CO_2 Concentration

A different approach to large-scale evaluation of terrestrial models (Prentice et al. 2000) makes use of high-precision atmospheric measurements of CO_2 concentration (http://www.cmdl.noaa.gov/ccgg/globalview/co2/). Both the amplitude and the timing of the seasonal cycle of CO_2 vary geographically, reflecting different seasonal patterns of biospheric activity. The amplitude is greatest in northern high latitudes because of the large vegetated area in the north and the large offset in the timing of NPP and heterotrophic respiration maxima in high latitudes. Heimann et al. (1998) ran the TM2 atmospheric transport model with monthly fields of net ecosystem exchange (heterotrophic respiration and combustion minus NPP) from four terrestrial models. The output was sampled at the locations of CO_2 monitoring stations. Knorr and Heimann (1995, 2001), Dargaville et al. (2002) and Sitch et al. (2003) continued this approach. The main caveat for such comparisons is that they rely on the realism of the transport model; this is an active research area (Denning et al. 1999; Gurney et al. 2003; Law et al. 2003; Gurney et al. 2004). Inversion of tracer transport models has also been used to infer regional sources and sinks of CO_2 directly from the CO_2 concentration network (Fan et al. 1998; Bousquet et al. 2000; Kaminski and Heimann 2001; Rödenbeck et al. 2003). Peylin et al. (2005) showed good agreement between interannual carbon exchanges over broad regions as calculated by inverse models and as simulated with a DGVM and a TBM. Most of the observed interannual variability in the atmospheric CO_2 growth rate was shown to be explained by the differential responses of NPP and heterotrophic respiration to climate.

15.4.4 Runoff

As all terrestrial biosphere models simulate the interaction of the carbon and water cycles, the models can be evaluated in terms of their performance in simulating measured water fluxes (Gordon and Famiglietti 2004; Gordon et al. 2004). Over multi-annual time scales, runoff – which is measured at gauging stations on rivers – is equivalent to the difference between precipitation and evapotranspiration, averaged over the catchment upstream of the station. Gerten et al. (2004) demonstrated that LPJ showed comparable skill to existing global hydrology models in predicting global runoff patterns. They went on to model the additional effect of changing CO_2 concentration (via changes in stomatal conductance) on runoff.

15.4.5 CO_2 and Water Flux Measurements

Measurements of CO_2 and water flux from towers by the eddy covariance technique provide a temporally highly resolved record, and a powerful new tool for model evaluation (Falge et al. 2002; Baldocchi 2003). The FLUXNET global network of flux measurement stations gathers data from as many as 200 sites, although these are still very unevenly distributed across the globe (Baldocchi and Gu 2002; http://www.daac.ornl.gov/FLUXNET/fluxnet.html/). The data record diurnal, seasonal and interannual variability. CO_2, water and energy fluxes are measured simultaneously and concurrently with meteorological measurements that can be used directly to drive the models. There are two main limitations: the data are typically incomplete (for reasons discussed by Dolman et al. 2003), and the results (in common with conventional NPP measurements) are site-specific so that accurate specification of local soil conditions and disturbance history may be important. The experience obtained so far (e.g., Amthor et al. 2001; Potter et al. 2001; Gerten et al. 2004; Krinner et al. 2005; Morales et al. submitted) suggests that TBMs and DGVMs can perform well in simulating seasonal cycles and interannual variability of measured CO_2 and water exchange, but that the annually integrated carbon balance may depend on site-specific and generally unknown historical management factors.

15.5 Examples of Applications of DGVMS

DGVMs can be used alone or coupled to other types of models as tools to understand changes in the Earth System. Here we summarize a selection of DGVM studies that have helped either to explain observed phenomena, or to predict the consequences of human activities in the future.

15.5.1 Holocene Changes in Atmospheric CO_2

The causes of changes in the atmospheric concentration of CO_2 since the end of the last glacial period, about 12 ka before present (BP), are controversial. Ice-core analyses show a drop of 7 ppm from 11 to 8 ka BP, followed by a gradual rise of 20 ppm towards the pre-industrial 280 ppm (Indermühle et al. 1999; Flückiger et al. 2002). Indermühle et al. (1999) attributed both the initial drop and subsequent rise primarily to changes in terrestrial carbon storage. Broecker et al. (2001) questioned this explanation for the rise, suggesting instead that CO_2 removed from the atmosphere and surface ocean water by terrestrial carbon uptake after the glacial maximum was slowly replaced due to the precipitation of $CaCO_3$ at depth ("calcite compensation"). Ruddiman (2003) on the other hand has ascribed the CO_2 rise to deforestation. This problem has been studied with DGVMs by Brovkin et al. (2002) and by Joos et al. (2004). Joos et al. (2004) forced the Bern-CC coupled carbon cycle model (which includes the LPJ DGVM for terrestrial carbon dynamics) with palaeoclimate model simulations (Kaplan 2002). The coupled model reproduced the observed CO_2 trajectory since 11 ka BP to within a few ppm. The initial drop was explained by vegetation regrowth. The subsequent increase in CO_2 concentration was mainly due to *(a)* rising sea surface temperature, and *(b)* calcite compensation, as Broecker et al. (2001) proposed. The ice-core record of $\delta^{13}C$ (Indermühle et al. 1999) rules out any large contribution from deforestation. This model version also simulates the terrestrial $\delta^{13}C$ budget, based on Kaplan et al. (2002) and Scholze et al. (2003). The modeled $\delta^{13}C$ history was consistent with the ice-core data.

15.5.2 Boreal "Greening" and the Contemporary Carbon Balance

Spectral reflectance observations have shown a persistent greening trend in northern high latitudes through the 1980s and 1990s (Myneni et al. 1997; Zhou et al. 2001). Maximum summer LAI in the boreal zone, estimated from these observations, increased by 0.19 between 1982 and 1998. Potential explanations include vegetation response to high-latitude warming, forest regrowth due to changed management, vegetation recovery from disturbance by fire or insect attacks, CO_2 fertilization, or (just possibly) incomplete correction for drifts in the response of the sensor. Lucht et al. (2002) investigated whether the greening trend could be explained by vegetation responses to climate. Simulations driven by monthly climate data (New et al. 2000) showed that the trend, its seasonal cycles and interannual variability could all be reproduced. The simulations were entirely independent of the satellite observations. Thus, it is most likely that the observed greening trend is real and was caused by the changing climate. Further simulations showed that virtually all of the effect has been due to warming. These findings are consistent with the over-riding control of temperature on vegetation growth in high latitudes. The controls are more complex in warmer climates. Figure 15.4 shows the simulated land-atmosphere flux averaged over the whole period, compared with climate anomalies. Some regions showed a large reduction in precipitation (e.g., the Sahel), others a large increase in temperature (e.g., southern Africa), both leading to a release of carbon because of reduced NPP and/or increased heterotrophic respiration. Some regions, such as the southeastern USA, experienced increased precipitation and decreased temperatures, leading to increased carbon uptake (cf. Nemani et al. 2002; Hicke et al. 2002; Rödenbeck et al. 2003).

15.5.3 The Pinatubo Effect

Atmospheric CO_2 concentration temporarily slowed its increase after the eruption of Mount Pinatubo in 1991. Aerosols from this eruption cooled the globe by around 0.5 °C (more in northern latitudes). DGVM simulations over this period have reproduced both a temporary drop in boreal LAI (also shown by the satellite data) and an enhanced high-latitude terrestrial carbon sink (Lucht et al. 2002). Although NPP and heterotrophic respiration were both reduced, the modeled effect on respiration was stronger, producing an enhanced carbon sink. But these changes at high latitudes were not large enough to provide the full explanation. The simulated *global* patterns of simulated NPP and heterotrophic respiration anomalies are more complex, and controversial. Roderick et al. (2001) and Gu et al. (2002) have argued that an increase in the fraction of diffuse vs. direct radiation caused large-scale enhancement of NPP during the post-Pinatubo period. In other words, an enhanced sink was produced by increased NPP. But Angert et al. (2004) have shown that this hypothesis is inconsistent with observed seasonal cycles of CO_2 during these years. Jones and Cox (2001) used GCM simulations incorporating the TRIFFID DGVM to suggest that post-Pinatubo climatic anomalies overall produced enhanced NPP in the tropics, while respiration globally was reduced.

15.5.4 Future Carbon Balance Projections

Schaphoff et al. (2006) predicted the response to climate and CO_2 changes during the 21st century, as simulated by five ocean-atmosphere GCMs, all driven by a standard "business as usual" CO_2 emissions scenario. The simulated change in terrestrial carbon storage ranged from a loss of 106 Pg C to a gain of 201 Pg C (neglecting land-use changes). This finding complements Cramer et al. (2001), who found large uncertainty *within* one climate change scenario, due to differences among six DGVMs. The spatial patterns of changes in carbon content found by Schaphoff et al. were more robust than the global total. Carbon storage was enhanced due to warming in the Arctic and at high elevations, but reduced over the temperate and boreal zones. Carbon storage was also increased in many semi-arid regions due to increased vegetation water-use efficiency and woody encroachment at high CO_2, with soil carbon loss inhibited due to drought. Tropical vegetation response varied due to precipitation differences among GCMs.

15.5.5 Carbon-Cycle Feedbacks to Future Climate Change

DGVM simulations based on climate projections of the 21st century have indicated that the time course of carbon storage depends on a balance of CO_2 fertilization and the positive effect on NPP of longer and warmer growing seasons in cold climates, vs. the general increase in heterotrophic respiration rates and the negative effect of high temperatures on NPP in warm climates (Cao and Woodward 1998; Kicklighter et al. 1999; Cramer et al. 2001; Schaphoff et al. 2006). CO_2 fertilization is expected to show a "diminishing return" while the effect of warming on respiration will continue (Jones et al. 2003). As a result, future projections of terrestrial carbon storage have often shown an initial increase in terrestrial carbon storage followed by a decline. Cox et al. (2000) used a fully coupled GCM, including the Hadley Centre (HADCM3) ocean-atmosphere model and the TRIFFID DGVM, to perform a comprehensive analysis based on a "business as usual" CO_2 emissions scenario. They found that the carbon-climate feedback had generated an additional 1.5 K global warming by 2100, mostly due to increased heterotrophic respiration. A similar analysis using the IPSL ocean-atmosphere model and the SLAVE TBM (Dufresne et al. 2002) also found a positive feedback, but the change was less, and was mostly due to reduced NPP in the tropics. Reasons for the difference include stronger vertical mixing in the IPSL ocean model, and greater initial soil carbon storage in the Hadley Centre model (Friedlingstein et al. 2003). Yet despite uncertainty about the size of carbon cycle feedbacks, the largest uncertainty in the future CO_2 concentration is still the unknown future of CO_2 emissions from fossil fuels. Joos et al. (2001) used the Bern-CC model to examine the consequences of six different emissions scenarios. A positive carbon-cycle feedback to climate change was found in all cases and atmospheric CO_2 rose to between 540 and 960 ppm, depending on the scenario and on assumptions about climate sensitivity, by 2100.

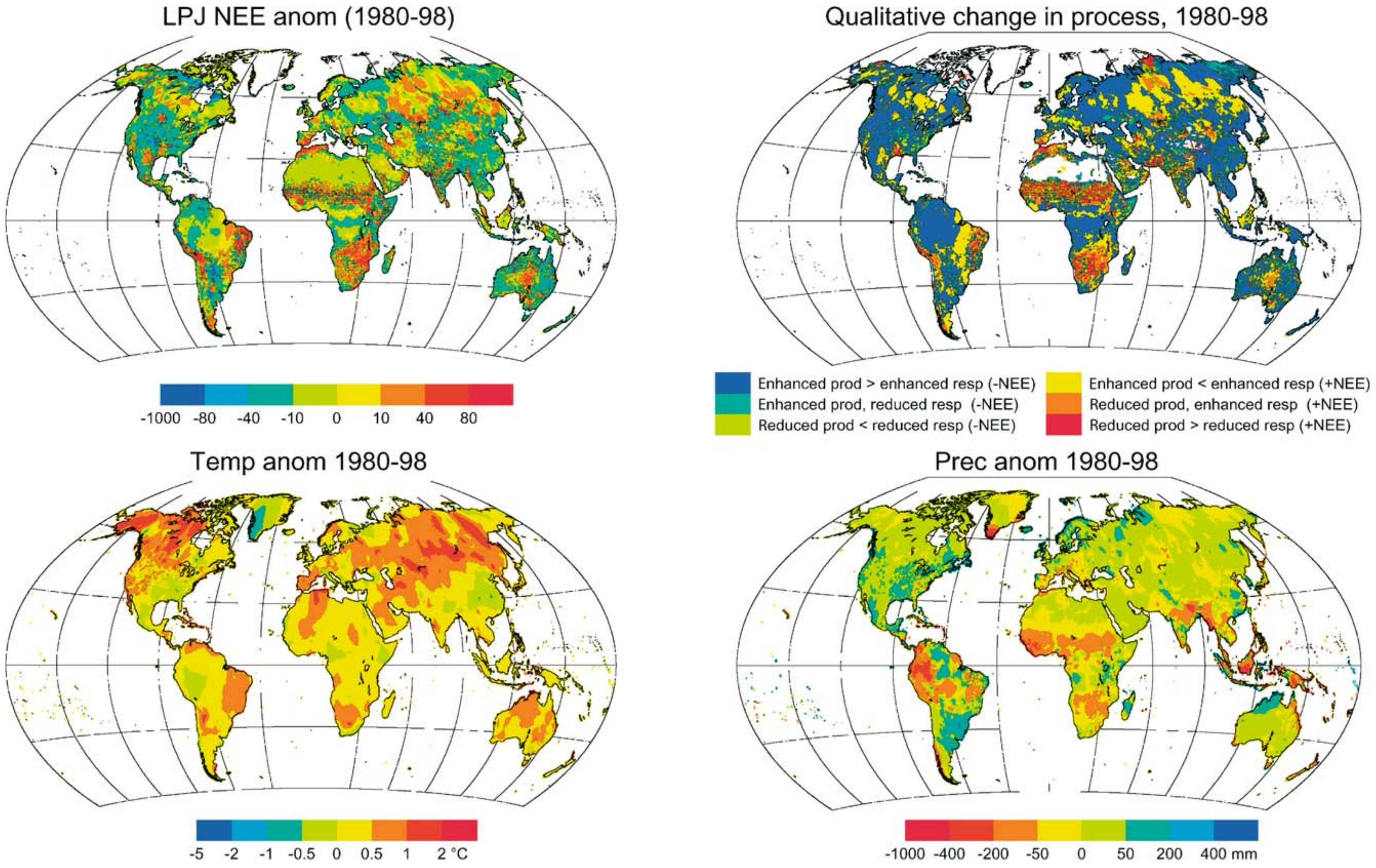

Fig. 15.4. Global patterns of the modeled terrestrial carbon balance during 1980–1998, simulated with the LPJ DGVM. The *top left panel* shows anomalies of net ecosystem exchange (*NEE* = heterotrophic respiration + combustion – *NPP*), i.e., mean *NEE* during 1980–1998 minus *NEE* for the standard climatological period (1931–1960). The *top right panel* shows the origin of the anomalies in terms of increases or decreases in "respiration" (strictly, heterotrophic respiration + combustion) and "production" (*NPP*). The corresponding annual mean anomalies of temperature and precipitation are shown in the *bottom panels*

15.5.6 Effects of Land-Use Change on the Carbon Cycle

Land-use change was the main cause of increasing atmospheric CO_2 in the early industrial period, and is still a substantial contributor. McGuire et al. (2001) used four terrestrial models to assess the relative roles of CO_2 fertilization, climate variation and land-use change through the industrial era. The simulated cumulative effect of cropland establishment and abandonment from 1920 to 1992 was a release of 56–91 Pg C. The concurrent simulated uptake, due mainly to CO_2 fertilization, was 54–105 Pg C. The modeled net terrestrial carbon budget proved broadly consistent with independent estimates from atmospheric measurements (Prentice et al. 2001; House et al. 2003). This global analysis has not yet been extended beyond 1992, nor carried into the future. Some possible consequences of future land-use change have been analysed, however. Cramer et al. (2004) used LPJ to estimate past and potential future losses of carbon from wet tropical ecosystems, which are the main site of deforestation today. During the 20th century, deforestation was estimated to have released 39–49 Pg C. Extrapolating a range of estimates for current rates of deforestation into the future yielded a projected additional loss of 158–243 Pg C by 2100. By comparison, CO_2 fertilization and climate change produced a response ranging from a gain of 80 Pg C to a loss of 50 Pg C. Direct human intervention, therefore, is likely to be the most important determinant of the fate of carbon in tropical forests.

15.6 Some Perspectives and Research Needs

The following discussion is by no means a complete overview of the aspects of DGVMs that are in need of further testing and development. However, it points to some key areas where an international collaborative effort, building on the achievements of GCTE, would very likely lead to more rapid progress than could be achieved by individual groups working alone.

15.6.1 Comparison with Field Experiments

Experimental studies of the response of terrestrial ecosystems to environmental changes has been a major focus for GCTE. For example, experimental evidence from studies with small trees in open-top chambers has shown an average stimulation of photosynthesis by ≈60% for a 300 ppmv increase in CO_2, while the annual increment in wood mass per unit leaf area increased by ≈27% (Norby et al. 1999). The Free-air CO_2 enrichment (FACE) methodology was introduced so that experiments on the effects of raised CO_2 concentrations could be conducted on intact ecosystems (Hendry et al. 1999; Nowak et al. 2004; Long et al. 2004). The first FACE study in an intact forest ecosystem was set up in a *Pinus taeda* plantation in the southeastern USA (DeLucia et al. 1999). Ambient CO_2 concentrations were increased to 560 ppmv in the replicated plots from autumn 1996. From 1997 to 2000, annual NPP was on average 23% higher in plots with elevated CO_2 than in the control plots (Delucia et al. 1999; Hamilton et al. 2002; Schäfer et al. 2003). F. I. Woodward and M. Lomas (personal communication 2004) used the SDGVM to simulate this experiment. They obtained a realistic 20% enhancement in net primary production after four years. Hickler et al. (2004b) obtained a range from 15 to 33% increase over the same period. There is considerable scope for rigorous testing of different process formulations in DGVMs using the data now available from experiments involving artificial warming, drought and N fertilization as well as an increasing range of FACE studies.

15.6.2 Plant Functional Types

PFT schemes in current DGVMs are simplistic, and the values of most PFT-specific parameters are neither agreed nor well founded. GCTE has stimulated new interest in PFT classification (Díaz and Cabido 1997; Díaz et al. 1999a; Gitay and Noble 1997; Lavorel et al. 1997; Lavorel and Cramer 1999; Lavorel and Garnier 2002; Lavorel et al. 2007, Chap. 13 of this volume), but this has not yet filtered through to influence DGVM design. Current approaches to PFT classification emphasize readily observable plant traits that confer characteristic responses to factors of the environment and disturbance or management regime (e.g., Díaz et al. 1999b; Díaz et al. 2002; Gurvich et al. 2002; Barboni et al. 2004; Díaz et al. 2004; Wright et al. 2004). This is precisely the kind of information that is needed for the more rational representation of PFTs in DGVMs. The development of an internally-consistent, global vegetation map explicitly based on PFTs and based on high-resolution multispectral reflectance data is a related but distinct goal, proposed by Nemani and Running (1996). Such a map would be extremely useful for testing DGVMs. Various satellite-based global land-cover maps are now available, but there are still considerable differences among them, and the procedures used to generate them are not entirely transparent.

15.6.3 The Nitrogen Cycle

Hungate et al. (2003) suggested that scenario analyses with current DGVMs (Cramer et al. 2001; Prentice et al. 2001) exaggerate the amount of carbon the biosphere could take up in response to a continued increase in atmospheric CO_2. In fact, the two DGVMs in Cramer et al. (2001) that explicitly allow for N cycle constraints on NPP produce lower estimates of future carbon storage than those that do not. But these estimates still fall above the range postulated by Hungate et al. (2003). Recent simulations with the LPJ model (Schaphoff et al. 2006) produce estimates within this range, even though this model does not yet include N cycle constraints on NPP. Whatever the correct view on future CO_2 uptake, improving the representation of N cycling within DGVMs is a research priority. This work is hampered by inadequate quantification of gain and loss terms in the N cycle at regional and global scales (e.g., amount of N in precipitation, controls of N_2 fixation and dissolved organic N losses, and the release and fate of N-containing trace gases). Incorporation of a realistic N cycle is also important for prediction of the influence of soil nutrient status controls on PFT distributions, and to assess the impacts of anthropogenic N deposition on the carbon cycle and ecosystems.

15.6.4 Plant Dispersal and Migration

Current DGVMs assume that the rate of plant dispersal and migration does not limit the response of vegetation to climate change. This assumption is called into question by the fact that large changes in climate could occur rapidly (i.e., over a few decades) in some regions, and by the potential barriers to plant migration caused by landscape fragmentation. The issue is hard to address observationally because of the difficulty in quantifying rare long-distance dispersal events, which are believed on theoretical grounds to be crucial to explaining how rapid, continent-wide plant migrations occurred in response to climate changes in the Quaternary (Pitelka and Plant Migration Working Group 1997; Clark et al. 1998). Model formalisms to represent plant dispersal (e.g., Higgins et al. 2003) have been devised, but not implemented in DGVMs.

15.6.5 Wetlands

Wetlands are a major carbon store and are sources of the greenhouse gases methane (CH_4) and nitrous oxide (N_2O). The lateral transport of water is generally less important as a determinant of terrestrial vegetation than the *in situ* water balance, but this is not so for wetlands. DGVMs to date treat only dryland ecosystems. Extension to wetlands will require DGVMs to be coupled to water routing models with high spatial resolution. It will also be important to account for specific wetland PFTs, and the controls on nutrient supply to different types of wetland.

15.6.6 Multiple Nutrient Limitations

Realistic simulation of nutrient constraints on vegetation productivity will require not only the incorporation of lateral transport of nutrients by water, but also lateral transport in the atmosphere. For example, on geological time scales, aeolian transport of dust is a major control on phosphorus supply to terrestrial ecosystems (Chadwick et al. 1999). Transport of sulfate-containing aerosols derived from the production of dimethylsulphide by phytoplankton is a unique natural route for the redistribution of sulfur to the land surface. Precipitation is a significant source of N even in remote, unpolluted regions. Models of plant growth have scarcely begun to address the way in which different nutrient limitations interact. Marine ecosystems are already beginning to incorporate the interactions of the cycles of nitrogen, phosphorus, iron and silicon and their consequences for competition among phytoplankton PFTs (Aumont et al. 2003; Blackford and Burkill 2002; Blackford et al. 2004; Le Quéré et al. in press) and may inspire further DGVM development in this field.

15.6.7 Agriculture and Forestry

Efforts are already underway to simulate crop productivity and yield generically using DGVMs (e.g., Kucharik and Brye 2003). One objective of this work is to predict the consequences of climate change for agriculture. Such predictions will also have to consider climatically induced changes in the suitability of different crops, and non-climatic as well as climatic drivers of changes in land use – requiring that DGVMs be embedded in an integrated assessment framework. Forest management likewise has been only partially treated in DGVMs. Global carbon cycle studies have taken into account the consequences of deforestation and reforestation (Houghton 2003; McGuire et al. 2001), but not changes in logging intensity although these are thought to have had a major role in creating a present-day carbon sink in northern temperate forests (Nabuurs et al. 2003). The representation of forest management places new demands on DGVMs to show the correct response of forest NPP to stand age and density. Progress in modeling economically important ecosystems must be matched by progress in the collection and standardization of statistical data on crop distribution, yields and farming practices, and past and present forest management regimes. Adequate representation of management is important for the assessment of practices designed to increase carbon storage in ecosystems, which the present generation of DGVMs is not well adapted to address (Bondeau et al. in press).

15.6.8 Grazers and Pests

The eventual expansion of DGVMs to cover components of the ecosystem other than autotrophic plants and heterotrophic soil organisms (bacteria and fungi) is unavoidable. The abundances of grazing animals, and of pests such as leaf- and bark-eating insects, exert an important control on vegetation productivity and disturbance in several biomes. It should be possible to simulate the impact of changes in both natural and managed grazing regimes by introducing a small number of animal functional types (AFTs). Models of marine ecosystems, where the ratio of secondary to primary production is much higher, already incorporate functional types of zooplankton grazers with different feeding preferences and population growth rates (Bopp et al. 2002; Aumont et al. 2003; Le Quéré et al. in press).

15.6.9 Biogenic Emissions of Trace Gases and Aerosol Precursors

Through various processes, the terrestrial biosphere emits the greenhouse gas N_2O, reactive gases that have a major influence on atmospheric chemistry including the greenhouse gas CH_4, carbon monoxide (CO), nitrogen oxides (NO_x), volatile organic compounds (VOCs) such as isoprene, and aerosol precursors in the form of dust, black carbon and VOCs. The extension of DGVMs to model sources and sinks of trace gases and aerosol components is a natural development. DGVMs will be called on to model CH_4 production in wetlands and oxidation in drylands (Kaplan 2002; Ridgwell et al. 1999), VOC production (e.g., Guenther et al. 1995), the N cycle including controls on the relative production of N_2, N_2O and NO in soils (Potter and Klooster 1999), ozone (O_3) uptake by vegetation, the relationships among dust emission, vegetation density and height (Tegen et al. 2002), the occurrence and intensity of fires, and the emissions of CO, CH_4, NO_x and black carbon associated with fires (Andreae and Merlet 2001; Thonicke et al. 2005). Progress has been made in most of these areas individually, but further efforts will be required to develop a comprehensive emissions model that can be coupled to an atmospheric chemistry and transport model (CTM) and ultimately to a GCM, in order to better understand the role of the biosphere in determining the atmosphere's changing chemical composition and, through this, the Earth's climate.

15.7 Summary and Conclusions

DGVMs exploit the power of modern computers and computational methods to yield a predictive description of land ecosystem processes that takes account of knowledge previously developed through long histories of separate disciplinary approaches to the study of the biosphere. The degree of interaction between the different scientific approaches still falls far short of optimal; thus, DGVM developers have a responsibility to be aware of progress in several disciplines in order to ensure that their models remain state-of-the-art. We have presented a series of case studies of the evaluation of DGVMs that demonstrate the predictive capability that current models have achieved. Nevertheless, there are plenty of unresolved issues – differences among models that are not well understood, important processes that are omitted or treated simplistically by some or all models, and sets of observations that are not satisfactorily reproduced by current models. More comprehensive "benchmarking" of DGVMs against multiple data sets is required and would be most effectively carried out through an international consortium, so as to avoid duplicating the large amount of work involved in selecting and processing data sets and model experiments. We have also presented a series of case studies that illustrate the power of DGVMs, even with their known limitations, in explaining a remarkable variety of Earth System phenomena and in addressing contemporary issues related to climate and land-use change. These case studies encourage us to believe that the continued development of DGVMs is a worthwhile enterprise. Finally, new directions in Earth System Science point to a range of aspects in which DGVMs could be improved so as to take account of recently acquired knowledge, such as experimental work on whole-ecosystem responses to environmental modification and new understanding of the functional basis of plant traits; complemented by an effort to represent semi-natural and agricultural ecosystems and the impacts of different management practices on these ecosystems; and extended to include processes such as trace-gas emissions, which are important in order to understand the functional role of the terrestrial biosphere in the Earth System. Together, these potential developments add up to an ambitious research program, requiring the economies of scale that only an international collaborative effort can provide.

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Part D

Managing Ecosystem Services

Chapter 16

Wheat Production Systems and Global Climate Change

John R. Porter · Pete D. Jamieson · Peter R. Grace

16.1 Introduction

The production and provision of food is central to the survival and well being of humans. Globally, more people are employed in the production, processing and distribution of food than any other socio-economic sector. Agriculture contributes between 2% of GDP in developed western countries to more than 30% of GDP in many African states. From the ample sufficiency of basic commodities in the developed world, we can forget the historical importance that food and fibre have played in human social and political development. During the Napoleonic Wars in Europe in the first years of the 19th century, the price of a tonne of wheat in the UK was five times its purchasing parity price today and food riots were common. Humans have cultivated the land for about 10 000 years when the global population reached one million. Before that time and for the preponderance of human history, humans have hunted and gathered their food, fiber and energy since *Homo sapiens sapiens* diverged from its ancestors about 200 000 years ago (Evans 1998). The effect of agricultural cultivation on human political and social development was explosive. In the 10 000 years leading to AD 2000, the human population increased 100-fold from 5 to 500 million people. In the second millennium, the effect was even more profound in absolute terms as 500 million people became 5 000 million. Today more than 75% of the land area of Europe is cultivated for either crop, grassland or forestry production and humans appropriate about 40% of terrestrial net primary productivity for their own use (Vitousek 1986). In rich, demographically stable countries the effects of agriculture and forestry on biodiversity and the cycles of carbon, nutrients and water are relevant social and political agendas. Land cultivation, and particularly its management intensity, is the most influential human practice for the dynamics of the terrestrial landscape and thereby the atmospheric, biogeochemical and water cycles of the Earth System. The production of food affects the main global biogeochemical cycles and is heavily reliant on inputs of fossil fuel energy. Farmers use such products of fossil fuels as nitrogen fertilizer, herbicides and pesticides and machinery to increase the proportion of solar energy that is captured by crops to drive dry matter production and thereby harvested yield. It is only in the past 250 years out of the 10 000 years that human beings have cultivated the land for food that they have been able to swap the toil of long hours in the field to increase solar energy capture for less humanly demanding methods.

Wheat yields have been steadily rising in most parts of the world for at least the past century. New cultivars provide part of the explanation (Moot et al. 1996; Evans and Fischer 1999), where the addition of dwarfing genes has meant that newer cultivars produce shorter straw, similar total biomass but a higher harvest index. Much of the increase in crop production is attributable to the use of N fertilizer, but better knowledge and methodology leads to improvement as well. Much of the increases in crop yields in the past century are due to substantially greater use of nitrogen fertilizer. Demographic changes and urban encroachment onto peri-urban farmland will cause a change in production patterns and trade over the next 30 years or so. For instance, since the 1960s China's wheat production has nearly trebled while the land area used for its production has fallen very slightly. In the absence of any effects of atmospheric changes, Chinese wheat production is nearing stabilization. There is no sign of a decrease in demand for wheat in China, so that the shortfall is likely to be met by imports. Marathée and Gomez-MacPherson (2001) estimate that by 2030, wheat production in the developed world will have needed to increase from 308 to 440 million Mg (43%), while in the developed world the increase will need to be from 272 to 418 million Mg (54%). Most of this increase will come from increased yield per ha, rather than increased area. Accompanying the increase in production will be a change in the trade balance. Exports from the developed world are projected to increase by 91 million Mg, all into the developed world. The biggest demand increases will be from China, North Africa and the near East.

Globally, the picture is different from that seen in Europe, the USA and the affluent parts of Asia. In these areas, we have a stable overall population with an aging population structure and with some countries experiencing negative population growth. In many parts of the developing world and, particularly in south-east Asia, populations are still expanding but fortunately at a decreasing rate. There are causes for optimism that, even with a global population of 9 to 10 billion people, the world will be able to feed itself on average. However, the average conceals that the relative gap between the richest and the poorest in the world is getting larger.

The base of the human food chain is largely formed by the grasses rice, maize, wheat and tropical species such as sorghum and millet. Amthor (2001), quoting FAO data (FAO 2003) notes that of the 1.4 billion ha of land (Evans 1998) devoted to arable cultivation, wheat is harvested from about 15% of it; direct consumption of wheat contributes 20% of the calories and 22% of the protein in the human diet. As more than 30% of harvested wheat is fed to animals and thence to humans as milk or meat, the place of wheat as the most important human food source is unrivalled. The versatility of wheat, both in terms of its versatility of food end-uses and its environmental adaptability, means that its importance is likely to increase in the future. Projections based on population driven demand suggest that the total production and productivity per unit area of wheat will need to increase by about 50% during the next 30–40 years to accommodate the projected extra 3 billion humans by that time. This will partly come about as wheat continues to displace other cereals, particularly rice in Asia. This makes it important to examine the vulnerability of the world wheat crop to changes in the global environment in the foreseeable future. As the total global arable area for all crops is about 1.4 billion ha (Evans 1998), most of the production increase will need to come from increased yields per hectare, rather than increases in production area since there is little extra available land and this is often of poor quality. In terms of a global average, wheat yields needs to double to about 5 Mg per ha from the current 2.8 Mg per ha over the next 30–40 years. So far, yield increases have been maintained post Green Revolution for wheat (Evans and Fischer 1999) but this trend will need to continue in the face of a changing climate that can act as a stimulant to production via 'CO_2 fertilization'. However, rising temperatures and drier conditions in areas already at the margins of production are expected to come under enhanced agro-climatic as well as enhanced human pressure. Therefore, the interactions, defined as impacts, adaptation and mitigation, between wheat and global climate change has formed an important element in the modeling and experimental activities of GCTE Focus 3 (Agroecology and Production Systems).

For almost all the time that humans have cultivated the land the atmospheric CO_2 concentration has been between about 260 and 280 μmol mol^{-1} and the northern hemisphere temperature anomaly has had an absolute value of about 1 °C with a decreasing amplitude since about 1500. However, since 1900 both the mean and variance of the temperature anomaly have been increasing, as has the atmospheric CO_2 level. The immediate questions for arable agriculture in these circumstances can be categorised as the damage potential of climate change for the basic arable food systems and their security, possible adaptations thereof and the mitigation potential of arable farming to slow the build-up of greenhouse gases (GHG). Agriculture is situated at the interface between ecosystems and society (Olesen and Bindi 2002) and is obviously affected by changes in global environmental conditions, but it also contributes to GHG emissions, notably carbon dioxide, methane and nitrous oxide (Rosenzweig and Hillel 2000). Agriculture contributes 24% of global CO_2 emissions from energy use (4%) and anthropogenic GHG emissions (20%, as CO_2 equivalents) mainly from CH_4 and N_2O as well as carbon from land clearing (IPCC 2001).

Wheat productivity in important wheat growing regions of the world is well below its potential (Aggarwal et al. 2000). Increases in production will therefore be associated with raising the lower end of the distribution via improved management, rather than by raising the theoretical ceiling of productivity (Sinclair 1992). Simulation studies suggest that these increases, associated mostly with improved technology, will be boosted by global atmospheric changes, where CO_2 fertilization will more than compensate for the yield reducing effects of increased temperature, provided these are not too extreme (IPCC 2001). A danger will be that yield increases may be accompanied by reductions in quality via reduced protein content. However, we believe that improved understanding of the internal nitrogen economy of wheat will provide solutions to this problem, both through cultivar development and improved management.

Increases in the productivity of wheat will mean that issues such as the future of the 23 Mha of the extended Indo-Gangetic Plain that is responsible for feeding about one third of humanity will assume ever greater importance. The direction of the Green Revolution, that enabled a halving of the globally undernourished even as the global population doubled (Conway 1997), will need to be in the direction of combining the best of modern technology while paying more attention to conservation and building of the agro-ecological resource, particularly water and soil organic matter. This so-called doubly Green Revolution will both be affected by and have consequences for the global climate, an issue that is addressed later in this chapter.

This paper highlights some of the research in which members of the GCTE Focus 3 community have participated and that has contributed to raise understanding of global change and wheat and wheat cropping system productivity. We focus on four issues, as representative of the GCTE Wheat Network's activities to date. These are the experimental and modeling analysis of wheat responses to elevated CO_2 in combination with water and nitrogen treatments in Free-Air (CO_2) Concentration Enrichment (FACE) experiments in Arizona, USA; the importance of climate variability on wheat growth, development and yield; the influence of climate on the quality of wheat and the contribution of the rice-wheat cropping system of the Indo-Gangetic Plain to global climate change.

16.2 Global Atmospheric Change, Climate and Yields

The one complete certainty is that atmospheric CO_2 concentration is increasing. Just how much it will change will depend on combinations of fossil fuel use and deforestation that will occur during over the next 100 years. A near certainty is that the changes in atmospheric composition will be accompanied by changes in climate. Climate scientists refer to emissions scenarios as the drivers of climate change. Biologists, who must assess the effects that the resultant climate changes will have on patterns of production, refer to these climate changes as their scenarios for assessment. Crops respond to temperature, rainfall and its temporal and spatial spread, fertilizer levels as well as direct responses to atmospheric CO_2 concentration. A main activity of Focus 3 scientists has been to make educated assessment of whether the integrated effects will be, on balance, positive or negative. Scientific members of GCTE Focus 3 have participated in many of the experimental studies that have attempted to measure the dependence of wheat grain yield on ambient CO_2 concentration, data reviewed by Amthor (2001) for mainly non-European ones (Fig. 16.1a) and Downing et al. (2000) and Olesen and Bindi (2002) for European sites (Fig. 16.1b).

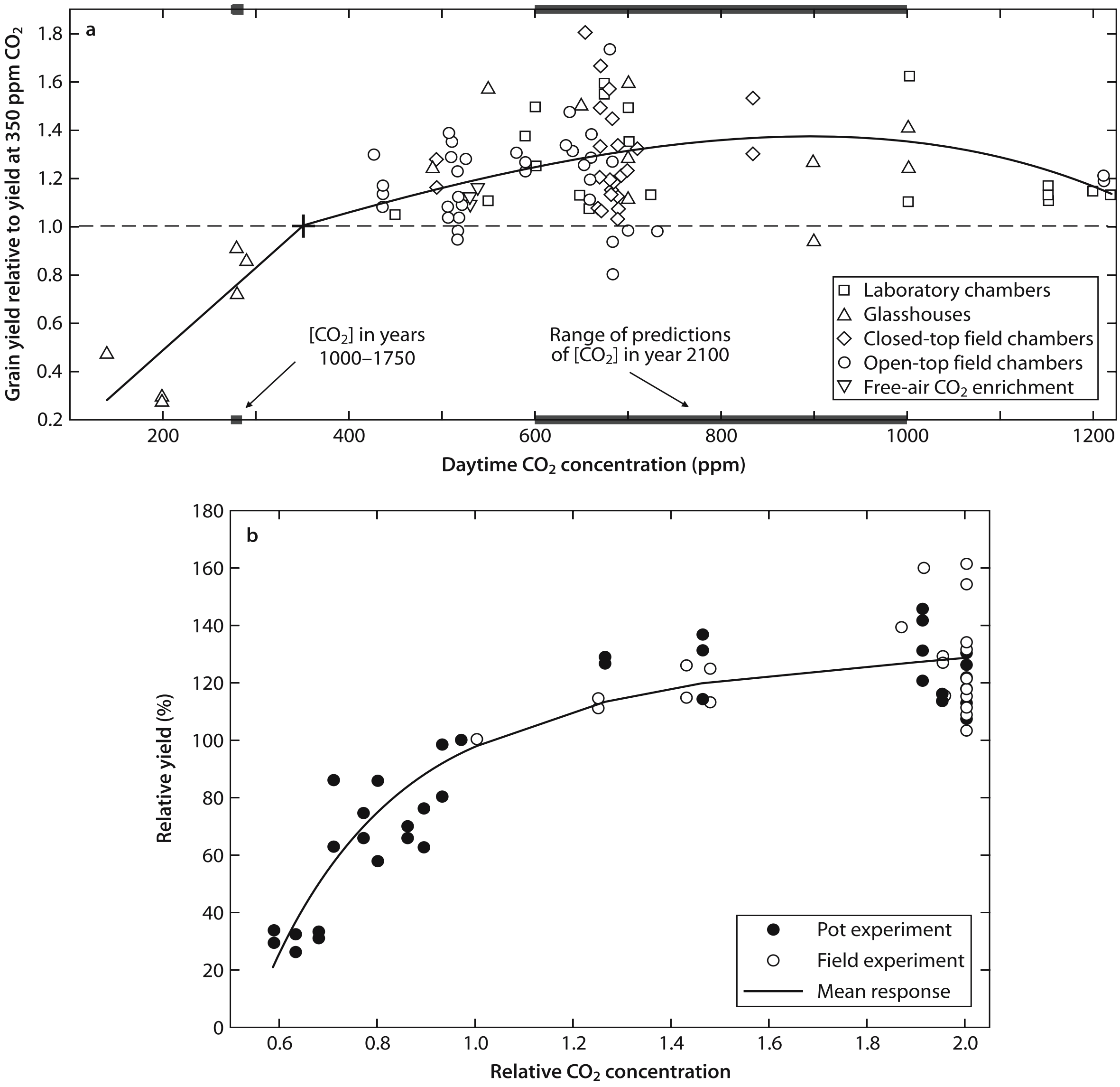

Fig. 16.1. Relative effects of CO_2 concentration on wheat grain yield in various experiments from mainly non-European (**a** Amthor 2001) and European sites (**b** Downing et al. 2001; Olesen and Bindi 2002) and where current ambient CO_2 is set to 1. In **b** *open symbols* represent data from field experiments (OTC, FACE); *filled symbols* represent data from pot or glasshouse experiments and the *solid line* shows the mean estimated response (Olesen and Bindi 2002). In both cases, values were taken from treatments in which adequate water and nitrogen were provided

Both graphs in Fig. 16.1 show that wheat grain yields, on average, rise by about 20% when the CO_2 concentration is double the pre-industrial level and it is difficult to detect an effect of experimental design in these results. There is considerable spread in the grain yield increase (or decrease) in both reviews but the curves are very congruent for ambient CO_2 levels between about 200 µmol mol^{-1} and 700 µmol mol^{-1}. The lack of dependence of the relative grain yield increase measurement on experimental design concurs with the conclusions of Kimball et al. (2002) that only two crop physiological parameters were substantially different between FACE and chamber-based approaches; namely FACE systems tended to reduce stomatal conductance by one and a half times compared with chambers and that root-to-shoot ratios were higher for FACE, as opposed to other, systems.

In both modeling and experimental studies, scientists associated with the GCTE Focus 3 Wheat group have been involved with studying the interactions between CO_2 level and temperature. Such studies have included the effects of temperature gradients on wheat responses to CO_2 (Batts et al. 1996, 1997, 1998) and have shown the extent to which rising temperatures can offset increases in growth and yield stimulated by higher CO_2, such that a whole season mean temperature increase of 2–4 °C can negate any CO_2 induced rise in yield, mainly by shortening the life-cycle of the wheat crop and speeding the rate of development through grain-filling. Episodic high temperature events, such as 30–35 °C in the few days around anthesis, have been shown to have yield reducing effects, caused by reduced seed fertility and a decline in seed number (Ferris 1998; Wollenweber et al. 2003) and the general effects of threshold temperatures (Porter and Gawith 1999) producing increased non-linear uncertainties of yield (Porter and Semenov 1999) has been an important new insight to come from work of GCTE Focus 3 and will be referred to later.

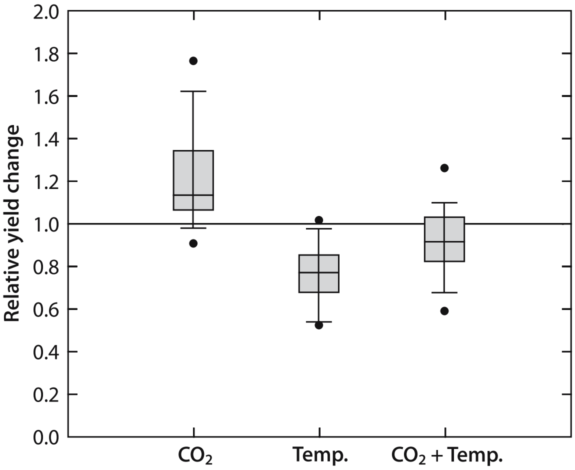

Fig. 16.2. Effects of elevated CO_2 and increased temperature, singly and in combination, on yield of wheat. The data represent the ratio of yield relative to current ambient CO_2 and temperature (relative yield change). Data are taken from the review by Amthor (2001, Table 7). *Plots* show median and standard percentiles ($n = 17$) (Fuhrer 2003)

In reviewing the interaction between temperature and CO_2 on relative yield change for wheat, Fuhrer (2003) presented a summary of data (Fig. 16.2) amassed and analysed by Amthor (2001) for 2 glasshouse, 13 closed-top chamber and two open-top chamber experiments. This showed that overall, warmer temperatures negate the CO_2 effects but that there is considerable overlap between the treatments. On average the effect of warming and higher CO_2 level on wheat yield is slightly to reduce yield in relation to current ambient conditions (Fuhrer 2003).

Studies of combinations of factors on the growth and yield of wheat have been extended by GCTE Focus 3 scientists to include the single and interactive effects of nitrogen level and irrigation. Collaborative research and modeling studies were made by using the FACE wheat experiments at Maricopa, USA and performed by Dr. Bruce Kimball and colleagues (www.uswcl.ars.ag.gov/edp/co2/co2face.htm). Although general conclusions of the effects of CO_2 enrichment on growth and yield are broadly similar, there are substantial effects of the chambers themselves on crop performance that vary among experiments. In any one experiment these are similar for both ambient and enriched treatments, but are sufficiently different from open field conditions to be difficult to simulate with models that assume uniformity over large areas and an absence of edge effects, (Ewert et al. 2002). Comparisons are facilitated when experiments are conducted in open field conditions such as those the FACE experiments at the University of Arizona Maricopa Agricultural Center (MAC), Maricopa, Arizona, USA. (Hunsaker et al. 1996; Kimball et al. 1995, 1997, 2001; Pinter et al. 1996). The experiments were conducted in replicated FACE rings of 25 m diameter with either no CO_2 enhancement or CO_2 enhancement for 24 h d^{-1} at either 550 µmol mol^{-1} (earlier experiments) or sustained at 200 µmol mol^{-1} above ambient CO_2 concentration. The FACE apparatus was placed well inside the boundaries of fields of substantial size, and therefore closely resemble the field scale that simulation models assume. The combined effects of CO_2 and water stress were studied in experiments in 1992–1993 and 1993–1994, and CO_2 and soil N restrictions in 1995–1996 and 1996–1997. A substantial scientific effort went into measurement of plant responses through time at a range of time scales and process levels within the crop, including gas exchange and micrometeorology. This allowed an analysis of the effects of elevated CO_2 on growth, biomass partitioning, yield, yield components, nutrient uptake and distribution, grain quality, evapotranspiration on time scales of less than an hour to seasonal totals plus biochemistry and other effects.

The major conclusions were that enhanced CO_2 increased production by about 10% in well watered conditions and by about 20% in drought stressed conditions – CO_2 compensated somewhat for water stress. Later analysis (Pinter et al. 2000) suggested that the CO_2 yield enhancement was probably understated by the results of the first experiments. The nitrogen experiments showed yield enhancements of about 15% at high soil N levels, but the enhancement was reduced when N was restricted, and the level differed between the two years. In general CO_2 decreased the transpiration rate although this was more obvious in the micrometeorological measurements than in long term water balance measurements. Grain protein content was decreased slightly by enhanced CO_2 unless N was not adequate; under low N conditions the protein reducing effects of enhanced CO_2 was increased.

Until the mid-1990s most studies of the impacts of climate change on agriculture (i.e., Rosenzweig and Parry 1994) focused on changes in CO_2 level and average conditions, such as a rise in mean global temperature or the amount of rainfall, on crop production. However, it was soon realized that these analyses were conceptually incomplete because *(i)* crops and plants in general, respond non-linearly to changes in their growing conditions exhibiting discontinuous threshold responses and *(ii)* because crops are often subject to combinations of stress factors that affect their growth and development (Fig. 16.3). The effect of climate variability, the frequency of extreme events and the effects of combinations of factors have since assumed greater importance (*i.e.,* Semenov and Porter 1995). IPCC reports since that time have highlighted the likely increase in extreme weather events associated with climate change. These would reveal themselves as higher maximum temperatures, hot days and heat waves over nearly all land areas and more intense precipitation events over many areas associated with El-Nino events and a likely increase in Asian summer monsoon precipitation variability. Variability at a range of spatial and temporal scales is now a key concern in impact studies on ecosystems in general and agroecosystems in particular.

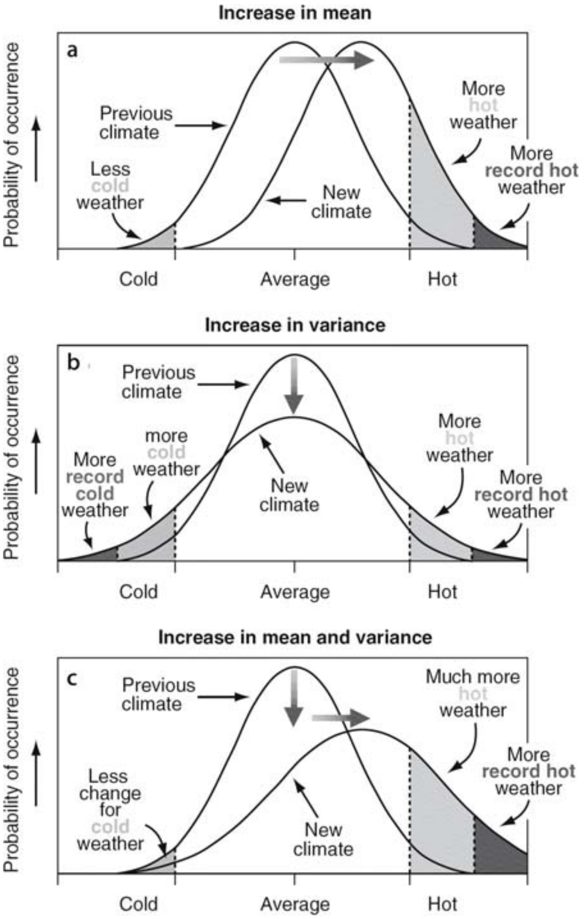

Fig. 16.3. Illustrations of the effects of increases in **a** mean temperature, **b** increase in temperature variance and **c** increase in both on the frequency of extreme hot weather

Crops models that incorporated mathematical descriptions of phenology, leaf area development, photosynthesis, respiration, water and nitrogen uptake were able to interact with climate scenarios that included changes in the variability of rather than the mean climatic driving variables. Simulation modeling of the effects of climatic variability has pointed to the general conclusion that increased annual variability in weather causes increased variation in yields. For wheat (Fig. 16.4), it was found by three simulation models that doubling the standard variation of annual temperature, while holding its mean value unchanged (*i.e.,* the scenario in Fig. 16.3b) gave the same decrease in yield as a 4 °C increase in mean temperature (Fig. 16.3a) but a more than doubled coefficient of yield variation. It remains a challenge for experimental studies to test these model predictions but there are sound reasons to expect verification of the predictions. The mechanisms that lie behind such responses are likely to be complex but will involve the non-linear relationship of respiration with temperature, and temperature threshold effects on reproductive fertility and phenology (Ferris et al. 1998; Porter and Gawith 1999).

16.3 Impacts on Wheat Productivity

With annual crops like wheat, the effects of increases in atmospheric CO_2 concentration and the accompanying temperature rises act in opposite directions. Broadly, the yield of wheat crop can be described as the product of its mean growth rate, duration or lifetime, and harvest index – that proportion of the crop that is grain. The primary effect of increased CO_2 concentration is to increase the mean growth rate by acting as an atmospheric fertilizer, provided enough N is present. A secondary effect is to reduce the transpiration rate for the same energy input, which has the effect of making more economical use of soil water. These effects are yield enhancing. However, the life cycle of a wheat crop occurs in thermal time, rather than chronological time. This means that higher temperature increases the development rate and shortens growth duration. This has the opposite effect of the

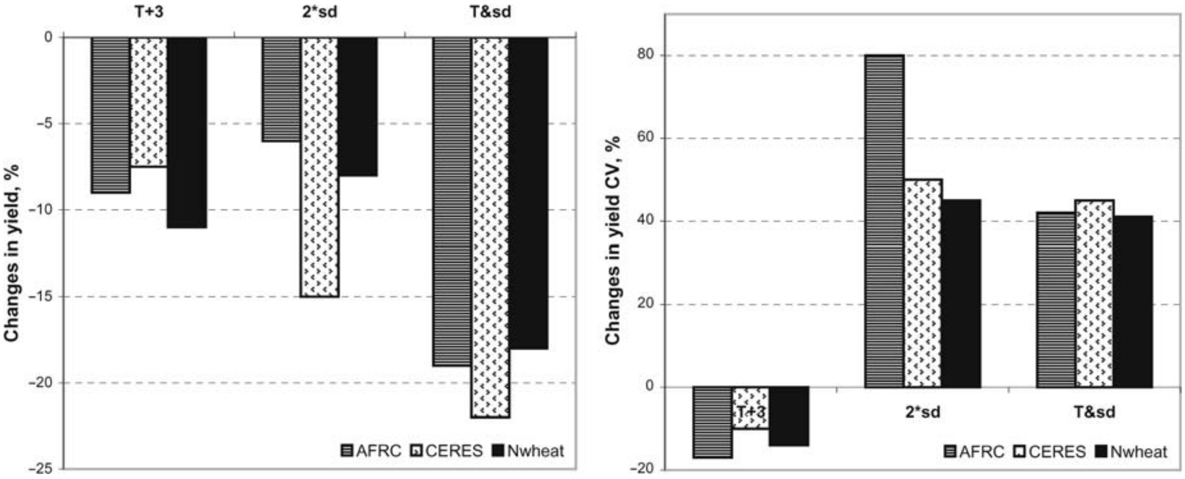

Fig. 16.4. Modeling of the effect of variation in temperature on crop yields and its variation (as *CV*) for wheat. *T*+3, mean temperature increased by 3 °C (c.f. Fig. 16.3a); *2*sd*, standard deviation of temperature doubled without change in its mean value (c.f. Fig. 16.3b); *T&sd*, combination of raised mean and standard deviation of temperature (c.f. Fig. 16.3c)

CO_2 increase – the crop has less time to grow and will hence produce less biomass. Effects on harvest index are less clear and may be positive, negative or neutral. Earlier maturity may avoid late season drought, for instance, and the yield depressing effects of shortened growth duration may be counterbalanced by a reduction in drought stress during grain growth. The main point of this discussion is that assessment of the effects of climate and atmospheric change on wheat production really needs the power of good simulation models that account for all these competing effects. Evaluation of such simulation models, particularly in comparison with data from experiments in elevated CO_2 and temperature environments, has been the core business of the GCTE International Wheat Network since its inception in 1991.

To be confident that simulation models give a reasonable assessment of likely response to changed environments, it is necessary to test them in a variety of conditions where these are well documented. If several models tend to give similar results, and at least give response in a similar sense to experiments, then some confidence can be attributed to their predictions in different circumstances. Examples of such studies, in collaborations reinforced by the GCTE network, are studies by Jamieson et al. (1998a) where the predictions of five models were compared with experiments under varying drought conditions, and Jamieson et al. (2000), where the predictions of three wheat simulation models were tested against data from wheat experiments in Arizona FACE experiments (Hendry and Kimball 1994; Grant et al. 1995; Grossman et al. 1995; Kimball et al. 1999) in which the amount of applied N and the atmospheric CO_2 concentration were both varied. This latter study complemented an earlier one (Tubiello et al. 1999) where simulations were compared with measurements from crops where CO_2 and water supply were varied.

16.4 Addressing the Yield Gap

Where are the projected yield increases to come from? Marathée and Gomez-MacPherson (2001) estimate large increases in production in both the developed and developing worlds, mostly from yield increases. Their analysis took no account of the posited increases associated with atmospheric changes discussed above. That necessarily means that increases must come via the better application of technology and knowledge. There is more opportunity to increase total average yield by raising the lowest yields, rather than by increasing the potential. Timsina and Connor (2001) noted that in the rice-wheat rotational system in the Indo-Gangetic Plain area of northern India, that "severe biological and/or technological limitations to productivity and … potential for substantial yield increase provided the environmental and management constraints can be identified and rectified, are evident". In other words, a substantial yield gap exists. The yield gap is the difference between what can be achieved in crop production systems (under climatic constraints), and what is achieved in practice. Much of the predicted increase in wheat yields is likely to be a consequence of the application of better knowledge of the causes of the yield gap and finding solutions for them.

16.5 The Protein Gap

An inevitable requirement for higher production will be increased use of nitrogen fertilizer. This is because of two reasons. The first is that maintaining the yield response to elevated CO_2 requires higher levels of the supply of Rubisco. The reasons for this are unclear but are possibly linked to the enhanced turnover of the CO_2 fixing enzyme as CO_2 level increases. A second reason is that elevated CO_2 on its own leads to an increase in crop C/N ratio (Triboï et al. 2003), meaning that the nutritional quality, in terms of grain protein will decrease in the absence of extra N. The link between climate change and food quality remains one of the main under researched areas in global change studies, yet is one of the issues most directly relevant to human needs. As new wheat varieties have been bred for improved yield, there has been a tendency for protein content to diminish. High yields call for a long-lived canopy, but most of the N in green tissue will end up as part of the storage protein in grain (Jamieson and Semenov 2000). So there is a tension between the physiologies of yield and protein formation. Recent work (Martre et al. 2003) has shown that transfer of N from vegetative to grain tissue is largely source regulated. That means that breeding attention to increase yield and quality, traditionally focused on the grain, must be directed to manipulating the N pools within the plant. Martre et al. (in press) recently showed, using simulation, that the dual aims of simultaneously increasing crop yield and protein content can be achieved by making the pool of labile N within wheat plants larger. Nevertheless, the building of protein requires a supply of N, and high yields coupled with high protein will always require N fertilizer. Such use will not make N pollution of waterways inevitable. Providing the tools so that farmers can target their N applications to periods of high demand can avoid that problem.

Over the ten years of its existence the study of managed ecosystems within GCTE has identified and been able to predict the responses of wheat to CO_2, N, H_2O and temperature alone or in combination and their effects on yield per unit area. We have identified the importance of changes in climatic variability for wheat growth and explained it as the interaction between nonlinear processes in crops and temperature thresholds. We have made progress in spatialising such predictions and also including the environmental effects of different production systems. We have started to examine and model the effects of environment on crop quality, particularly protein content and composition. The consequences of climate change for the technical, nutritional and environmental quality of food has barely been raised as a question for agricultural science to date and this situation needs to change. Finally, we have started to identify how cropping systems may respond to climate change and also may contribute to it via how they are managed. The most globally important of these is the rice-wheat system of Asia.

16.6 The Rice-Wheat System

The double or sometimes triple, cropping rice-wheat system of Asia is a regional cultivation system that is responsible for the food security of between a quarter and a third of humanity. The central Indian region of the rice-wheat system is alone responsible for the food, security and livelihood of 1.1 billion people in India, a value that is predicted to rise to about 1.5 billion by 2050. In its full extent the rice-wheat cropping system covers a region from western Pakistan to eastern China, covering 15° of latitude and more than 40° of longitude (Fig. 16.5, Timsina and Connor 2001). The major producers, with a

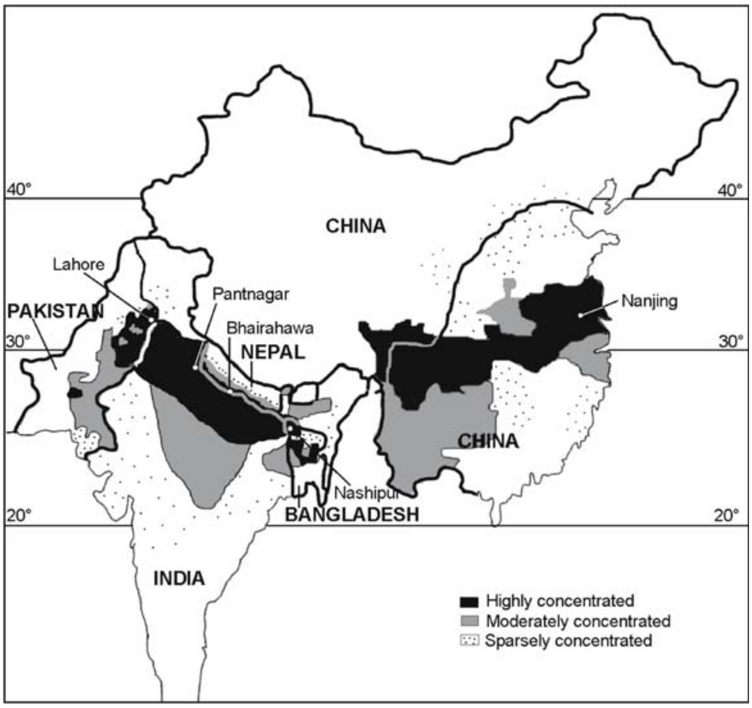

Fig. 16.5.
Distribution of the rice-wheat production areas in South Asia and China. The *curve* passing from northeast to southwest China represents the limits for growing rice-wheat sequences in China (Timsina and Connor 2001)

total area of around 23 Mha, are India and China, with *ca.* 10 and 13 Mha, respectively. Other countries in the region have rice-wheat areas that are at most 10% of the combined Indian and Chinese total. Food from rice-wheat systems contributes between 55% (China) and 95% (Bangladesh) of the national calorie intake of countries in the region (Timsina and Connor 2001). Yields of both wheat and rice have increased from the extremely low levels (ca. 1 Mg ha^{-1}) of the 1960s such that mean national yields for rice range from 2.4 Mg ha^{-1} in Nepal to 6.3 Mg ha^{-1} in China. Wheat yields less than rice and national values range from 1.6 Mg ha^{-1} in Nepal to 3.9 Mg ha^{-1} in China. National yields are in all cases superseded by yields from long-term trials in national research institutes, such that with applications of moderate amounts of nitrogen (120 kg N ha^{-1}), rice yields can increase by 50–70% and wheat yields by more than 30% (Timsina and Connor 2001). However, the trend over recent years has been for yield increases to stagnate or even decline, even in research plots (Grace et al. 2000a). Two issues considered by GCTE Focus 3 have been the impact of climate change on the rice-wheat system and the extent to which the rice-wheat system contributes to climate change via emissions of the major GHG gases, CO_2, N_2O and CH_4.

16.7 The Effect of Climate Change on the Rice-Wheat System

The medium to long-term viability of the rice-wheat system is very susceptible to global climate change for, at least, two reasons. The first is the dependence of the system on the monsoon rains that fall from June to August and provide about 600 mm (China) to 1 200 mm (India) of water that recharge the soil for rice cultivation in the autumn. Any changes in the spatial or temporal pattern of monsoon rains would be critical for production. The second reason for concern is high and rising temperatures associated with climate change. Long-term annual temperature records from sites in India and China show that temperatures in the late spring and early summer are already close to critical values for physiological processes in wheat and rice (Fig. 16.6). For example, temperature above 32 °C at anthesis induces anther sterility in wheat and rice and, as C_3 plants, both rice and wheat show large decreases in photosynthetic rates and elevated respiration and water use as temperatures rise above 35 °C (Porter and Gawith 1999). Given even the low (1–2 °C) IPCC (2001) predictions of mean global temperature increase by 2100 via the enhanced greenhouse effect, this will push temperatures, particularly in the wheat phase of the rice-wheat system, closer to known physiological thresholds for these crops. Pessimistic predictions of 5–6 °C increases in mean global temperature will mean that these are crossed. Thus, Gregory et al. (1999) concluded that wheat yields in the system are unlikely to increase by more than 10% for a doubled pre-industrial CO_2 concentration, with 5–7% being more likely under current management practices, and the negative effect of raised temperatures on crop duration and thereby yield. Major rice models concur in predicting a 5% decrease in yield per °C increase in temperature above 32 °C as a result of spikelet sterility.

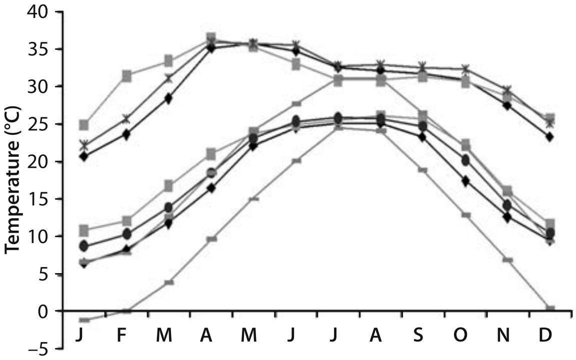

Fig. 16.6. Long-term temperature averages for a range of rice-wheat sites in south Asia and China (Timsina and Connor 2001)

In conclusion, the rice-wheat system is coming under ever increasing pressure as a result of moribund yields coinciding with population increase and income growth while, at the same time, the agro-ecological resource base is eroding, via lowering of ground water levels and decline in soil fertility. Global climate change that leads to warmer temperatures and more variable weather patterns can be expected to inflict significant limitations on the productivity of the rice-wheat system.

16.8 The Contribution of the Rice-Wheat System to Climate Change

A second important global issue is the impact that the rice-wheat system has on global biogeochemical cycles of C and N and the environment via its emissions of the GHG of CO_2, methane and nitrous oxide. Of course, these questions are linked in that crop management, such as the burning of crop residues, both reduces soil carbon levels while promoting greenhouse gas emissions. Future consideration of global land processes need to acknowledge the capacity that intensity of cultivation has to affect biogeochemical cycles (Grace et al. 2000a,b; Gregory et al. 2002). The direct cause of climate change is primarily the enhanced greenhouse effect. Different gases persist for different lengths of time in the atmosphere, and they also trap heat to different degrees. The global warming potential (GWP) is used to compare the effectiveness of each greenhouse gas to trap heat in the atmosphere relative to some standard gas, by convention CO_2. The GWP for CH_4 (based on a 100-yr time horizon) is 21, while that for N_2O is 310. Although present in concentrations lower than either CO_2 or CH_4, N_2O is a very potent greenhouse gas, accounting for about 6% of the enhanced greenhouse effect. By using GWP values for CH_4 and N_2O emissions of 21 and 310, respectively, it is possible to convert all our emission estimates to either a CO_2 or carbon equivalent (CE) basis. Carbon dioxide equivalents can be calculated by multiplying the CE values by 3.7.

Increased food-grain production in the rice-wheat system over the past 40 years has arisen mainly from the intensification of production rather its extensification, since almost all the productive arable land had been used prior to the Green Revolution. The intensification practices have included mechanical tillage of the soil, earlier sowing, increased use of inorganic fertilizer and irrigation. Crop residue burning is also used as a disease control practice. To a greater or lesser extent such management practices have an impact on the emissions of GHGs and estimates can be made of the emissions of each of the GHGs.

16.9 Carbon Dioxide

The main source of CO_2 to the atmosphere in the rice-wheat system is through tillage. Two on-site tillage sources exist: the biological decomposition of soil organic matter and the production of CO_2 as a by-product of machinery fuel usage. The burning of crop residues is not considered a CO_2 source to the atmosphere because an amount of CO_2 equivalent to the amount released will be taken up by the following crop; in other words, on an annual basis, there will be only small changes in standing C stock as a result of this activity. Carbon dioxide from this source is therefore not counted in the accounting procedures adopted by IPCC.

During tillage, soil aggregates are broken, thus increasing oxygen supply and surface area exposure of organic material. This promotes the decomposition of organic matter. An example of the effect of three to four cultivations per year on soil organic C (SOC) content can be drawn from CIMMYT's long-term wheat-maize trial at El Batán in central Mexico (Grace 2000 unpublished). Initial levels of SOC in the top 20 cm were 1.37%. After 8 yr of continuous wheat, with residue retention and conventional tillage, SOC had declined to 1.12%, a total decline of nearly 6.5 Mg C ha^{-1}, or 800 kg ha^{-1} yr^{-1}. In the adjacent no-till treatment, where yields were similar, the total decline was only 3.6 Mg C ha^{-1}, or 450 kg ha^{-1} yr^{-1}, a saving of 350 kg ha^{-1} yr^{-1}. In cultivated ecosystems, the rate of decline (or accumulation) of SOC therefore depends on several interacting factors: the amount of residue retained, the quality of residue retained, soil temperature and moisture interactions, tillage, and a reduction in fallow periods. For residue quality, high-quality (i.e., high N) residues from grain legumes or fodders can accelerate the decomposition of soil organic matter because of the additional N being available to the microbial population. Usually, the additional N being released will also be taken up by the following crop, thereby enhancing yields and biomass production; however, where high temperatures coincide with high water-holding capacity, the conditions are ideal for the promotion of SOC decomposition and the emission of CO_2. Soils therefore are generally considered to be a source of CO_2, unless the inputs outweigh the outputs, which is not usually the case in conventionally tilled low- to medium-input production systems. Fossil fuel energy sources form a large component of the total emissions from the rice-wheat system. Heavy use of diesel fuel occurs with current land preparation practices. For every liter of diesel fuel consumed, 2.6 kg of CO_2 are released to the atmosphere. Assuming that 150 l ha^{-1} yr^{-1} of fuel are used for tractor usage and irrigation pumping in conventional systems, this would amount to nearly 400 kg of CO_2 being emitted. For the entire 25 Mha under rice-wheat, this amounts to 12.0 Mg CO_2 yr^{-1} or 3.2 Mt C equivalents (MMTCE). To put this in perspective, this value is approximately three-quarters of the CH_4 emissions (expressed as MMTCE) from rice paddy fields in the entire IGP. Diesel use is a greatly underestimated source of GHGs in agriculture in general and the IGP in particular. An off-site source that is also often neglected is the production of CO_2 in the manufacture of fertilizers (Schlesinger 2000). Although not strictly relevant to on-farm environmental effects, 0.58 mol of C is produced per mol of N fixed in fertilizer production, resulting in 1.8 kg CO_2 produced per kilogram of N fertilizer manufactured. Full cost accounting that includes fertilizer transportation and application would raise this value to 1.4 mol of C per mol N fixed. In a no-till cropping system, this cost can significantly negate the mitigation gain by soil C sequestration.

16.10 Methane

Methane is produced in soil during microbial decomposition of organic matter and reduction of CO_2 under strictly anaerobic conditions. Methane emissions are regulated by two microbial processes: CH_4 production by methanogenic bacteria and CH_4 oxidation by methanotrophic bacteria. Continuously flooded rice fields are a source of CH_4 because anoxic conditions that favor methanogenesis predominate, and rice plants serve as conduits for its release to the atmosphere once it is formed in sediments (Neue et al. 1997). Under the UNDP-IRRI Inter-Regional Programmem, CH_4 emissions from rice fields were measured at eight locations in five rice-producing countries covering the main rice ecosystems – irrigated, rainfed, and deepwater systems (Wassmann et al. 2000a,b). Irrigated rice fields had the highest emission rates. Seasonal emissions varied from 1 to 50 g m^{-2}, with continuously flooded fields emitting the most (Wassmann et al. 2000a). Depending upon local precipitation, emissions from rainfed rice fields may be less than 50% of the emissions from irrigated fields. On the basis of results obtained by various rice-growing countries, IPCC has suggested that emission reduction factors under single and multiple aeration are 0.5 and 0.2 of those in continuously flooded fields. Using IPCC accounting methodology and the country default value of 10 g m^{-2}; CH_4 emissions from rice cultivation in the whole of India (45 Mha) are calculated to be 2.5 Mt yr^{-1} (14.3 MMTCE). In the 25 million ha of rice-wheat; this would equal about 1.8 Mg CH_4 yr^{-1} (or 6.5 MMTCE yr^{-1}). The main reason for relatively low CH_4 emissions from rice fields in India is that the soils of major portions of rice-growing areas have very low organic C or receive very little in the way of organic amendments (Jain et al. 2000). Incubation studies have shown that large differences in CH_4 production potential are related to organic C content (Majumdar et al. 1998). The use of organic manuring is also not very common in India, although where it occurs it can affect methane emissions (Debnath et al. 1996). The burning of crop residues also contributes to the global CH_4 budget. For each tonne of crop residue burned, 2.3 kg CH_4 are emitted, equivalent to 48 kg CO_2, using a GWP of 21. If we assume average annual residue production for rice and wheat on the IGP to be 10 Mg ha^{-1}, then, if one-half of the 25 Mha under rice-wheat is burned, a total flux of about 0.3 Mg CH_4 is emitted. This is equivalent to 50% of the total CH_4 emitted from paddy rice fields in the IGP, that has a total 1.8 Mg CH_4, as outlined above. Thus the total emission of CH_4 from the rice-wheat system is about 2.1 Mg equivalent to about 44 Mg CO_2 in terms of GWP.

16.11 Nitrous Oxide

Both fertilized and unfertilized soils emit N_2O. Although nitrogenous fertilizer is a source in the case of fertilized soils, the built-in N of the soil itself also contributes to the release of this GHG. It has long been recognized that soil water content and the availability of C enhance the production of N_2O provided a suitable NO_3 source is available. The total fluxes of N_2O have been reported to be many times higher in organic soils and mineral soils with higher contents of soil organic matter (Terry et al. 1981). The primary effect of water on N_2O production in aerobic and partially aerobic soils is the restriction of oxygen levels, which produces anaerobic conditions. Because of the relatively slow diffusion of oxygen through water (10 000 times slower than through air), denitrification in soil is highly affected by the relative amount of air- and water-filled porosity (Robertson 2000). Generally, an increase in denitrification and potential N_2O losses is observed following irrigation and precipitation. However, rice paddies are not considered an important source of atmospheric N_2O because N_2O, as the intermediary product of denitrification, would be further reduced to N_2 under the strong anaerobic conditions found in paddies (Granli and Bockman 1994). Thus, nitrous oxide is not usually detectable during the normal growing season of flooded rice (Bronson et al. 1997a,b) but is significant after mineral N fertilizer applications. During the rice-wheat dry season, Bronson et al. (1997a,b) reported N_2O fluxes that were 2.5 times higher with ammonium sulfate than with urea. The N_2O flux also increased sharply during the drainage period at mid-tillering until reflooding, when it dropped back to near zero. Experiments in rice fields conducted at the Indian Agricultural Research Institute (IARI) have shown that, as the redox potential becomes positive, CH_4 emissions decrease but N_2O emissions increase. There is much uncertainty about the amount of N_2O released; however, it is suspected that 0.1 to 6% of applied N is lost as N_2O. IPCC methodology assumes that 1.25% of fertilizer N is lost as N_2O. Crops such as wheat and maize, which receive nitrogenous fertilizers, are expected to release more N_2O than crops grown in flooded environments. The burning of crop residues also contributes to the global N_2O budget. For each tonne of crop residue that is burned, 40 g N_2O are emitted, equivalent to 12 kg CO_2, using a GWP of 310. If we assume that the average annual residue (rice plus wheat) production on the IGP is 10 Mg ha^{-1}, then, if one-half of the 23 million ha under rice-wheat is burned, a total flux of 4 000 t of N_2O is possible; that is, about 1.2 Mt CO_2 equivalent is emitted.

16.12 Comparative Greenhouse Gas Budgets for Rice-Wheat Farming Systems

The management of the rice-wheat system in the IGP is extremely diverse in terms of the amount of N applied and the rotation and tillage options that exist. As such, the GHG emission and production potential of this system is influenced by management intensity in terms of the quantity of inputs. Emissions and productivity both depend on both inputs (inorganic N, organic manure) and tillage. One useful statistic of the efficiency of resource use is overall productivity in relation to the amount of GHG emissions. To make this comparison, a carbon/productivity ratio (CPR) (Grace et al. 2000b) is used to assess how environmentally efficient various production systems are with respect to GHG emissions and how much food is placed on the table. Systems with higher CPRs are more inefficient at producing food with respect to the damage to the global environment. The CPR for Latin America, Africa, and Asia for the 30 yr of the Green Revolution was 0.52 (Grace et al. 2000b).

As an example of such a calculation for the rice-wheat system, data were analysed from a long-term rice-wheat trial in northern India at Pantnagar (Ram 2000).

Table 16.1.
Agronomic details (yields, applied N fertilizer and manure and soil organic C) of a 20-yr irrigated rice–wheat–cowpea trial at Pantnagar, Uttar Pradesh, India (Ram 2000)

System	Rice ($Mg\ ha^{-1}$)	Wheat ($Mg\ ha^{-1}$)	Fodder ($Mg\ ha^{-1}$)	N fertilizer per crop ($kg\ ha^{-1}$)	Manure ($Mg\ ha^{-1}$)	Soil organic C (%)
Control	3.74	1.71	1.86	0	0	0.49
Trt. 1: 50%	5.02	3.13	1.93	60	0	0.64[a]
Trt. 2: 10%	5.67	3.97	2.36	120	0	0.84
Trt. 3: 150%	5.92	4.38	2.32	180	0	1.06[a]
Trt. 8: FYM	6.41	4.6	2.47	120	15	1.48

[a] Estimated for 0–15 cm based on published measurements in other treatments.

Table 16.2.
Estimated annual (on-site) emissions of greenhouse gases (GHG) from the irrigated rice–wheat system in the Indo-Gangetic Plains based on 20-yr long-term trial data of Ram (2000). This example assumes conventional tillage with all crop residues being retained

GHG source	GHG emissions ($kg\ ha^{-1}$)				
	Control	Trt. 1	Trt. 2	Trt. 3	Trt. 8
CO_2: Soil tillage	3 539	3 003	2 288	1 502	0
CO_2: Diesel[a]	260	260	260	260	260
N_2O: Burning residues	0	0	0	0	0
N_2O: Manure application[b]	0	0	0	0	3
N_2O: N fertilizer application[b]	0	2.4	4.7	7.1	4.7
N_2O: Cereal residues retained[b]	0.1	0.1	0.1	0.1	0.1
N_2O: N-fixing crops[c]	1.1	1.1	1.4	1.4	1.5
CH_4: Burning residues	0	0	0	0	0
CH_4: Rice cultivation[d]	100	100	100	100	200
CE[e]	3 496	4 103	4 721	5 232	7 137
CPR[f]	0.64	0.50	0.49	0.51	0.64

[a] 2.6 kg CO_2 released per l of diesel consumed and 100 l yr^{-1}.
[b] 1.25% of applied N.
[c] 1.25% of fixed N.
[d] 10 g CH_4 m^{-2}, doubled if manure added.
[e] Carbon equivalents, global warming potentials (GWPs) of 21 and 310 used for CH_4 and N_2O, respectively.
[f] Carbon/productivity ratio, kg C emitted (equivalents) per kg of edible dry product (cereals).

This trial started in 1971 and its objective was to assess the effects of nutrient management (NPK) on productivity and soil fertility. The rice-wheat-cowpea trial consisted of 12 treatments with 50, 100, or 150% of the recommended dose of NPK fertilizer. The recommended dose of N was 120 kg ha^{-1} for each crop of rice and wheat. In the assessment, annual GHG budgets were constructed for individual gases (CO_2, CH_4, N_2O) for five of the 12 treatments (Table 16.1) on the basis of the activities outlined in the earlier part of this chapter. We included one treatment that incorporated farmyard manure.

In all budgets, we then converted this information to C equivalents to give an overall assessment of C lost to the atmosphere in relation to total edible product. Table 16.2 outlines the conventional tillage budget with all crop residues being retained, which we assume represents the experiment most closely.

The highest total emissions in terms of C equivalents were found in Treatment 8 (7 Mg C ha^{-1}), which included FYM. Treatment 2, which received the recommended dosage of fertilizer only, had emissions of 4.7 Mg C ha^{-1}, but it had the lowest CPR, which meant that it was the most efficient of all the nutrient management systems in this analysis of conventional tillage with residue retention. However, Treatments 1 and 3, which supplied 50 and 150% of the recommended dosage, respectively, had similar CPRs. In Treatment 3, the higher fertilizer N input may also result in leaching of excess fertilizer. In terms of recommendations, obviously Treatment 1, with the reduced N input (and hence reduced cost), would be the most suitable, particularly if we consider the off-site environmental costs (i.e., fertilizer production) discussed earlier. Tables 16.3 and 16.4 give GHG budgets where burning of all residues and no-tillage are alternative managements. The no-till scenario assumes complete retention of all crop residues and a hypothetical two-thirds reduction in on-site fuel use (cultivation only). Both scenarios exhibit the same trend as the earlier conventional residue-retained scenario in the final treatment analysis. The seemingly small amount of N_2O and CH_4 being emitted from residue burning in fact contributed an additional 15% to the overall C emission budgets of all treatments (ranging from 457 to 895 kg C ha^{-1} yr^{-1}). These increased emissions with residue burning exceed any benefit of moving from conventional to no-tillage,

Table 16.3. Estimated annual (on-site) emissions of greenhouse gases (GHG) from the irrigated rice–wheat system in the Indo-Gangetic Plains based on 20-yr long-term trial data of Ram (2000), assuming conventional tillage with all crop residues being burned

GHG source	GHG emissions (kg ha^{-1})				
	Control	Trt. 1	Trt. 2	Trt. 3	Trt. 8
CO_2: Soil tillage	3 539	3 003	2 288	1 502	0
CO_2: Diesel[a]	260	260	260	260	260
N_2O: Burning residues	0.4	0.6	0.6	0.7	0.7
N_2O: Manure application[b]	0	0	0	0	3
N_2O: N fertilizer application[b]	0	2.4	4.7	7.1	4.7
N_2O: Cereal residues retained[b]	0	0	0	0	0
N_2O: N-fixing crops[c]	1.1	1.1	1.4	1.4	1.5
CH_4: Burning residues	17	25.3	29.9	31.1	34.1
CH_4: Rice cultivation[d]	100	100	100	100	200
CE[e]	3 953	4 774	5 510	6 086	8 032
CPR[f]	0.73	0.59	0.57	0.59	0.73

[a] 2.6 kg CO_2 released per l of diesel consumed and 100 l yr^{-1}.
[b] 1.25% of applied N.
[c] 1.25% of fixed N.
[d] 10 g CH_4 m^{-2}, doubled if manure added.
[e] Carbon equivalents, global warming potentials (GWPs) of 21 and 310 used for CH_4 and N_2O, respectively.
[f] Carbon/productivity ratio, kg C emitted (equivalents) per kg of edible dry product (cereals).

Table 16.4. Estimated annual (on-site) emissions of greenhouse gases (GHG) from the irrigated rice–wheat systems in the Indo-Gangetic Plains based on 20-yr long-term trial data of Ram (2000), assuming no-tillage and all crop residues being retained in this example

GHG source	GHG emissions (kg ha^{-1})				
	Control	Trt. 1	Trt. 2	Trt. 3	Trt. 8
CO_2: Soil tillage[a]	1 769	1 501	1 144	751	366[h]
CO_2: Diesel[b]	86	86	86	86	86
N_2O: Burning residues	0	0	0	0	0
N_2O: Manure application[c]	0	0	0	0	3
N_2O: N fertilizer application[c]	0	2.4	4.7	7.1	4.7
N_2O: Cereal residues retained[c]	0.1	0.1	0.1	0.1	0.1
N_2O: N-fixing crops[d]	1.1	1.1	1.4	1.4	1.5
CH_4: Burning residues	0	0	0	0	0
CH_4: Rice cultivation[e]	100	100	100	100	200
CE[f]	2 966	3 646	4 362	4 981	6 724
CPR[g]	0.54	0.45	0.45	0.48	0.61

[a] Assuming 66% fuel savings and soil organic C levels decrease only by 50% compared with conventional till.
[b] 2.6 kg CO_2 released per l of diesel consumed and 33 l yr^{-1}.
[c] 1.25% of applied N.
[d] 1.25% of fixed N.
[e] 10 g CH_4 m^{-2}, doubled if manure added.
[f] Carbon equivalents, global warming potentials (GWPs) of 21 and 310 used for CH_4 and N_2O, respectively.
[g] Carbon/productivity ratio, kg C emitted (equivalents) per kg of edible dry product (cereals).
[h] Assuming a C accumulation of 100 kg yr^{-1} in the topsoil.

which showed only a 9% reduction in the C emission budget. In other words, no-till must be complemented by residue retention. The use of FYM increased GHG emissions, and Treatments 1 to 3 showed similar CPRs. Again, the tendency to use a less N-intensive system would be desirable, but it is not essential provided N losses through leaching can be minimized, perhaps through better timing and placement of fertilizers (i.e., Jamieson et al. 2003). The judicial timing of application of fertilizers can produce yields similar to those from application of larger amounts. Crop simulation models developed during the lifetime of GCTE Focus 3 can mimic these systems in terms of water, N movement, and yield responses. They offer the opportunity to examine the bi-directional nature of the interaction between climate and the rice-wheat system.

16.13 Summary and Conclusions

Over the past ten years of GCTE, Focus 3 scientists have contributed to understanding of the effects of CO_2, temperature, water and nutrition on the growth and development of wheat and other crops. The effects of environmental factors have been looked at in isolation and in combination. Focus 3 scientists were among the first to realize the importance of climate variability as opposed to changes in mean climate for food production and quality and to model these effects. Challenges for the future as IGBP moves into its second phase include further modeling of cropping systems, modeling genomics and breeding strategies and genotype by environment by management relationships. Linkage to global programmes, such as GECAFS (Global Environmental Change and Food Systems), concerned with food systems and that concentrate on the effects that global environmental change on the interplay between biological and social aspects of food systems, define a clear role for the work of GCTE Focus 3 in the future. In terms of experiments, FACE systems that allow the interaction between gases such as O_3 and CO_2 need to be supported and used by the international wheat community. In agricultural systems including wheat production, non-CO_2 GHG emissions dominate (IPCC 2001) and their contributions in terms of CO_2 equivalent emissions need to be taken account of more than has been the case to date. Generally, soil organic carbon (SOC) levels in arable agricultural soils are lower than those found in undisturbed ecosystems as a result mainly of tillage and carbon removal in crops. Paradoxically, this means that a large potential C sink exists in agricultural soils that can be exploited as a mitigation option via agricultural management. The UK Royal Society (Royal Society 2001) concluded that the largest enhancement of the terrestrial carbon sink would result from changes in agricultural management (Fig. 16.7) that would include practices such as non-inversion tillage, residue return, rotational cropping and energy crops. The rate of increase of soil carbon, in all circumstances, would be very slow and finite as the SOC level moves to a new equilibrium that is potentially reversible but this depends greatly on the intensity of management (Schlesinger 2000; Smith et al. 2000). This means that management that increases SOC has to be maintained but with hopefully other benefits by way of improved soil physical and chemical quality.The vast majority of analyses of the effects of climate change on arable crops have concerned themselves with production, either per unit area or for a region. A major neglect has been studies of the influence and mechanisms by which climate change may affect crop and food quality, for either human or animal nutrition. Crop quality is a multi-faceted and complicated subject involving the growing, storage and processing pre- and post- harvest and quality has nutritional, technological and environmental definitions. For herbivores, it is possible to have a carbohydrate sufficiency but still suffer from malnutrition – as protein, mineral or vitamin deficiencies. From closed chamber experiments with wheat in which nitrogen, temperature and CO_2 level have been manipulated, we know that there is a strong weather signal in the determination of total protein content and, as importantly, its fractional composition that affects its nutritional and bread-making rheological properties (Martre et al. 2003). The effect of climate change on food quality will be an important issue for future research as we develop our perceptions of what constitutes a healthy and sustainable diet.

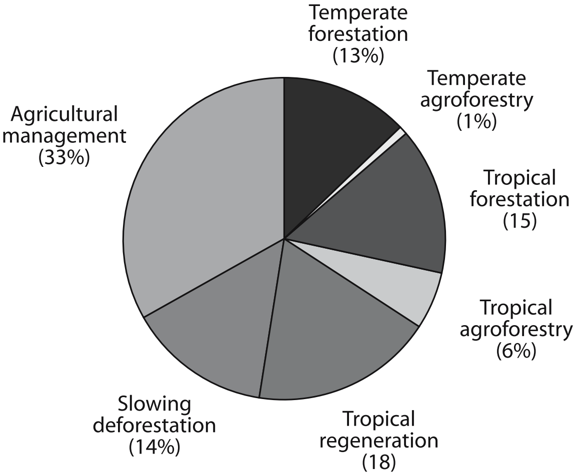

Fig. 16.7. Potential contribution of measures to increase soil carbon levels (Royal Society 2001)

Adaptation is the attempt to reduce or at least minimize the negative effects and maximise the benefits of climate change by changing management and agricultural practices, including breeding (Olesen and Bindi 2003). Management changes include earlier planting or sowing of crops that increases the length of the growing season thus increasing yield potential, provided moisture is adequate and the risk of heat stress is low. Combining the advantages of earlier planting with drought avoidance places emphasis on the importance of the crop phenological cycle in breeding. An adaptive strategy of a slowly developing vegetative period followed by rapid reproductive 'self-destruction' that transports nutrients and carbon to the grain sites as quickly as possible, thus avoiding stress, has been proposed for low latitude cereals. Profiting from increased atmospheric CO_2 for yield will mean an increase in demand for nitrogen by crops but climate change will also alter the magnitude and the balance of nitrogen losses as between leaching and gaseous losses. The links between the global carbon and nitrogen cycles will both affect the productivity of crops but will, in turn, be affected by the suite of gaseous emissions from arable and other forms of agriculture. Global warming will also likely lead to a higher incidence of pests and weeds and thus to a potentially larger use of biocides, although their use can be reduced via integrated pest management. Breeding and management have led to rises in crop yields of about 1–2% yr^{-1} since the 1960s, mainly because of changes in yield harvest index and the responsiveness of crops to nitrogen. The speed of breeding for higher yields and the release of new crop varieties is currently faster than the rate at which the climate is changing – about 0.01 °C increase in mean global temperature per year for the past several decades. It this appears that breeders may be able to stay ahead of climate change for sometime to come and incorporate climate change effects in their selections as part of the breeding process. In order to do this crop breeding needs to use both traditional and biotechnological techniques to allow the introduction of heat and drought resistant crop varieties.

Agriculture is the oldest human production industry that has withstood moderate changes in climate over the 10 000 years that humans have practiced it. It is probable that arable agricultural production can adapt to changes in mean global temperatures over the next century of the order of 1–2 °C (about 0.01 to 0.02 °C yr^{-1}) via breeding, selection and management. The agricultural genotype management environment envelope is flexible and spacious enough to accommodate small to medium changes in the weather signal for crops. However, if global warming results in mean temperature changes over the next century of 4–5 °C (i.e., 0.04 to 0.05 °C yr^{-1}) then it will be a case of global agriculture struggling to survive. Mitigation options from farming are substantial but are slow to implement and to have their effect. In the rich world, we need to keep our agricultural options open but our thinking should include a new vision for agriculture that seeks to change humankind's oldest production industry into its newest service industry. This means providing the ecosystem services of food, fiber and energy provision, biogeochemical regulation, biodiversity and soil conservation and cultural and aesthetic benefits for the landscape.

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Chapter 17

Pests Under Global Change – Meeting Your Future Landlords?

Robert W. Sutherst · Richard H. A. Baker · Stella M. Coakley · Richard Harrington · Darren J. Kriticos · Harald Scherm

17.1 Introduction

The term global change embraces a range of natural and anthropogenic environmental changes that are occurring around the world (Vitousek 1994), including changes in atmospheric composition, climate, land use and land cover, and the prevalence of non-indigenous species. This synthesis describes contemporary approaches to the assessment of the vulnerability of ecosystems and human societies to plant pests (arthropods, plant pathogens and weeds that are injurious to plants) in relation to global change. Animal and human health have been covered elsewhere in recent reviews (Sutherst 2001, 2004). While the detailed impacts of global change on the status of pests will only be known as events unfold, it is already clear that some pests will be able to invade new areas and become increasingly problematic for the maintenance of biodiversity, the functioning of ecosystems and the profitability of crop production. Some pests which are already present but only occur in small areas, or at low densities may be able to exploit the changing conditions by spreading more widely and reaching damaging population densities. Our objective is to discuss these potential changes in pest status and to present a framework for effective adaptation.

17.2 Methods

17.2.1 IPCC Processes

In addition to assessing the direct impacts of global change on agriculture and natural ecosystems, the global scientific community faces the task of understanding indirect impacts caused by pests of animals and plants. The numerous interacting species, the myriad of stakeholder interests, and great variation in the quality of available data make this a daunting prospect requiring generic approaches with a hierarchy of analytical tools (Sutherst et al. 1996). In order to develop a holistic approach we need to integrate the methodologies developed by the different research and policy communities into a comprehensive risk analysis framework. Pest risk analysis procedures developed by the International Plant Protection Convention (IPPC) (FAO 2004) provide an accepted standard for analysing the risks posed by pests to areas where they are not currently present or, if present, not widely distributed and under official control. At present, although assessments may focus primarily on impacts under current conditions, the risk analysis framework does allow the effects of global change to be taken into account (Baker et al. 2000; Sutherst 2000). In addition, although designed for invasive non-indigenous species, the procedures can also be used to analyze future threats posed by indigenous species.

The concept of vulnerability is used by the scientific and policy communities investigating the likely threats from climate change (Houghton et al. 1996; IPCC 2001a). *Vulnerability* is a measure of the potential *impacts* of a given change, taking into account the *adaptive capacity* available to respond to that change. The term avoids the consideration of risks in the absence of a natural or societal response, which can give an incomplete picture. *Impacts* are a combination of a change in *exposure* of ecosystems to pests and the *sensitivity* of the system to that change. *Adaptive capacity* depends on the adaptation technologies, cultural tools, and the infrastructure and resources available to implement appropriate management responses:

$$\text{Vulnerability} = \text{Impacts} \times (1 - \text{Adaptive capacity})$$

where

$$\text{Impacts} = \text{Exposure} \times \text{Sensitivity}$$

and

$$\text{Adaptive capacity} = (\text{Adaptation products and practices}) \times \text{Resources}$$

The general issues of adaptive capacity relative to climate change have been reviewed by Smith et al. (2003), who delve into both theoretical considerations and practical examples.

17.2.1.1 *Exposure*

A shift in the geographical distribution of a pest exposes new ecosystems to that pest for the first time. Climate change may enable such shifts to take place as pests track suitable climates. Immigration to new environments may occur through anthropogenic or natural pathways. Anthropogenic pest entry to new areas is already a major cause of invasion, and the numbers of species carried by traded commodities and with passengers are unlikely to be influenced directly by global change. However, entry by natural means may increase with global change if, for example, migrant species extend their range and move closer to threatened areas. While natural spread is generally undertaken by the pests themselves, movement of hosts or vectors with their associated pests may also be responsible for pest entry.

Following entry, a number of abiotic and biotic factors coupled with the intrinsic attributes of a species, e.g., its reproductive rate and adaptability, determine the success of establishment in the new area (Baker et al. 2003; FAO 2004). Climate is usually the first feature of the habitat considered in a risk assessment for pragmatic reasons, but other variables such as the spatial distribution of host plants also need to be considered. The extent to which exposure is affected by climate change will depend on the position of the particular habitat relative to the species' climatic envelope (Sutherst 2001). Populations closer to the edges of a species' range are likely to respond more quickly to climate change than populations near the center where conditions are closer to the optimum. Natural enemies of the pests may be left behind so the pest can proliferate unchecked (the enemy release hypothesis; Colautti et al. 2004), although predators and parasites may adapt to the invading species over time. Genetic observations can also contribute to understanding patterns of invasions by pests in new environments, as shown by studies of population structure of a non-pest fruit fly, *Drosophila subobscura*, in the Americas (Balanya et al. 1994; Noor et al. 2000).

Predictions of current and future distribution based on climate have been enhanced by the availability of monthly local and global gridded climatologies, e.g., the 1961–1990 global climatology interpolated to a 10' latitude/longitude grid (New et al. 2002). Where climate change scenarios are available at the same resolution as the baseline climatologies, predictions of changes in potential distribution under climate change can be made (Baker et al. 1998; Baker et al. 2003; Kriticos et al. 2003a).

17.2.1.2 *Sensitivity*

Sensitivity is the degree to which a system responds to a perturbation such as climate change (IPCC 2001a). Responses are often complex and non-linear due to a number of features of biological systems (Sutherst 1998) including thresholds (Scherm and van Bruggen 1994; Scherm 2004), discontinuities at the edges of species' ranges including hybrid zones (Barton and Hewitt 1989), multiplicative effects of population growth in multivoltine species (Sutherst 1983), the Allee effect (Stephens et al. 1999; Garrett and Bowden 2002; Taylor and Hastings 2005) and competition or predation (Silvertown 2004). A consequence of these effects is the need to augment empirical and descriptive approaches, such as statistical models, with dynamic and mechanistic simulation models (Sutherst 2001).

Once the sensitivity of the target system or species has been defined, a measure of the likely impact on the population can be derived, in the absence of any intervention. This provides a baseline measure of risk against which to estimate the benefits of alternative adaptation options.

17.2.1.3 *Impacts*

Both 'top-down' and 'bottom-up' approaches have been recommended for analyses of impacts of climate change (Parry and Carter 1998). The former is based on scenarios from global climate models (GCMs) while the latter uses sensitivity analyses (Sutherst 1998; Sutherst 2001). The two approaches have been combined into a risk management approach (Jones 2000). Integrated assessment frameworks are under development to bring some of these elements together, e.g., in a framework for analysing impacts on parasites (Sutherst 2001). The science needed to assess impacts of global change on pests is the same as for other species. However, the emphasis is different in that pests usually reproduce, disperse and colonize new habitats faster than many species of conservation value.

17.2.2 Monitoring, Benchmarks and Indicators for Measuring Impacts

We need *monitoring* data for pest-related *indicators*, covering long time-series in order to detect changes in ecology and impacts associated with global change. Such indicators need to relate to environmental, economic and social systems. We also need *benchmarks* to provide reality-checks for attribution of changes in status of populations.

The 1961–1990 climatology has become a standard from which to gauge climate change impacts, although, as climate change accelerates, its use as a baseline reflecting current climatic conditions is becoming less justifiable. Records of species presence need to include collection dates so that potential range expansion can be detected reliably. Records of absence are also useful. The difficulty of accurately determining the distribution of even well-known pest species (Yonow et al. 2004) suggests that more emphasis is needed on incorporating high-quality pest data into databases of species distributions.

A benchmark for the effects of temperature change *per se* is provided by the relationships with altitude and latitude (Linacre 1992). Each 1 °C increase in global temperature corresponds to a potential increase of ~170 m in a species' altitudinal range. As warming over the past century has been about 0.6 °C (IPCC 2001a), altitudinal range changes caused by global warming are unlikely to exceed 100 m. Similarly, in the absence of other factors, latitudinal shifts of about 1.7° (~200 km) can be expected for each 1 °C increase in temperature, corresponding to a shift of ~118 km with the observed temperature increase of 0.6 °C.

Whether changes of this order are achieved by a pest, i.e., whether the species is able to track temperature change, will depend on its rate of dispersal through fragmented habitats. In this context, it is worth drawing attention to the 'conservation-regulation' paradox. Those working on pests, i.e., species that require regulation, generally claim that, under global change, their species will become more abundant and widespread. By contrast, those working on species that require conservation generally state that their species will become less abundant and less widespread (Thomas et al. 2004). There are many exceptions on both sides, and some of the conclusions may be artefacts of the assessment tools employed (Thuiller 2003). Nonetheless, the paradox can be explained in part by the fact that the characteristics which tend to make an organism a pest, i.e., high reproductive and dispersal potentials, are the same ones that allow it to adapt to environmental change. For example, if the ability to migrate in fragmented habitats is impaired in plant species of conservation concern compared with weeds, climate change is likely to favor the weeds (Collingham et al. 2000).

Yamamura and Kiritani (1998) developed an indicator for tracking change in seasonal population dynamics of invertebrates. They devised a formula for the expected increase in the number of generations (voltinism) per year with a given temperature increase, based on values of the lower developmental threshold (T_0) and generation time (K). Using this index, those species with the largest increase in voltinism will be those with the lowest T_0 and the shortest K. Of 12 invertebrate orders examined, aphids are expected to show the greatest increase in voltinism with an extra two to three generations per 1 °C warming. Naturally, an increase in voltinism will not necessarily translate into larger population densities if, for example, required moisture conditions are not satisfied or if there is strong density-dependent parasitism, predation or lack of food.

The establishment of a global network of long-term monitoring sites will facilitate the development and implementation of indicators to monitor effects of global change. Examples of such measurements include the number of non-indigenous species in each country, the number of species extinctions, losses of agricultural production, and incidence of disease in humans (Pimentel et al. 2000b). In the context of biodiversity, suitable indicators include measures of physiological processes such as photosynthesis, metabolism and development rates, geographical distributions, phenology, and microevolutionary adaptation (Hughes 2000).

Perhaps most intuitive for policy makers is the expression of impacts in monetary terms. For agricultural crops, Oerke and Dehne (2004) gave potential yield losses for a range of commodities and regions. According to their synthesis, weeds currently cause losses of 32% with animal pests and pathogens causing 18 and 15%, respectively. Costs of pests in six countries (United States, UK, Australia, South Africa, India and Brazil) were estimated at US$336 billion, with about 9% of those representing costs of control. Extrapolated to the world the estimate was US$1.4 trillion. These figures would be multiplied several times if losses of biodiversity and ecosystem services in natural systems were included. How these costs will be impacted by global change is difficult to project, but Pimentel et al. (2000a) provide an example of how this can be estimated. Their estimate for a single global change driver (non-indigenous species) for a single country (the United States) suggests annual environmental and economic costs of nearly US$137 billion, of which almost 20% are due to non-indigenous plant pathogens and associated control costs. These figures may underestimate the problem (Perrings et al. 2002).

17.2.3 Estimating Impacts

A comprehensive assessment of impacts of pest risks under global change requires a conceptual framework that encompasses the pest and its interactions with physical and biological factors, including other species in the same or different trophic levels. It also needs a balanced program of field observations to help identify variables that affect species populations, experimental studies to elucidate mechanisms, and models to synthesize and test knowledge and understanding. Networks of researchers are also invaluable in the context of global change in order to facilitate sharing of information and comparative regional studies (Scherm et al. 1999; Hijmans et al. 2000). Some examples illustrate how these activities can contribute to ecological research to form the basis for the design of adaptation strategies for global change.

17.2.3.1 *Field Observations to Detect Population Changes*

Field observations are the grist of ecology and yet there is reluctance to fund such efforts due to the open-ended commitments necessary to obtain long time-series of observations. Many important revelations have been obtained by analysing such data. For example, long-term monitoring of the wheat stem rust pathogen (*Puccinia graminis* f. sp. *tritici*), initiated in the early 1900s in the central United States, clearly documented the effects of the deployment of specific host resistance genes and of the eradication of the alternate host, barberry (on which sexual reproduction occurs) on the pathogen's virulence dynamics (Roelfs 1982).

In community ecology, the changing correlations in rankings of abundance of each species and drifts in species compositions in communities over time provided insights into the natural behavior of species communities (Lawton 2000). Species in higher trophic levels were more sensitive to climate change (Voigt et al. 2003) suggesting that some communities may break down under global change.

There is increasing global scientific interest in developing Long-Term Ecological Research (LTER) sites and programmes, most of which are concerned with species of conservation interest. The most enduring long-term, standardised network for monitoring arthropod pest species is the suction trap network operated by the Rothamsted Insect Survey for studying aphids (Woiwod and Harrington 1994). The long run of data has enabled statistical relationships to be established between aphid phenology (e.g., annual time of first capture) and a range of climate and land-use variables. The time of first flight was strongly correlated with temperature for some species at some sites, with earlier first flights after higher winter temperatures. In the case of the important pest species *Myzus persicae* at Rothamsted, the relationship accounted for 80% of the variance.

Within the United States, several LTERs are now being used to study pest populations. In a 12-year warming experiment at a site in the Rocky Mountains of Colorado, Roy et al. (2004) documented an overall trend of increasing damage from herbivores and plant pathogens in plots with warmer temperatures and earlier snowmelt, although some pathogens and herbivores preferred the cooler plots. Results support the idea that the community composition within a particular area is likely to change with global warming. Other LTER sites in Alaska are currently being used to study how climate warming may impact pest occurrence under various temperature/moisture combinations (Mulder and Roy 2003). It would be prudent to include more climate impact studies in LTER sites in the future; assessing the effects of pest control will add to the value of biodiversity information being collected without significantly increasing the cost of maintaining these research sites.

Regardless of the species being monitored, there is a need for much more spatial distribution data coupled with geophysical measurements, including soil types, topography, vegetation type and cover and land use. Such measurements are particularly valuable if they are spatially explicit, cover a wider range of parameter values than measurements at any single location, and contain multiple combinations and permutations of environmental conditions (Sutherst 1998). In addition, spatial information is becoming valued due to the trend towards landscape-scale management of non-indigenous species (Jules et al. 2002).

17.2.3.2 *Empirical Data from Experimental Manipulations*

Reductionist experiments are traditionally employed to isolate each component of a system and examine its relative contribution. Such an approach has been used to dissect the effects of elevated CO_2 on the dynamics and intensity of anthracnose disease on the tropical legume *Stylosanthes scabra* (Chakraborty et al. 2000a; Chakraborty and Datta 2003; Pangga et al. 2004). Elevated CO_2 was found to reduce disease in growth chamber experiments by delaying pathogen spore germination, germtube growth and appressorium production and by inducing host resistance to anthracnose. In the field under elevated CO_2, however, these disease-reducing effects were counterbalanced by increased pathogen fecundity and by an enlarged canopy of *Stylosanthes* which trapped more pathogen spores and provided a more humid microclimate, leading to increased lesion numbers. Follow-up studies should include additional treatment levels in order to detect possible non-linear responses (Körner 2000).

In general, it is difficult to predict field responses from experiments involving changes in a few selected variables. For example, although the intrinsic growth rate of populations of the pest aphid *Aulacorthum solani* was enhanced in elevated CO_2 (Awmack et al. 1997a), a decrease in the insect's response to alarm pheromone could make it more vulnerable to attack by natural enemies, thus potentially offsetting the population increase (Awmack et al. 1997b). Experiments are needed to show how these and other changes interact.

Artificial ecosystems in controlled conditions, such as the Ecotron (Jones et al. 1998), can act as a useful intermediate step between laboratory experiments and the field and assist in the scaling-up process. Whole-system studies in controlled ecosystems provide insight into the complexity of simplified synthetic communities and so help to elucidate patterns and mechanisms behind specific responses of those communities to changes in environmental variables (Lawton 2000).

In one such laboratory-based study, interactions between three species of *Drosophila* fruit flies (*D. melanogaster*, *D. simulans* and *D. subobscura*) were studied in temperature clines with dispersal, with or without a hymenopteran parasitoid (*Leptopilina boulardi*) present (Landsberg 1989). As with other similar experiments, e.g., Davis et al. (1998), each of the treatments altered the balance of species numbers. The latter authors criticized the use of climatic mapping techniques (see below) on the basis of these laboratory results, and called for inclusion of population sinks and species interactions when trying to predict ranges under climate change. However, while recognising that species interactions are important in the field, Hodkinson (1999) and Baker et al. (2000) argued that experiments in confined spaces may overestimate species interactions since they do not provide species with the heterogeneous habitats that allow fauna such as these *Drosophila* spp. to coexist (Jenkins and Hoffmann 2001). A protocol has been described for ensuring that climate-based projections of species ranges do not overlook the roles of non-climatic variables (Sutherst 2003). Regardless, community-level impacts of global change will remain very uncertain due to their inherent complexity and multiple linkages.

Manipulation of whole systems in the field offers opportunities to study species interactions in more natural conditions. Free-Air CO_2 Enrichment (FACE) experiments (Hendrey 1992) have been particularly popular in global change research, but few have included pest components. A recent exception is a study on the interactive effects of CO_2 and ozone (O_3) on aspen trees infected with the rust fungus *Melampsora medusae* f.sp. *tremuloidae* (Percy et al. 2002; Karnosky et al. 2002). The results showed that O_3 predisposed the host to rust infection and that elevated CO_2 was unable to compensate for this effect. Exposure to O_3 or CO_2 increased the amount of hydrocarbons in leaf surface waxes, which aid host recognition by certain herbivorous insects; as a result, aphids were more abundant in trees treated with O_3 and/or CO_2 (Percy et al. 2002).

A complicating factor in controlled experiments is the potential for genetic adaptation to climate change. This is difficult to mimic in laboratory experiments that generally utilize populations of single strains or of a few strains with limited genetic diversity and do not investigate how populations may adapt as climate changes over long time periods with many generations. Indeed, there is now increasing evidence from field studies that some organisms can evolve rapidly in response to the strong directional selection pressures exerted by global change. For example, genetic adaptation to elevated temperature (Rodriguez-Trelles et al. 1998) and increased length of the growing season (Bradshaw and Holzapfel 2001) associated with global warming have been documented for certain insect species. The potential for genetic adaptation will be particularly important for host-parasite interactions, for which a changing climate could lead to temporal asynchrony between pest phenology and the availability of host tissue (Visser and Holleman 2001). In such cases, there will be a very strong selection pressure to maintain that close temporal synchrony (Dixon 2003).

17.2.3.3 *Modeling Tools*

Many modeling approaches have been applied to the assessment of risks from pests under global change because opportunities for large-scale experimentation are so limited. One group of models simulates the detailed population dynamics of species at a point scale. These tools have focused on software engineering to create modular and generic simulation models (Reynolds and Acock 1997; Sutherst et al. 2000). However, comprehensive, process-based models are inevitably complex and expensive to parameterise and so will be applicable only to the most intensively studied species or systems.

Simplified, inferential and dynamic simulation models (Sutherst and Maywald 1985; Sykes and Prentice 2004) can avoid the inherent problems of complex and over-parameterized models. They are also amenable to investigation of competitive interactions between species across geographical distributions. For example, in some cases where the CLIMEX model was used to project the potential range of a pest species in exotic habitats, strong evidence was found for biotic interactions truncating their ranges (Sutherst et al. 1985; Kriticos and Randall 2001; Wharton and Kriticos 2004). Inferential simulation tools that exploit the richness of spatial climatic data (Sutherst 1998) to infer the climatic responses that drive and limit species populations are highly informative, offering insights into the climatic factors that limit species distributions in different parts of their ranges (Yonow and Sutherst 1998; Kriticos et al. 2003a,b). Inference is less certain than deduction but complements mechanistic studies using traditional reductionist approaches. To date, models of combinations of species have only included species in additive form, such as the need for conditions to suit a weed and its biological control agent (Julien et al. 1995), crop tree and its arthropod pest (Wharton and Kriticos 2004), pathogen and host plants (Yonow et al. 2004), or both pathogen and vector in vector-borne disease transmission (Sutherst 2004). Recent progress has now included explicit species interactions within and between trophic levels (Sutherst et al. In press). This has allowed predation, competition and facilitation to be simulated on geographical scales. These advantages have been partially offset by the extra operational demands in estimating parameter values, a lack of probabilistic outputs, and difficulty in handling GCM climate change scenarios.

Another modeling approach consists of a heterogeneous collection of statistical, rule-based and simulation approaches with variations, such as neural networks (Berry et al. 2002) or genetic algorithms (Peterson et al. 2002), designed to predict potential changes in geographical distributions of species (Kriticos and Randall 2001; Scott et al. 2002; Cocu et al. 2005). Potential geographical distributions tend to be based on ecological (realized) rather than physiological (fundamental) niches and so involve assumptions about the extent of specific and non-specific biotic resistance. This is a pragmatic approach that demands caution in the selection of appropriate tools, in the ability to detect significant biotic interactions and in choice of predictive variables. It has been claimed that species distributions are usually limited by fewer than ten factors (Brown et al. 1996); thus the use of descriptive, pattern-matching of meteorological data to create 'climate envelopes' has become very popular (Sutherst 2003). Descriptive species distribution models often do not have predictive capability and need validation against independent geographical distributions before being used to predict effects of global change.

17.2.3.4 *Networks*

International, interdisciplinary collaboration is crucial in order to accelerate progress by creating synergy, capitalising on existing infrastructure and pooling data (Scherm et al. 1999). This involves activities such as the compilation and standardisation of input data sets and models, the development of metadata (information describing the data and data collection methods), as well as formal model comparison experiments to identify the appropriateness of specific models for global change assessments. The potato late blight disease simulation network established jointly by the IGBP Global Change and Terrestrial Ecosystems (GCTE) Programme and the Global Initiative for Late Blight (GILB) is an example of a formal research network designed to conduct such activities. The aim of this group is to develop an operational platform for simulating the effects of selected global change drivers on late blight intensity and potato yields on a global scale (Hijmans et al. 2000).

17.3 Impacts

Several examples of the effects of selected global change drivers on plant pests have been given in the previous section, and we now consider the evidence for changes in the impacts more systematically. Rather than repeating what has already been summarised and synthesised in previous comprehensive reviews (Teng et al. 1996; Sutherst et al. 1996; Coakley et al. 1999; Chakraborty et al. 2000b; Bale et al. 2002; Scherm and Coakley 2003), we focus on selected examples from the most recent literature. All the environmental changes considered here are global in nature, but their intensity may vary on a regional scale; thus, the degree of exposure of each pest system will vary with both the driver involved and with geographical location. In the absence of a unifying principle, the risks associated with each type of change need to be addressed on a pest-by-pest and location-by-location basis.

17.3.1 Atmospheric CO_2 and Climate

The widespread pattern of upward shifts in the freezing isotherm and retreat of glaciers in the tropics, changes in the geographical ranges of species at higher latitudes, earlier spring migration and breeding by birds, and earlier seasonal activity of insects have been cited as examples of impacts of gradual global warming (Root et al. 2003; Parmesan and Yohe 2003). These surveys provide strong evidence that the recent climatic changes have already affected up to 50% of the species examined in a survey of the literature.

There has been difficulty in attributing the relative magnitude of causal effects because factors other than climate are often involved and observations cannot easily be verified experimentally. We urgently need to establish baseline data on abundance and geographical distributions, benchmarks to assess their consistency with physiological processes, and monitoring data to track the changes (AtKisson 1999). In addition, the implications of the asymmetrical increases of temperature with global warming (Karl et al. 1993) for the ecology of species and species interactions need to be clarified. For example, increased cloud cover at night coupled with higher minimum temperatures could lead to reduced dew formation which, in turn, could lead to less favourable conditions for infection by foliar plant pathogens. As another example, plants are often limited by a lack of sufficient thermal accumulation or by extreme temperatures. There are several cardinal temperatures (Woodward 1987) below which specific sets of adaptations are required for survival (e.g., deciduous or coniferous leaves, thick bark, ability to adjust osmotic concentrations, etc.). As these climatic limits shift pole-ward in response to global warming, some plants will be able to migrate with them, applying increasing competitive pressure on species that presently occupy hitherto unsuitable habitat.

17.3.1.1 *Weeds*

Temperature drives the development of plants, changing their seasonal phenology and geographical distributions. Moisture affects survival and growth, while CO_2 acts as a fertilizer for plants when other nutrients are not limiting.

Ziska (2003b) reports on a recent comparison of six non-indigenous weed species in the continental United States in three levels of CO_2. They used concentrations roughly similar to those that existed at the beginning of the 20th century (284 μmol mol^{-1}), currently (380 μmol mol^{-1}), or are anticipated for the end of the 21st century (719 μmol mol^{-1}). Results indicate that there has already been a stimulation of growth of these species (average of 110% increase) and that there is likely to be a further increase by about 50% on average. This research is notable because the overall CO_2-induced growth associated with the increase of 285–382 µmol mol^{-1} was about three times greater than in earlier studies of other species. It also provides support for the hypothesis that many organisms have been evolving with the increase in CO_2 concentration.

CO_2 reduces water loss in plants as they close their stomata in response to higher concentrations (Körner et al. 2007, Chap. 2 ofthis volume). One consequence of the increase in water use efficiency may be the spread of woody weeds into lower rainfall zones (Farquhar 1997; Kriticos et al. 2003a; Kriticos et al. 2003b). We can expect changes in the balance of C_3 vs. C_4 plants, legumes vs. non-nitrogen fixing species, and woody plants vs. grasses to occur on a wide scale (Farquhar 1997; Gavazzi et al. 2000). Thus there is likely to be a shift in the importance of different weedy species. An increase in the frequency of extreme climatic events will alternately aid dispersal and establishment of woody weeds in the case of floods, and reduce productivity in the case of droughts. Rangeland habitats currently support extensive pastoral activities, and the cost of weed control typically exceeds the productive value of the land. The evidence for relative competitiveness of temperate C_3 crop species against their C_4 weeds is equivocal. Increased competitiveness due to increases in CO_2 may be offset by reduced competitiveness due to increased temperatures (Fuhrer 2003).

The invasion of ecosystems by weeds will also have important second-order effects such as the alteration of fire cycles (D'Antonio and Vitousek 1992) or soil nutrient conditions that can facilitate additional weed invasions (Ramakrishnan and Vitousek 1989). Plants can be constrained from spreading into cooler habitats either by insufficient thermal accumulation to grow and reproduce or by extreme low temperatures that cause stress or mortality by damaging tissues. If introduced beyond their thermal accumulation limits, perennial weeds can sometimes persist as 'sleeper' populations in marginally cold climates where they frequently fail to reproduce. There may also be microhabitats, e.g., with favourable combinations of altitude, slope, aspect and proximity to water bodies enabling founder populations to colonize very small areas from where they can expand as temperatures rise. Increasing temperatures are likely to shift heat-sum limits on tropical and sub-tropical weeds such as *Acacia nilotica* and *Cryptostegia grandiflora* toward the poles allowing them to invade areas that currently lack sufficient heat for them to reproduce (Kriticos et al. 2003a,b). Following climate warming, these established sleeper populations may form nascent foci for potentially rapid increase in abundance.

Assuming movement is possible, montane and alpine communities are likely to shift pole-ward as temperate species invade upward in altitude and the limits of minimum growing season length shift pole-ward (Fig. 17.1). Weeds will likely be able to disperse pole-ward across inhospitable habitats more effectively than other species with which they currently share habitat. These weed species typically have little reliance upon specialized pollinators, in addition to having effective dispersal methods (frequently human-mediated).

The focus on weeds has been in terrestrial ecosystems. Equally important, however, is the likelihood of climate change impacting pest species in aquatic ecosystems. Specifically, research in a marine ecosystem along the Dutch coastal zone shows that an increase in temperature of 4 °C results in increased harmful dinoflagellate and raphidophyte blooms (Peperzak 2003). It is likely that the rise in water temperature in fresh water bodies may also result in an increase in weedy species including numbers and growth of phytoplankton. Toxic algal blooms are likely to increase in frequency as a result. Additional research on biodiversity and the functioning of marine and freshwater ecosystems will be needed to protect valuable ecosystem services such as fisheries.

Recent research has shown enhanced growth of weed species that produce allergenic reactions, contact dermatitis, mechanical injury, or internal poisoning in elevated CO_2. Common ragweed (*Ambrosia artemisiifolia*) produces more pollen in elevated CO_2 (Ziska and Caufield 2000; Wayne et al. 2002; Ziska et al. 2003). Various weeds responsible for contact dermatitis, including stinging nettle, may also increase in vegetative biomass in increased CO_2 (Ziska 2003d), and nitrogen availability is unlikely to limit this response (Ziska 2003c). Ziska (2003a) also reviewed a number of plant species producing poisonous compounds (such as ricin from castor bean) and concluded that both laboratory and field studies indicate significant growth response to CO_2 and increased temperature. There is also the possibility that increased CO_2 and temperature reduce the effectiveness of herbicides, requiring an increase in frequency of application and concentration of herbicide to obtain adequate control (Ziska 2003a).

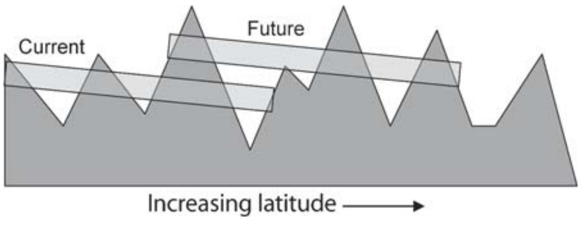

Fig. 17.1. Simplified schematic representation of the effects of a warming climate on alpine or montane vegetation (ignores topographic shading effects. The climatically suitable zone is represented by the lightly shaded parallelograms superimposed over a mountain range in the darker shading. A warmer climate will shift the suitable zone upward in altitude and toward higher latitudes. This may require dispersal across climatically unsuitable valley habitats. The climatically suitable zones are tilted to represent the compensating factors of decreased insolation at higher latitudes taking into account the effect of slope and aspect, and decreasing temperatures with increased altitude due to the adiabatic lapse rate

17.3.1.2 *Arthropods*

As described earlier, aphids are expected to be particularly responsive to climate change because of their low developmental threshold temperature, short generation time and dispersal abilities. They are key pests of agriculture, horticulture and forestry throughout the world, but especially in temperate regions. A long-term monitoring system for aphids (Woiwod and Harrington 1994) has demonstrated advances in aphid phenology that are compatible with the expectation of climate change (Fleming and Tatchell 1995). Correlations between phenology and temperature are strongest for species which pass the winter in the active stages rather than as eggs (Harrington et al. 1990; Harrington et al. 1995), presumably because, although the active stages are far less tolerant of low temperature, they are better able to take advantage of warm winters for development and population build-up.

The aphid monitoring network is now co-ordinated throughout Europe (Harrington et al. 2004). Analyses using the pan-European network and involving 29 pest aphid species suggest that under the Hadley Centre climate change scenario A1FI (Nakicenovic et al. 2000), the phenology of these species will advance on average by 8 days over the next 50 years (Harrington et al. in press). How this affects the status of aphids as pests will depend partly on the extent to which crop phenology advances in parallel with pest phenology. Indications so far are that sowing or planting dates of spring crops in Europe are not advancing because they are more dependent on rainfall than temperature. Winter rainfall is expected to increase in Europe, especially in northern regions.

Due to the inability of trees to disperse rapidly, forests are particularly prone to long-term disturbances caused by herbivores or from pathogens vectored by arthropods. Ayres and Lombardero (2000) reviewed the effects of climate change on forest distribution and health. They point out that there may be feedbacks to climate change due to impacts on water and carbon flux in forest ecosystems that are heavily damaged by herbivores or pathogens. In addition, insect or disease outbreaks in boreal forests could increase the number of forest fires that would further exacerbate climate change. Any major forest disturbance may impact biodiversity, water quality, property value, recreation, and the forest industry in general.

Hódar et al. (2002) and Hódar and Zamora (2004) report evidence that the pine processionary caterpillar (*Thaumetopoea pityocampa*) is increasingly attacking relict population of Scots pine (*Pinus sylvestris nevadensis*) that existed where winter conditions previously were unfavourable for survival and feeding of this pest. Given that this pine has poor regeneration ability, human intervention may be necessary to prevent its elimination from the Mediterranean region. Moving the pine into higher altitudes could provide insurance against losses.

17.3.1.3 *Plant Pathogens*

Long-term time-series data for plant pathogens are rare, owing primarily to the difficulties in monitoring and identifying these microscopic organisms. In cases where such data sets do exist (e.g., the time-series on wheat stem rust mentioned above), changes in management practices that have occurred over the years tend to override climate-related trends. Coordinated efforts are therefore needed to initiate standardized long-term monitoring programmes for pathogens in unmanaged ecosystems in which the confounding effect of anthropogenic disease management is minimized (Scherm and Coakley 2003).

The incidence of the aphid-borne *Barley yellow dwarf virus* (BYDV) in the UK has risen in recent years with the increase in the frequency of mild winters which permit aphid survival, movement and hence virus transmission (Harrington 2003). Problems from BYDV in the UK are likely to become more severe due to (1) changes in cropping patterns (in particular increase in the area of maize); (2) increased survival of a vector species, *Rhopalosiphum maidis*, that prefers maize and requires warm winters; (3) increased prevalence of a BYDV strain transmitted efficiently by this vector species; and (4) increased efficiency of transmission of this and other strains of BVDV in all cereals at higher temperatures. The incidence of the virus is expected to increase most in the west of the UK where milder winters are expected to be accompanied by wetter summers than will occur in the east. Both of these factors aid aphid survival.

Another example of the spread of a vector-borne disease comes from Japan, where an increase in epidemics of oak dieback in the past 10 years appears to be associated with the movement of the insect vector into more northern latitudes and higher altitudes as a result of a warmer climate. The symbiotic ambrosia fungus *Raffaelea* sp., vectored by the ambrosia beetle *Platypus quercivorus*, is implicated in the dieback (Kamata et al. 2002). With the expansion of its range, the vector has encountered *Quercus crispula*, an oak species that did not co-evolve with the fungus. This has led to a mortality of about 40% of the oaks each year. The pattern is consistent with the hypothesis that absence of regulating factors (e.g., natural enemies) in the newly invaded area allows outbreaks to occur for an extended time. The pattern is consistent with the enemy release hypothesis (Colautti et al. 2004).

Apart from being the cause of severe epidemics, introductions of non-indigenous plant pathogens can be problematical as they may enable the rapid evolution of novel plant pathogens via interspecific hybridization when the introduction occurs in areas where related but allopatric species are already present. Such new pathogen hybrids can have a wider host range and behave more aggressively than the two parent species (Brasier 2001). Thus, when one considers the movement of pathogens and their hosts into new geographic regions, one needs to be alert not only to a potential increase in disease severity, but also to the types of pathogens that may occur.

17.3.1.4 *Integrated Impact Assessments*

Integration of impact assessments remains a challenge in global change science and involves a number of different dimensions. Within a crop, growth and yield responses need to be linked with changes in the incidence and severity of pests. A spatial dimension then needs to be added to enable extrapolation to assess regional or industry-wide impacts. Such studies invariably require both environmental and socio-economic measures of impacts.

Since previous syntheses (Teng et al. 1996; Gregory et al. 1999; Sutherst et al. 2000) there has been limited progress in integrating host and pest models with socio-economic models to investigate impacts on regional or industry-wide scales, particularly for plant pathogens and weeds. The following section will therefore focus on recent integrated assessments involving vertebrate and insects pests.

Rats and Plant Hoppers in Rice

In 1998, participants from seven countries were introduced to global change issues in a workshop under the auspices of the Biotrop-GCTE/Impacts Centre for South-East Asia (IC-SEA) (Sutherst et al. 1999). The effects of two key pests on rice yields, the rice field rat (*Rattus argentiventer*) and the brown plant hopper (*Nilaparvata lugens*) in the presence of a coccinellid predator were examined. Participants collaborated to build CLIMEX models for each species and an integrated DYMEX 'RatHopper' crop-pest population model to investigate likely changes in the population dynamics of the species and to explore long-term adaptation options. The CLIMEX model indicated a shift in the potential geographical distribution of the rat as the environment became too hot. Use of the RatHopper model showed the importance of fallow in reducing pest numbers and revealed a danger in trying to increase total yields by inserting another crop cycle each year.

Queensland Fruit Fly

The Queensland fruit fly, *Bactrocera tryoni*, is one of the most important pests of horticulture in Australia. It is excluded from a large area of south-eastern Australia by quarantine restrictions and treatments of local outbreaks. There is concern about the impact of global warming on its potential geographical distribution and resultant regional and industry consequences. The Murrumbidgee Irrigation Area is an important source of citrus exports that requires freedom from endemic fruit fly infestation to meet market specifications. An analysis of the potential risks to the horticultural industries in the region raised doubts about the long-term viability of the current containment program as the pressure from higher fruit fly populations and demographic performance increases at higher temperatures (Sutherst et al. 2000).

17.3.2 Land Use, Land Cover and Biodiversity

Global climate change may increase the rate of loss of ecosystem diversity (Hartley and Jones 2003). With a change of diversity of organisms at one trophic level, it is likely that there will be a resultant change at the next level. Two experimental systems (a long-term field study on heather moorlands and an Ecotron controlled-environment experiment) were used to determine whether plant species richness influences insect herbivores (Hartley et al. 2003). Despite the different scales and different ecological communities, the two systems showed certain similarities in response to environmental change. Site was more important than grazing regime in affecting the number of species that occurred in an insect herbivore community, and there were interaction-specific effects of environmental change, which varied with the specific plant and its insect herbivores as well as with the site. To complicate matters further, indirect factors, including below-ground processes, may ultimately impact on a particular insect-plant interaction in addition to the more obvious above-ground factors.

Disturbances resulting from climate change are apt to exert pressure on ecosystems and result in stresses on the organisms within them. For example, the analysis of aspen tree rings shows that there has been an impact of climate change that is likely to have been related to stresses including attacks by insects and pathogens. As with most crops, simulation models for growth in the net primary productivity of such forests do not currently include the potential impact of pests (Hogg et al. 2002).

17.3.3 Trade and Travel

Between 1940 and 1970, fewer than five non-indigenous plant pathogen species entered the United States per decade but that rate more than tripled during the 1990s. Simultaneously, the import value of floriculture and nursery products into the United States increased more than 17-fold between 1976 and 2000 (USDA-ERS 2002). Most of the recent plant pathogen introductions have been documented or are strongly suspected to have been associated with plant material (Scherm and Coakley 2003). This is a global phenomenon, tapping into new species pools as trade expands to new areas, e.g., eastern Asia (Levine and D'Antonio 2003).

17.4 Adaptation

The IPCC has developed general guidelines for the design of adaptation measures to climate change, and these are applicable to other drivers of environmental change. Responses can be either *autonomous* (part of everyday business) or planned (requiring a new policy) (IPCC 2001b). Adaptive measures have also been classified as behavioral, engineering or administrative/legislative (Parry and Livermore 1999).

Adaptation measures rely on application of innovative approaches or products to prevent or control pests in a changing environment. The attributes of management tools that make them more likely to be available for adaptation to global change in the decades ahead are evaluated against specific objectives using criteria such as effectiveness and constraints (Parry and Carter 1998) or sustainability and robustness (Sutherst et al. 1998). Their performance needs to comply with the concept of 'triple bottom-line' accounting, i.e., social and environmental considerations need to be included in addition to economic values.

Ideally, responses to changes in pest incidence and severity under global change would be proactive rather than reactive. Unfortunately, the Earth's climate system is so complex and non-linear that we can never be sufficiently confident of predicting climate change to avoid surprises. Examples of so-called climate flip-flops (Calvin 1998), changes in regional rainfall (Hennessy et al. 1999) and temporal variation in the correlation of the Southern Oscillation Index (SOI) with tropical rainfall (Cai et al. 2001) illustrate the extent of the uncertainties. Rather than only designing adaptation responses strategically and well ahead of time, there is an additional need to respond quickly to unanticipated environmental changes. This calls for managers to be 'nimble' and respond rapidly to changes as they occur. Such a capability will have to be based on a thorough understanding of the ecology of the target pest or community of species in an ecosystem at each location. The most likely pathway to developing such a capacity is to adopt a knowledge-based, rather than a product-based, approach to pest management (Lewis et al. 1997) with sophisticated decision support systems for our major agricultural enterprises.

17.4.1 Natural Adaptations

Species rely on dispersal, phenotypic plasticity and genetic selection to respond to environmental change. In human-dominated landscapes, pests tend to disperse and be moved by humans more effectively than many less numerous species and so are less likely to be constrained from moving to track changing climates than rarer or more sessile species. Phenotypic plasticity is an important strategy for coping with a variable environment, such as the timing of onset of low temperatures in autumn (Taylor and Spalding 1989). If ecological responses are insufficiently plastic or are too slow to keep pace with the rate of environmental change, there is the potential for micro-evolutionary adaptations that are better able to exploit the new conditions. This has been documented for plants (Geber and Dawson 1993), a plant-associated mosquito (Bradshaw and Holzapfel 2001), and *Drosophila* (Rodriguez-Trelles et al. 1998). In addition, as species move with climate change they may be exposed to a new set of abiotic factors (e.g., soils and topography), as well as a modified community of competitors and predators, which will also exert new selection pressures.

17.4.2 Adaptive Management Options

Without foresight into future technologies, we can only assess the suitability of currently available practices. However, technologies, including those used in agriculture and ecosystem management, are rapidly evolving (Giampietro et al. 1999) and are not predictable. This is a major limitation, as it requires the attributes of existing and new technology to be extrapolated into the uncertain physical and biological environments of the future. While global climate models are able to generate scenarios of climate change, they can not yet be used to make predictions.

Legislative

Legislative or administrative options to adapt to environmental change include strengthening of barriers to entry of non-indigenous species, improved detection procedures for incursions, monitoring of pest abundance and geographical distribution (Baker et al. 2000), as well as enhanced knowledge-management using a hierarchy of information technologies such as expert systems, simulation models, remote sensing and GIS (Sutherst et al. 1996).

Engineering and Behavioral

Preventative measures based on environmental management are robust but depend on ongoing management inputs, which are easily downgraded in times of economic stringency. Selecting for plant species that are tolerant of drought and resistant to pests could be considered 'engineering' to the degree that biotechnology is used for genetic modification. Classic tools of breeding will also be needed to ensure plant and animal adaptability to climate change. Based on the results of an assessment of the effects of future climate change on sugar beet production in Europe, efforts are being made to incorporate appropriate disease tolerance into species that will be used increasingly in northern parts of the growing range (Jones et al. 2003).

Effective responses to ongoing or accelerating invasions by non-indigenous species require a multi-pronged approach that addresses sources, pathways and destinations of potential pests (Baker et al. 2000). The chances of such species leaving their source area can be reduced by attacking the pest populations using biological control agents at their source (Sands et al. 1993), or by strengthening inspection procedures to prevent them from entering the pathway to other countries. Prevention of international trade in horticultural plants with potentially weedy or insect-harbouring attributes (Lok 2001) necessitates a greater understanding by industry. As part of the Montreal process (http://www.mpci.org), the temperate and boreal forestry sector has adopted sustainability protocols that include features such as reductions in pesticide use. This has seen an attitudinal change to pests as well as an interest in issues such as crop species becoming weeds (e.g., wilding pines) and managed forests as sources of weed invasions into adjacent areas.

Biological control using natural enemies can be valuable in adapting to new invasions or threats. Restoration of habitats around agricultural fields can rectify the loss of natural vegetation which shelters generalist predators. Some predators have low mobility and so do not find their way into fields fast enough after each new crop to provide useful contributions to pest management. Provision of artificial shelters for generalist predators can be a useful technique for managing pests in field crops (Halaj et al. 2000).

To address the potential impacts of woody weeds on rangelands effective quarantine procedures need to be implemented to prevent weed spread, establish education programmes to assist in the early detection of new invaders, and develop more effective biological control programmes aimed at vulnerable life-stages of the weeds (Kriticos et al. 1999). Biologically-based adaptation measures have the desirable characteristic of low implementation costs per unit area.

17.4.3 Adaptation of Control Measures in Response to Global Change

Following the processes developed for increasing the sustainability of cities (AtKisson 1999) we need to address three issues in relation to adaptation:

1. Indicators of change are required in order to track pest movements and feed information back to inform the decision-making process. We have addressed this issue in relation to measuring and monitoring impacts.
2. Steps need to be taken to accelerate development and strengthen guidance of the use of new technologies and approaches to pest management. This will include knowledge-based decision support systems that measure outcomes in terms of the 'triple-bottom-line' of environmental, economic and social benefits.
3. Processes have to be implemented to accelerate the adoption of new approaches because global change is accelerating and society needs to fast-track adaptive management responses if it is to keep pace with the changes.

The ever-present risk of researchers finding solutions in isolation from those who are expected to adopt the technology can be averted by pooling the efforts of scientists, policy-makers, managers, advisers, teachers and students to develop adaptation strategies jointly. The use of modular simulation modeling networks as a vehicle for facilitating such activities has been encouraging in both developed and developing countries (Sutherst et al. 2000). It can form the basis of measures to inform the community and ensure its involvement in and ownership of adaptive measures, leading to accelerated adoption. Scenario-planning is another useful tool for generating and evaluating options to enhance sustainability (Schoute et al. 1995). This approach is easier for groups with no formal technical training to follow (Sutherst et al. 1999).

17.4.4 Threats to Sustainability of Adaptation Options

Pesticide Resistance

Synthetic pesticides are used widely to reduce damage to agriculture, and there has been a long history of development of resistant strains of arthropods, plant pathogens and weeds. Loss of susceptibility of pests to pesticides has the potential to reduce the capacity of communities to adapt to global change.

Entomologists concerned with protection of crops (Georghiou 1994) or livestock (Sutherst and Comins 1979) pioneered the development of resistance management strategies, and such strategies are now used widely in all disciplines dealing with pest management (Russell 1999; Vaughn 2003). Sutherst and Comins (1979) used the terms '*saturation*' and '*moderation*' to describe strategies aimed at either intensive control or less aggressive measures designed to reduce selection pressures. Pesticide resistance needs to be managed by avoiding a high-risk 'magic bullet' (*saturation*) approach and adopting multi-pronged measures (*moderation*).

Human Safety and Non-Target Effects

The widespread use of pesticides has had detrimental effects on both humans and animals. The early effects of

DDT on bird life are well known but the replacement chemicals were also associated with significant risks (Marco et al. 1987). Very low concentrations of some agricultural chemicals can mimic the activity of estrogen and thyroid hormones in humans and animals (Colborn et al. 1996). They are referred to as 'endocrine disrupting chemicals' and include organochlorine pesticides and some synthetic pyrethroids and herbicides (Krimsky 2000). Their disruptive effects threaten their availability for adaptation to global change. In the United States, all registered pesticides are under review under the Food Quality Protection Act (Ragsdale 2000) with an initial focus on active ingredients that have high mammalian toxicity, pose a threat to ground water resources, or have shown carcinogenic or teratogenic effects in laboratory animals.

17.5 Vulnerability

The vulnerability of affected natural and managed ecosystems to pests is assessed by combining impacts and adaptation with the adaptive capacity of the affected ecosystem. Regions or industry sectors vulnerable to pests under global change will be those that are unprepared or do not have suitable options to respond to major changes in pest status. Such changes are more likely to occur in regions adjoining endemic areas, where they rely on freedom from infestation for market access. An example is the Murrumbidgee Irrigation Area in south-eastern Australia where the citrus industry is focused on exports but has an ongoing problem with exclusion of the Queensland fruit fly. Under climate change, pest pressure is likely to increase in the temperature-limiting region, making eradication of incursions more difficult (Sutherst et al. 2000).

Tropical rangelands, where invasions with leguminous woody weeds are expected to occur with rising temperatures and concentrations of CO_2, are located mostly in less-developed countries. As such weeds spread into semi-arid rangelands, the low economic value of these lands limits human capacity to undertake adaptation measures. Economic options are restricted to biological control and in some situations, hygiene measures to stop the spread of seed by livestock. As biological control options are often limited by fear of non-target damage (Thomas and Willis 1998; Brimnen and Boland 2003) and by an apparent shortage of suitable agents, there are few options available. The problem is magnified by resource shortages and the absence of government control over animal movements in many developing countries. Indeed, all industry and public health sectors in developing countries are vulnerable to increases in impacts because they do not have the resources or infrastructure to respond effectively.

17.6 Summary and Conclusions

Pests have major effects on both natural and managed ecosystems. Their impacts are expanding as more species are spread around the world and often become an irreversible extra burden on the affected systems. Environmental change creates disturbances and the many pest species involved ensure that there will be some species available to exploit opportunities arising from disruption of native communities or vacant niches. Climatic volatility is a concern and recent predictions of the increasing frequency and intensity of extreme events demand greater attention. Environmental change results in shifts in species' geographical ranges, seasonal phenology, host preferences, population densities and population genetics. To date, results from limited experimental studies have shown a wide range of negative and positive responses by different species to the same environmental changes. This limits our ability to make generalizations about likely responses to global change. The problem is compounded by interactions between species in the same or different trophic levels in communities.

The resources necessary to enable researchers to provide managers with the information needed to adapt to global change include: baseline data on driving variables, indicators of change, strategies and tools to analyze problems and design adaptive management responses, and information delivery systems to accelerate adoption of new technologies or approaches to keep pace with the accelerating rate of change. Among the available management options, biological approaches based on either host resistance or natural enemies tend to be more robust because they have built-in flexibility and, in the most successful cases, avoid the need for extra contributions by human management, which is so often the weakest link.

There is a conundrum where strategic decisions on adaptation need to be made, but they require a sound understanding of the environmental, social and economic consequences. We support evidence-based policy and yet we acknowledge the great uncertainties associated with both the scenarios of environmental change and the responses of ecological systems to these changes. Further, we recommend *nimbleness* in adaptive management responses in order to respond to unexpected changes, and yet that relies on having sufficient understanding of the systems involved to make sound decisions. The two long-standing questions 'How much knowledge is enough?' and 'Is that knowledge attainable given the complexities of natural systems?' still have not been resolved.

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Chapter 18

Greenhouse Gas Mitigation Potential in Agricultural Soils

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18.1 Introduction

Agricultural soils can act as sources and sinks for carbon dioxide and other greenhouse gases. Whether soils act as a sink or source, and the sink/source strength depends critically upon the management of the soil. Agricultural soils emit carbon dioxide (CO_2; through soil and root respiration / decomposition of soil organic matter), nitrous oxide (N_2O; formed during nitrification and denitrification processes) and may either emit or remove (oxidize) methane (CH_4) from the atmosphere. The greenhouse gas mitigation potential for agricultural soils results from reducing these emissions. For CO_2 this entails reducing the CO_2 efflux from the soil or sequestering carbon in the soil. For N_2O, this entails reducing N_2O emissions. For CH_4, this entails reducing CH_4 emissions from soils emitting CH_4 (e.g., rice paddy soils) and maximising the methane oxidation potential of other soils.

18.1.1 Soil Carbon and Carbon Dioxide

Globally, soils contain about 1 500 Pg (1 Pg = 1 Gt = 10^{15} g) of organic carbon to a depth of 1 m (Batjes 1996), which is about three times the amount of carbon in vegetation and twice the amount in the atmosphere (IPCC 2001). The annual fluxes of CO_2 from atmosphere to land (global Net Primary Productivity [NPP]) and land to atmosphere (respiration and fire) are of the order of 60 Pg C yr^{-1} (IPCC 2000b). During the 1990s, fossil fuel combustion and cement production emitted 6.3 ±1.3 Pg C yr^{-1} to the atmosphere, while land-use change emitted 1.6 ±0.8 Pg C yr^{-1} (Schimel et al. 2001; IPCC 2001). Atmospheric C increased at a rate of 3.2 ±0.1 Pg C yr^{-1}, the oceans absorbed 2.3 ±0.8 Pg C yr^{-1} and there was an estimated terrestrial sink of 2.3 ±1.3 Pg C yr^{-1} (Schimel et al. 2001; IPCC 2001).

The amount of carbon in the soil is therefore large compared to gross and net annual fluxes of carbon to and from the terrestrial biosphere. Manipulating the size of the soil carbon pools is at the heart of soil carbon sequestration.

Soil carbon pools are smaller now than they were before human intervention. Historically, soils have lost between 40 and 90 Pg C globally through cultivation and disturbance (Paustian et al. 1998; Houghton et al. 1999; Lal 1999). Soil carbon sequestration can be achieved by increasing the net flux of carbon from the atmosphere to the terrestrial biosphere, by increasing global NPP (thus increasing carbon inputs to the soil), by storing a larger proportion of the carbon from NPP in the longer-term carbon pools in the soil, or by slowing decomposition. For soil carbon sinks, the best options are to increase C stocks in soils that have been depleted in carbon, i.e., agricultural soils and degraded soils (Lal 2004a; Smith 2004a).

Estimates of the potential for additional soil carbon sequestration vary widely. The most recent global estimate is that of Lal (2004a) of 0.9 ±0.3 Pg C yr^{-1}. Over 50 years, this level of C sequestration would restore a large part of the carbon lost from soils historically. Cropland soils can be a large source of carbon dioxide (e.g., Janssens et al. 2003). There is significant potential to reduce the efflux of carbon from agricultural soils, and to sequester carbon in them. However, soil carbon sequestration rates have a limited duration and cannot be maintained indefinitely. Mitigation options for agricultural soil carbon are given in Table 18.1.

18.1.2 Trade-Offs between GHGs in Agriculture

In addition to carbon dioxide, nitrous oxide and methane are important greenhouse gases emitted from agriculture. Nitrous oxide is formed primarily from nitrification (the conversion of ammonium to nitrate, via nitrite) and denitrification (the conversion of nitrate, ultimately to N_2 gas). N_2O is a by-product of nitrification and an intermediate product during denitrification. N_2O fluxes from agricultural soils (0.53 Pg C equivalents yr^{-1}) account for more than 50% of the global anthropogenic N_2O flux (Robertson 2004). Options for N_2O mitigation are given in Table 18.2.

The majority (52%) of the methane flux from agriculture arises from enteric fermentation (microbial fermentation in the rumen of ruminants), with biomass burning (19%) and animal waste treatment (8%) accounting for other significant proportions (Robertson 2004). Most aerobic soils actually oxidize CH_4 but there is good evidence that the capacity of soils as a sink for methane is reduced upon cultivation. The only significant soil source of methane in agriculture arises from rice cultivation

Table 18.1. Soil carbon sequestration measures in agricultural land (after Smith 2004c)

Cropland	Grazing land
Zero/reduced tillage Set-aside/conservation reserve program Convert to permanent crops Convert to deep-rooting crops Improve efficiency of animal manure use Improve efficiency of crop residue use Agricultural use of sewage sludge Application of compost to land Rotational changes Fertilizer use Irrigation Bioenergy crops Extensification/de-intensification of farming Organic farming (a combination of many different individual practices) Convert cropland to grassland Management to reduce wind and water erosion	Improve efficiency of animal manure use Improve efficiency of crop residue use Improve livestock management to reduce soil disturbance Improve livestock management to maximize manure C returns Agricultural use of sewage sludge Convert to deeper-rooting species Application of compost to land Fertilizer use Irrigation Extensification/de-intensification of farming Improved management to reduce wind and water erosion

Table 18.2. Nitrous oxide mitigation options for agricultural soils (after Smith et al. 2004e)

Practices	
Inorganic fertilizer	▪ Suitable type and characteristics e.g. – ammonium providing fertilizer vs. nitrate fertilizer – slow-release – inhibitors ▪ Application techniques – synchronisation/timing (e.g., split-application to coincide with crop demand) – placement, burial may reduce flux ▪ Amount/rate of application, appropriate fertilizer recommendations required
Organic fertilizer	▪ Type – farm yard manure, (flux dependent on degree of maturity/degradation, moisture content) – liquid fertilizer/slurry (give higher fluxes than dried material; avoid spreading with mineral fertilizer) – industrial waste – household waste – biogas residue – fermented manure ▪ Timing (less critical than inorganic) ▪ Application techniques ▪ Storage, processing, and handling (temperature, duration, capacity, cover, etc.) ▪ Amount/rate of application (apply at recommended rate to coincide with crop demand)
Biological N fixation	▪ Avoid mono cropping, flux dependent on legumes/grass mixture ratio and is mostly after ploughing (net effect is unknown)
Crop residue	▪ (Important for C sequestration) ▪ Quality and size (C : N ratio, total N) ▪ Quantity (weight) ▪ Application/incorporation techniques (note the interaction with tillage; priming effect on soil N_2O flux mainly with incorporation) avoid wet conditions
Farming system and management	▪ Extensive cropping may be better than intensive – further research needed for to assess this difference and the effect of the arable/livestock ratio. Also compare to intensive areas with other land use on spare land
Tillage	▪ Important for C sequestration but interacts with soil physical conditions ▪ Ploughing or deep ploughing may reduce trace gas emissions but decrease carbon sequestration ▪ Conservation (reduced) tillage may be intermediate but more information required
Crop rotation	▪ Catch crops reduce bare soils (possible link to BNF) ▪ Amelioration crops (crop type i.e. deep rooting or shallow rooting)
Water management	▪ Drainage useful but irrigation should be avoided, flooding water buffers may have an effect
Compaction status	▪ Appropriate timing and size of machinery required ▪ Manage grazing to avoid poaching

(0.25 Pg C equivalents yr^{-1}), which accounts for 22% of agricultural emissions or 12% of total anthropogenic fluxes (Robertson 2004). Mitigation of CH_4 fluxes from agricultural soils needs to focus almost entirely on this rice land flux. Rice crop management to reduce CH_4 emissions includes yield improvement with well-managed, high yield rice crops have significantly lower CH_4 emissions due to more C being allocated to the grain than to the rhizosphere where it can undergo methanogenesis. Other mitigation options in rice include residue management and irrigation scheduling (Robertson 2004). Methane mitigation is not discussed further in this chapter.

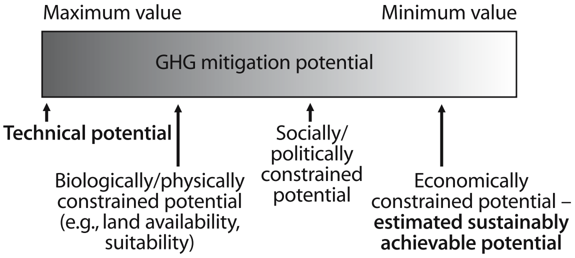

Fig. 18.1. How different constraints reduce the GHG mitigation potential from its theoretical biological maximum to realistically achievable potentials that are much lower (adapted from Smith 2004a)

Robertson (2004) emphasises the needs for a systems approach for assessing GHG mitigation potential in agriculture. For example, increasing soil carbon stocks in the soil through reduced tillage can lead to anaerobic zones in some soils and thereby increase N_2O emissions (MacKenzie et al. 1998; Smith et al. 2001; Six et al. 2004). Similarly, management to reduce CH_4 emissions in paddy rice fields might increase N_2O emissions. Trade-offs between the GHGs are complex (Robertson et al. 2000), but should always be considered.

18.2 What Is Meant by GHG Mitigation Potential?

Estimation of mitigation potential is often confounded by the choice of constraints. Some authors quote biological potentials (Metting et al. 1999), others quote potentials as limited by available land or resources (Smith et al. 2000), and others also consider economic and social constraints (Cannell 2003; Freibauer et al. 2004). Smith (2004a) provided a figure showing how these mitigation potential estimates differ and how the potential is reduced by a number of constraints (Fig. 18.1).

Table 18.3. Carbon sequestration potentials limited only by availability of land, biological resources and land-suitability, and those estimated to be achievable by 2012 (Smith 2004c; after Freibauer et al. 2004)

Practice	Soil carbon sequestration potential ($t\ C\ ha^{-1}\ yr^{-1}$)	Estimated uncertainty	Total soil carbon sequestration potential for EU15 ($Mt\ C\ yr^{-1}$)[a]	Realistic soil carbon sequestration potential for EU15 ($Mt\ C\ yr^{-1}$) by 2012
Zero-tillage	0.38 (0.29)*	>50%	24.4	2.4
Reduced tillage	<0.38	≫50%	<24.4	<2.4
Set-aside	<0.38	≫50%	2.4 (maximum)	0
Permanent crops	0.62	≫50%	0?	0?
Deep-rooting crops	0.62	≫50%	0?	0?
Animal manure	0.38 (1.47)*	≫50%	23.7	?
Cereal straw	0.69 (0.21)*	≫50%	5.5	?
Sewage sludge	0.26	≫50%	2.1	?
Composting	0.38	≫50%	3	3?
Improved rotations	>0	Very high	0?	0?
Fertilization	0	Very high	0	0
Irrigation	0	Very high	0	0
Bioenergy crops	0.62	≫50%	4.5	0.9
Extensification	0.54	≫50%	11	?
Organic farming	0–0.54	≫50%	3.9	3.9
Convert cropland to grassland	1.2–1.69 (1.92)*	≫50%	8.7–12.3	0
Convert cropland to woodland	0.62	≫50%	4.5	4.5 (maximum)

[a] Carbon sequestration potentials limited only by availability of land, biological resources and land-suitability. All estimates based on extrapolation from Smith et al. (2000) except those marked *, where the figure in brackets is derived from Vleeshouwers and Verhagen (2002). For full list of assumptions, limitations and sources, see Freibauer et al. (2003).

An analysis of the estimates presented in Freibauer et al. (2004) and the assumptions used by Cannell (2003) suggest that the realistic sustainable (or conservative) achievable potential of GHG mitigation (taking into account limitations in land use, resources, economics, and social and political factors) may be about 10–20% of the biological potential (Table 18.3).

Although this value is derived predominantly from expert judgment, it may be useful in assessing how different estimates of GHG mitigation potential can be compared and how they might realistically contribute to GHG stabilization. More robust methods to develop estimates of socioeconomic potential are being developed, e.g., McCarl and Schneider (2001).

In a study of European agricultural GHG mitigation potential, a range of estimates of carbon sequestration potential were compared (Smith et al. 2004e). The results (Fig. 18.2) show that by including more constraints in the calculation, the estimated mitigation potential is drastically reduced.

Estimates on the left of the graph are for biological potential while those on the right extrapolate from current trends. These findings show that, despite a high biological potential for carbon sequestration in European agricultural soils, lack of policy incentives to implement carbon sequestration measures means that virtually none of this potential will be realized by the end of the first Kyoto commitment period in 2012.

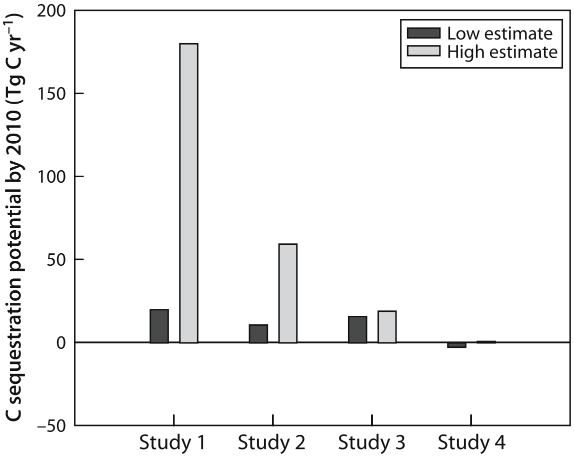

Fig. 18.2. Estimates of cropland soil carbon sequestration potential in EU-15 from previous studies and from this study. *Study 1* is from Vleeshouwers and Verhagen (2002) with the low estimate for straw incorporation and the high figure for conversion of all cropland to grassland. *Study 2* is from Smith et al. (2000a) with figures scaled from geographical Europe (including Baltic States but excluding Russia) to EU-15 as per Smith et al. (1997). The low estimate is from the combined land management scenario with extensification of surplus arable land and straw incorporation; the high estimate is for the combined "optimal" scenario (see Smith et al. 2000 for further details). *Study 3* is from Freibauer et al. (2004) with values assessed for realistically achievable potential by 2010 (about 1/5 of the estimated biological potential). *Study 4* uses figures based on measured trends 1990 to 2000 and extrapolations to 2010 (Smith et al. 2004e)

18.3 Regional Case Studies

Greenhouse gas mitigation potential can be estimated at a range of scales, from the region to the continent to the globe. In this section, we provide some examples of regional estimates of carbon sequestration.

18.3.1 Sustainable Soil Management in the Moscow Region to Enhance Soil Carbon

In the Moscow region, the soil-weather C static model, which is based on an equilibrium approach to predict changes in soil organic carbon (SOC) as a function of climate and changes in management practices, was used for the zone of podzoluvisols of the Russian Federation (Shevtsova et al. 2003).

Analysis of different initial SOC stocks, crop rotations and fertilization rates has revealed that the most important resource for preventing SOM decrease in the long-term for intensive agricultural systems is an increase in the percentage of grasses used in crop rotations at the expense of row crops. This is especially true on coarse-textured soils. Farm-yard manure (FYM) application has a smaller potential of increasing soil sustainability while changes in the rates of mineral N fertilization are the least important (Romanenkov et al. 2001).

Simulation of the influence of climate change using the IPCC-SRES A1FI scenario (IPCC 2000a) to 2050 (as implemented by the HadCM3 climate model) will increase soil C gain as a result of a net increase in the amount of residue returned to the soil (higher plant productivity with higher temperature), and a reduced rate of C loss with declining soil moisture, resulting in slower decomposition of residues and SOC. These regional studies in the Moscow region are a good example of how GHG mitigation studies can advise policy requirements as they show, for most of the regions, that FYM application rates can be decreased and percentage of perennials in crop rotation in 2050 can be reduced by 10–20% to sustain current SOC level in arable soils (Sirotenko et al. in press). Increases of SOC of up to 30% are possible with increased addition of FYM, but the necessary application rates are both economically unprofitable and ecologically unsafe. Change in the ratio of perennial grasses to row crops in rotations is a more realistic measure.

Similar results were found using the CANDY model (Franko 1997; Franko and Schenk 2001) for the whole territory of Russia. The average increase of SOC storage in arable soils from 1990 to 2070 for the business as usual scenario was about 0.09 kg m^{-2} ranging from a decrease of 0.4 kg m^{-2} to an increase of 1.8 kg m^{-2} (Fig. 18.3). The majority of the arable land (62%) was classified as invariant (±0.1 kg m^{-2}).

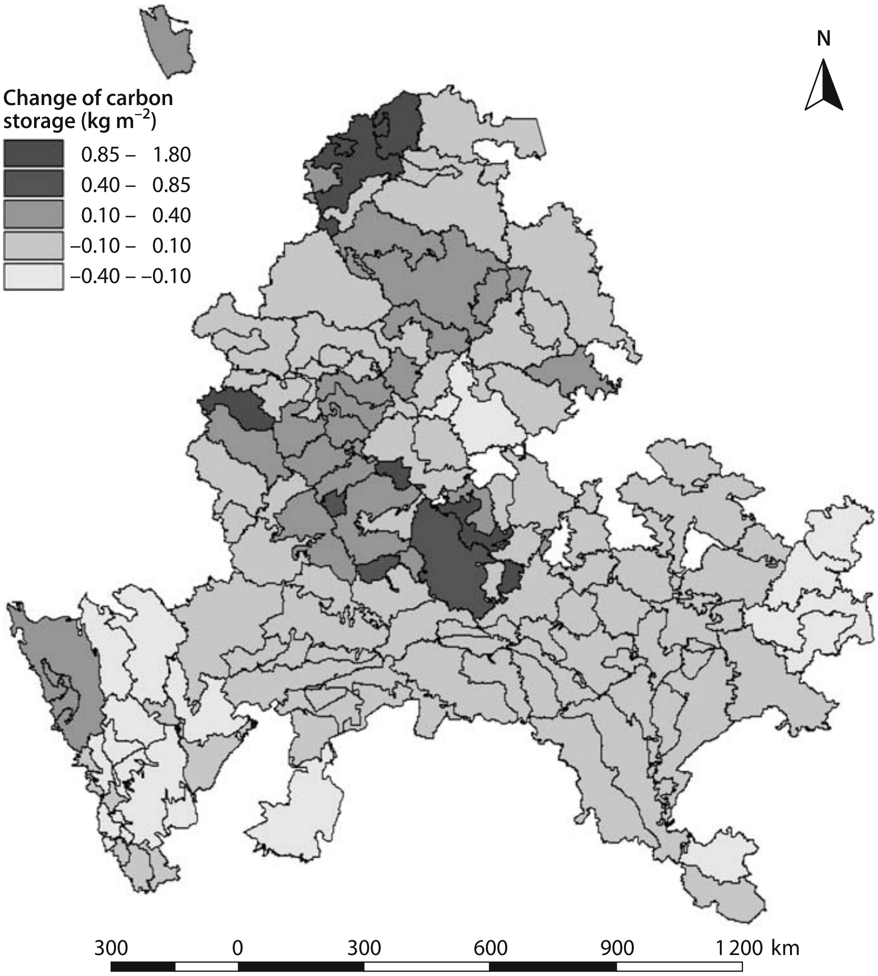

Fig. 18.3. Change of carbon storage in Russian cropland soils (1990 to 2070) assuming no land-use change and the SRES B1 climate change scenario

18.3.2 Soil Carbon Sequestration Potential in the US

Lal and colleagues estimated that total C sequestration potential in the soils of the U.S. is 144 to 432 Tg C yr^{-1} or an average of 288 Tg C yr^{-1} (Table 18.4). Of the total potential, 25% is from croplands, 22% from forest lands, 14% from grazing lands, 15% from land restoration, 17% from land conversion and 7% from improving other lands. In comparison, CO_2 emissions from agricultural activities in the U.S. are 43 Tg C yr^{-1}, and the hidden, additional carbon costs of adopting recommended management practices (e.g., increased fossil fuel use) are 27 to 32 Tg C yr^{-1} (Lal et al. 2003).

A model-based assessment of soil C sequestration potential for US agriculture was conducted by Sperow et al. (2003). To represent regional differences in sequestration potential, soil, climate and land-use/management attributes were broken out for approximately 240 major ecoregions in the country. To assess potentials, scenarios entailing adoption of 'best management practices' for C sequestration were designed. These included conversion of all highly erodible annual cropland to conservation set aside, eliminating summer fallow in semi-arid regions, adding winter cover crops to annual crop rotations in humid climates and adopting conservation tillage practices on annual cropland. Potential sequestration rates totalled about 100 Tg C yr^{-1}, compared to current (1990s) estimated rates of C accumulation of around 10–15 Tg C yr^{-1}. Potential increases in C storage above baseline rates come from adoption of no-till (47 Tg C yr^{-1}), use of cover crops (22 Tg C yr^{-1}), set-asides (11 Tg C yr^{-1}) and elimination of summer fallow (3 Tg C yr^{-1}).

Table 18.4. Soil carbon sequestration potential in the U.S. (adapted from Lal et al. 2003)

Strategy	Total potential (Tg C yr^{-1})
1. Land use conversion	21 – 77
2. Land restoration	25 – 60
3. Cropland	45 – 98
4. Grazing land	13 – 70
5. Forest land	25 – 102
6. Other land uses in forestry	15 – 25
Total	144 – 432

18.4 Carbon Sequestration in the Future

Smith (2004b) recently calculated how future carbon emissions and CO_2 stabilization targets might influence the relevance of soil carbon sequestration as a GHG mitigation measure.

The future trajectory of carbon emissions over the next century depends upon many factors. The IPCC recently developed a range of standard reference emission scenarios (SRES) to provide estimates of possible emissions under a range of different possible futures (IPCC 2000a). These possible futures depend upon the degree to which greenhouse gas mitigation policies become global and upon whether environmental or economic concerns take precedence over the next century.

Among the A1 family of scenarios (global – free market), a number of possible emissions trajectories exist depending upon whether the energy sector remains fossil fuel intensive (A1FI), whether the rapid introduction of new energy technologies allows a move away from carbon intensive energy sources (A1T) or whether there is a mix of fossil fuel/alternative energy sources (A1B).

In all of these scenarios, the global population will grow, the population will become wealthier and per-capita energy demand will increase over the next century (IPCC 2000a). The extent to which these changes will occur differs between different scenarios, with some showing larger increases than others, but in all of them, these trends are observed. For each of the scenarios carbon emission trajectories have been determined (IPCC 2000a). Annual carbon emissions (Pg C yr^{-1}) by 2100 would be A1FI ~ 30, A1B ~ 17, A1T ~ 7, A2 ~ 28, B1 ~ 6, B2 ~ 18.

Emissions trajectories can also be calculated for a range of atmospheric CO_2 stabilization targets (e.g., 450, 550, 650, 750 ppm). For each stabilization target, the allowed carbon emission trajectories, which cannot be exceeded if the target is to be reached, can be calculated. The difference between the allowed emission trajectory for stabilization at a given target concentration, and the emissions associated with the estimated global energy demand is the carbon emission gap. For a stabilization target of 550 ppm, carbon emission gaps for each scenario by 2100 (Pg C yr^{-1}) are A1FI = 25, A1B = 12, A1T = 2, A2 = 22, B1 = 1, B2 = 13 (IPCC 2001).

The current annual emission of CO_2-carbon to the atmosphere is 6.3 ±1.3 Pg C yr^{-1}. Carbon emission gaps by 2100 could be as high as 25 Pg C yr^{-1} meaning that the carbon emission problem could be up to 4 times greater than at present. The maximum annual global C sequestration potential for all soils (mostly agricultural) is 0.9 ±0.3 Pg C yr^{-1} meaning that even if these rates could be maintained until 2100, soil carbon sequestration would contribute a maximum of 2–5% towards reducing the carbon emission gap under the highest emission scenarios. When we also consider the limited duration of carbon sequestration options in removing carbon from the atmosphere, we see that carbon sequestration could play only a minor role in closing the emission gap by 2100. It is clear from these figures that if we wish to stabilize atmospheric CO_2 concentrations by 2100, the increased global population and its increased energy demand can only be supported if there is a large-scale switch to non-carbon emitting technologies for producing energy.

Given that soil carbon sequestration can play only a minor role in closing the carbon emission gap by 2100, is there any role for carbon sequestration in climate mitigation in the future? The answer is yes. If atmospheric CO_2 levels are to be stabilized at reasonable concentrations by 2100 (e.g., 450–650 ppm), drastic reductions in emissions are required over the next 20–30 years (IPCC 2000a). During this critical period, all measures to reduce net carbon emissions to the atmosphere would play an important role – there will be no single solution (IPCC 2000a). Given that carbon sequestration is likely to be most effective in its first 20 years of implementation, it should form a central role in any portfolio of measures to reduce atmospheric CO_2 concentrations over the next 20–30 years while new energy technologies are developed and implemented (Smith 2004b).

18.5 Win-Win Strategies for Greenhouse Gas Mitigation by Agricultural Soils

Soil carbon sequestration is a process under the control of human management and, as such, the social dimension needs to be considered when implementing soil carbon sequestration practices. Since there will be increasing competition for limited land resources in the coming century, soil carbon sequestration cannot be viewed in isolation from other environmental and social needs. The IPCC (2001) have noted that global, regional and local environmental issues such as climate change, loss of biodiversity, desertification, stratospheric ozone depletion, regional acid deposition and local air quality are inextricably linked. Soil carbon sequestration measures clearly belong in this list. The importance of integrated approaches to sustainable environmental management is becoming ever clearer.

In any scenario, there will be winners and losers. The key to increasing soil carbon sequestration, as part of wider programmes to enhance sustainability, is to maximise the number of winners and minimise the number of losers. One possibility for improving the social/cultural acceptability of soil carbon sequestration measures would be to include compensation costs for losers when costing implementation strategies. By far the best option however, is to identify win-win measures (Lal 2004a), i.e., those which increase carbon stocks while at the same time improving other aspects of the environment, e.g., improved soil fertility, decreased erosion, or greater profitability by improved yield of agricultural or forestry products. There are a number of management practices available that could be implemented to protect and enhance existing C sinks now, and in the future, i.e., a no regrets policy. Smith and Powlson (2003) developed these arguments for soil sustainability, but the no regrets policy option is equally applicable to soil carbon sequestration. Since such practices are consistent with, and may even be encouraged by, many current international agreements and conventions, their rapid adoption should be encouraged as widely as possible.

18.6 Future Challenges

18.6.1 Improving Carbon Sequestration

The soil carbon sequestration strategy is the common link between three U.N. Framework Conventions: Climate Change, Biodiversity and Desertification Control. Soil C sequestration could potentially reduce the rate of enrichment of atmospheric CO_2 by 0.6 to 1.2 Pg C yr^{-1} over about 50 years, while enhancing biodiversity and controlling desertification (Lal 2004b). Restoration of degraded/desertified soils and ecosystems is an important ancillary benefit of soil C sequestration.

Of all the ancillary benefits, the impact of soil C sequestration in advancing the global food security can neither be ignored nor over-emphasized. Severe soil degradation is a common problem among all regions threatened by food insecurity including sub-Saharan Africa, Central and South Asia, Andean region, the Caribbean etc. The soil C pool in these regions has been strongly depleted because of the extractive agricultural practices such as complete residue removal for fodder and fuel, uncontrolled and excessive grazing, nutrient mining caused by low external input of chemical fertilizers and organic amendments etc. Increasing the soil C pool is necessary to improving its quality and enhancing productivity of crops, pastures and tree plantations grown on them. The soil C pool of many soils of South Asia and sub-Saharan Africa is as low as 0.1 to 0.2%, in contrast to the critical limit of the soil C concentration of 1.1% for maintenance of an adequate level of soil quality (Aune and Lal 1998). The entry point for breaking the vicious cycle of: degraded soils-depleted soil C pool-low crop yields-poverty-hunger-further degraded soils, is through adopting land-use and management systems which restore soil C pools (Lal 2004b). Lal (2004b) argues that because of the beneficial role of soil organic matter content and soil fertility, there is a very close link between soil C sequestration and the global food security. Indeed, soil C sequestration is an important ancillary benefit of the inevitable necessity of enhancing soil quality for feeding the global population of 6 billion in 2000, which is expected to reach 7.5 billion by 2020 and 9.4 billion by 2050.

18.6.2 Monitoring Soil Carbon Sequestration

Since there is a significant role for carbon sequestration in climate mitigation in the next 20–30 years, it will be essential to accurately monitor the amounts of carbon sequestered in order to estimate its role in closing the carbon emission gap. Signatory nations to the United Nations Framework Convention on Climate Change (UNFCCC) are required to report detailed inventories of greenhouse gas emissions due to Forestry and Land-Use Change, while Article 3.4 of the Kyoto Protocol lays the foundations for inclusion of human-induced changes in fluxes of C from agricultural soils and Land-Use Change and forestry in Annex I countries' commitments. Under Article 3.4, parties electing to include cropland management, grazing land management and re-vegetation need to account for changes in these soil carbon sinks and sources on a net-net basis, comparing the net flux of carbon from a given activity during the commitment period with the equivalent net flux of carbon in the baseline year. Sinks and sources of carbon must be accounted for 'taking into account uncertainties, transparency in reporting, verifiability'. Table 18.5 summarises measurement methods for assessing losses or accumulation of carbon on land (compiled from IPCC 2000b).

There are methodological, and other issues, such as cost, associated with each of the assessment methods described in Table 18.5 (Smith 2004d). For example, levels of soil sampling adequate to represent spatial variation, overcome resolution problems (detectable levels of change) and satisfy verification requirements could be extremely costly, depending on the scale and design of C sequestration projects. To achieve the highest levels of certainty, any chosen method (such as stock changes) would need to be backed up by a second independent assessment method such as flux methods, or models. However, the IPCC currently consider that flux methods are not sufficiently reliable to be used as a primary estimation method, and in addition, flux measurement is expensive and it is difficult to factor out the individual contributions of soil, roots and above-ground vegetation. Further, with any measurement system, it is very difficult to demonstrate that changes in carbon stocks are directly due to human induced activity rather than other causes such as nitrogen deposition or carbon dioxide fertilization – although models could have a role to play in this regard.

At its most stringent, verifiability under Kyoto activities would require the sampling of each geo-referenced piece of land subject to an Article 3.4 activity at the beginning and end of a commitment period, using a sampling regime that gives adequate statistical power. Soil and vegetation samples would be archived and the data from each piece of land aggregated to produce a national figure. Separate methods would be required to deliver a second set of independent verification data (Smith 2004d). Such an undertaking at the national level would likely be prohibitively expensive. At its least stringent, verifiability would entail

Table 18.5. Measurement methods for assessing losses or accumu-lations of carbon on land. Compiled from information in IPCC (2000b) after Smith (2004d)

Stock change measurements methods	Vegetation inventory Stemwood volume – forest inventory Total tree biomass – allometry Wood products – models of wood products Soil and litter Woody debris – volume and mass measured Litter – sampling and carbon analysis – highly spatially variable Mineral soil – sampling and carbon analysis – highly spatially variable (*Sampling strategy, methods and sampling depth all need to be considered*)
Flux measurement methods	Chambers, eddy covariance – for scales less 1 km^2 Tall towers, balloons for convective boundary layer budgeting – landscape, regional scale Flask measurements and flux measurements from aircraft; coupled with inversion analysis – continental scale
Remote sensing to determine geographic extent and change	Current resolution (NOAA-AVHRR) is 1 km^2 but 30 m possible soon Geographic extent possible, vegetation type possible, residue over, tillage, and perhaps soil organic carbon and moisture content of bare soil will become possible in near future
Models	To be used in combination with the above methods

the reporting of areas under a given practice (without georeferencing) and the use of default values for a carbon stock change for each practice, to infer a change for all areas under that practice. A less stringent definition of verifiability would allow simple methods, such as those derived from IPCC default values for CO_2 fluxes from soil, to be used for estimating changes in soil carbon. These may enable low-level verifiability to be achieved by most parties by the beginning of the first commitment period (2008–2012).

The need to provide information on uncertainty in carbon sequestration estimates presents further challenges, not least given that IPCC (2000b) recommended the use of models in combination with direct sampling methods. For example, consider the use of a dynamic modeling approach for carbon sequestration estimates. Such models are usually tested against data sets of long-term changes in SOC, but many data sets have only mean SOC values available at each sample date, with no estimates of error about the mean. Falloon and Smith (2003) showed that when using data sets that do not include estimates of error about the mean, it is not possible to reduce the error (root mean squared error) between modeled and measured values below 6.8–8.5%, even with site-specific model calibration. Using error as an indicator of the certainty that can be attached to model projections, a significant reduction in uncertainty would be needed for Kyoto Protocol accounting. This could be achieved by better replication of soil measurements at benchmark sites, which would allow model error to be separated from measurement error. Thus more comprehensive model testing could be completed, and more certainty could be attached to model projections. This would be a practical option for benchmark testing of models at a small number of global sites, but would be prohibitively expensive to implement were it needed for more routine monitoring assessments at a large number of sites. At the national scale, information on uncertainty is even scarcer (Smith 2004d).

The challenges for the future lie in developing robust, transparent carbon accounting and verification systems which combine models with a variety of direct and indirect measurement techniques which are repeatable and can be performed quickly and cheaply, allowing for projections to be verified by two independent data sets where possible. Collection of information to contribute to uncertainty estimates in these assessments is crucial, and replication of soil measurements at global benchmark sites is an example of how this might be achieved. Modeling techniques which can separate the influence of human-induced changes in activity on changes in carbon stocks from changes driven by other causes will help contribute to these aims. These issues should be met with urgency if carbon sequestration is to play the significant role it deserves in climate mitigation in the next 20–30 years.

18.7 Summary and Conclusions

There is considerable biological potential to reduce greenhouse gas emissions from agricultural soils but many factors prevent the full biological potential being realized. When considering greenhouse gas mitigation, it is important to consider all of the greenhouse gases together as a management practice suitable for reducing one gas may increase emissions of another. Successful greenhouse gas mitigation options for agricultural soils will likely be those that provide other economic and environmental benefits and win-win strategies should be targeted. In the long term, soil-based greenhouse gas mitigation options (including carbon sequestration) can play only a small role in reducing the gap between projected emissions and the reduction in emissions necessary to achieve atmospheric CO_2 stabilization. Nevertheless, since it is critical to reduce greenhouse gas emissions over the next 20–30 years to achieve CO_2 stabilization within a century, and since there is no single solution, soil-based greenhouse gas mitigation options should form part of a broad portfolio of measures aimed at reducing greenhouse gas emissions.

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Chapter 19

Carbon and Water Tradeoffs in Conversions to Forests and Shrublands

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19.1 Introduction

Carbon sequestration programs on land and in the oceans are gaining attention globally as a means to offset increasing fossil fuel emissions and atmospheric carbon dioxide concentrations (e.g., DeLucia et al. 1999; Caldeira and Duffy 2000; Schimel et al. 2000; Pacala et al. 2001; Hoffert et al. 2002; Jackson et al. 2002; Hungate et al. 2003; McNeil et al. 2003). Many industrialized nations now have national plans to foster land-based sequestration; Australia's Plantations 2020 program is one example of such a national effort (Polglase et al. 2000). Ocean based sequestration, particularly deep ocean pumping of CO_2 and iron fertilization, is also receiving considerable attention, although it remains even more controversial than land-based programs (e.g., Chisholm et al. 2001; Lawrence 2002; Buesseler and Boyd 2003; Tsuda et al. 2003). Despite uncertainties about the size and sustainability of sinks and markets, programs for emissions trading and carbon credits are underway, including the Chicago Climate Exchange and the European Union Greenhouse Gas Emission Trading Scheme.

On land, many biological sequestration programs emphasize storing carbon in soil organic matter in agricultural fields, in woody encroached sites, and in the soils and wood of plantations. Land-based sequestration in agricultural soils restores all or part of the soil organic carbon (SOC) lost with plowing and intensive agriculture (Gebhart et al. 1994; Lal et al. 1999). No-till and low-till management are additional approaches proposed for increasing soil organic carbon in croplands.

For plantations, the most controversial factors for carbon sequestration and management include the feasibility and permanence of the carbon sequestered, the scale of management needed to offset anthropogenic emissions, and the accompanying biogeochemical changes that would occur. As an example, a carbon sequestration rate of 3 000 kg C ha^{-1} annually in plantations would require an area the size of Texas or Pakistan to offset 0.2 Pg C yr^{-1} of emissions; such a rough calculation ignores economic and biophysical limitations to storage and downstream losses of carbon as the wood is processed. A more complete evaluation of the feasibility of carbon storage by vegetation management, both scientifically and economically, is needed, including a more complete biogeochemical accounting of the consequences. The biogeochemical interaction that we examine in this chapter is water availability; other key interactions, such as with nitrogen, are beyond the scope of this chapter (e.g., Vejre et al. 2001; Dalal et al. 2003).

Here we will examine some of the potential benefits of biological sequestration programs on land, some of the uncertainties surrounding them, and some unintentional consequences if they are initiated broadly. We will also address a related land-cover change, woody plant encroachment, which has important consequences for carbon and water cycling. Woody plant encroachment differs from afforestation and abrupt land-cover changes because it occurs over many decades. However, its global extent, potential for carbon sequestration, and similarities to afforestation make it important to address. For these land cover and land-use changes we will estimate potential carbon sequestration rates, explore key biophysical interactions, and discuss examples of other biogeochemical and hydrological changes that may occur. For example, plantations may be the most beneficial environmentally when they are used to ameliorate groundwater upwelling, but they may also decrease water yield (defined as the amount of water from a unit area of watershed) (Herron et al. 2002; Farley et al. 2005). Our long-term goal is to identify these biogeochemical and hydrological costs and benefits that accompany sequestration scenarios.

19.2 Afforestation

19.2.1 Afforestation: Carbon Storage Potential

For purposes of this chapter, afforestation is defined as the conversion of rangelands and agricultural lands to tree plantations. Forest plantations grown on rangelands or agricultural lands have large sequestration potentials because carbon can be stored rapidly in biomass pools that are large, have relatively slow turnover times compared to the previous vegetation, and have wider carbon to nutrient ratios (e.g., Paul et al. 2002; Halliday et al.

2003). Depending on land-use history, plantations can also increase or decrease carbon storage in the soil (e.g., Post and Kwon 2000; Guo and Gifford 2002; Farley et al. 2004). Summary data across plantations for total carbon storage in soil and wood reveal an average rate of C storage of ~3 600 kg C ha^{-1} yr^{-1} (e.g., Hamilton et al. 2002), an order of magnitude larger than that in agricultural soils (Post and Kwon 2000). Based on this coarse estimated rate of carbon storage, ~280 million ha of plantations would be needed globally to reach a target of 1 Pg C yr^{-1}, approximately one-sixth of global carbon emissions in fossil fuels.

Sequestration rates a little higher than 3 600 kg C ha^{-1} yr^{-1} are possible in some locations and in the short term, but significantly higher rates are unlikely over large areas (Jackson and Schlesinger 2004). Moreover, back-of-the-envelope estimates such as the one described above do not address issues such as permanence of carbon storage and leakage, defined as activities shifted to locations outside of a sequestration program that counteract some of its carbon benefits (e.g., Murray et al. 2004). One alternative that acknowledges these uncertainties is carbon "rental" payments, where landowners contract to store carbon for specific periods of time (Lewandrowski et al. 2004).

Additional costs also need to be included to estimate the technical and economic potentials of carbon storage, including site preparation and planting, potential carbon losses from disturbance (e.g., storms, pests, and fires), and post-harvest losses in timber use and processing (Jackson and Schlesinger 2004; Murray et al. 2004). Carbon stored in the soil or wood must be protected from plowing, fire, storm damage, and decomposition to keep the carbon from returning to the atmosphere. If long-term uses for the wood are not found, some of the plantation carbon will almost certainly return to the atmosphere after harvesting through uses such as burning for fuel or pulp and paper supply. Economic competition for land use must also be considered. Recent economic models for U.S. agriculture and forestry suggest that C prices would need to be ~U.S.$125 to $400 per metric ton C equivalents for potential sequestration in plantations to approach 0.2 Pg C yr^{-1} (McCarl and Schneider 2001; Lewandrowski et al. 2004).

19.2.2 Afforestation: Evapotranspiration and Water Yield

National policies promoting afforestation can lead to considerable carbon storage for decades, but the amount stored, the economic subsidies needed, and the environmental changes that would result require careful evaluation (e.g., McCarl and Schneider 2001). If economic incentives are provided to convert agricultural or range lands to plantations, what other social, economic, or biogeochemical changes might occur?

To provide a concrete example of such "ancillary" changes with afforestation, we examine changes in water yield. We explore the evidence for this interaction at a range of scales, including long-term catchment measurements and potential atmospheric feedbacks operating over large areas. The outcomes of those feedbacks depend on the initial land use, climate, and location of afforestation in complex but predictable ways.

Large changes in evapotranspiration (ET) and water yield are common with shifts between herbaceous and woody vegetation (Bosch and Hewlett 1982; Zhang et al. 2001; Brown et al. 2005; Farley et al. 2005). The effects of deforestation on water balance have been examined extensively at a range of scales that include eddy covariance measurements of canopy fluxes, multi-year catchment manipulations, and general circulation models examining regional mass and energy fluxes (e.g., Bosch and Hewlett 1982; Rannik et al. 2002; Werth and Avissar 2002). As just one example, Grace et al. (1998) found that daily evapotranspiration from a Brachiaria pasture in Brazil was 39% lower than in a nearby undisturbed rain forest, 2.74 mm d^{-1} compared with 4.48 mm d^{-1}, respectively. However, research has clearly shown that deforestation and afforestation are not opposite and reversible processes in terms of water yield (Robinson et al. 1991; Scott and Lesch 1997; Vertessy 1999).

In grasslands and agricultural lands, afforestation can reduce water yield from rivers and streams because canopy interception and evapotranspiration generally both increase (e.g., Herron et al. 2002; Farley et al. 2005). Interception tends to be relatively small in grasslands but can account for 10–20% of rainfall in hardwood systems and 20–40% in conifer plantations (e.g., Rao et al. 1979; Le Maitre et al. 1999; Levia and Frost 2003). For evapotranspiration, afforestation can alter leaf area, stomatal characteristics, surface roughness (a measure of the aerodynamic properties of the land surface), albedo, and the depth and density of root systems (Vertessy 2001; Brooks et al. 1997; Jackson et al. 2000). Holmes and Sinclair (1986) and Zhang et al. (1999) suggested that annual evapotranspiration from catchments planted to eucalypts or other plantation species could increase anywhere from ~50–250 mm compared to a grassland catchment. This change in ET could then affect other terms in the water budget, potentially decreasing annual stream flow, deep drainage, and rates of baseflow, as well as altering salinity.

In humid grasslands like those in the Pampas of Argentina, evapotranspiration is less than precipitation (P), and hydrological recharge takes place through deep drainage. Where groundwater is available, trees reverse the relationship between ET and P, initiating a net discharge regime (ET > P) in which groundwater use exceeds deep drainage (Fig. 19.1). The discharge regime is sustained by groundwater recharge and lateral transport from the surrounding grassland. Ground-

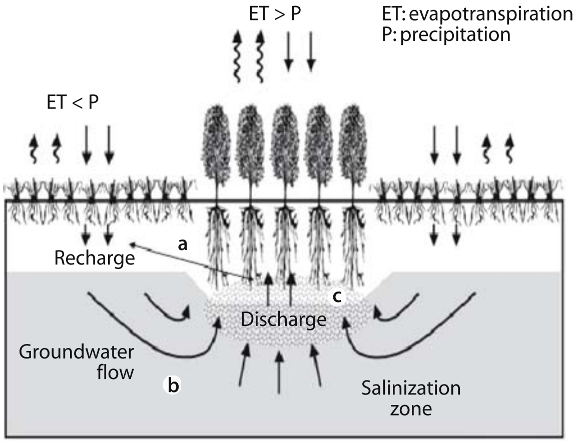

Fig. 19.1. Mechanism of groundwater use and salinization after afforestation of grasslands. Tree establishment reverses the net vertical flux of groundwater when absorption exceeds recharge. Groundwater exits the system through transpiration, leaving salts in the afforested stand (from Jobbagy and Jackson 2004)

water use through transpiration leaves dissolved salts behind that accumulate in the system if this net discharge regime is sustained. In the framework in Fig. 19.1, salinization is predicted to occur when three ecohydrological conditions are met: *(a)* grasses allow a moderate net hydrological recharge that is interrupted by trees, *(b)* the terrain and soil conductivity allow a sustained horizontal flow of groundwater and dissolved salts towards the tree stands, and *(c)* trees access groundwater. In the Pampas, afforested plots (10–100 ha in size) showed 2–19-fold increases in groundwater salinity (Jobbágy and Jackson 2004) compared to adjacent grasslands; in addition, surface soil pH typically decreased by a full pH unit, a change comparable in magnitude to the effects of acid rain (Jobbágy and Jackson 2003).

Globally, one of the best tools for examining the effects of afforestation on streamflow is long-term catchment datasets (e.g., Holmes and Sinclair 1986; Zhang et al. 2001). More recently, Farley et al. (2005) compiled catchment data in afforested grasslands and shrublands from 26 catchment studies with 504 annual observations, in part to stratify changes by original vegetation type and climate, and to quantify the effects of plantation age. Across the dataset, annual runoff decreased consistently in afforested catchments (Fig. 19.2, grassland data only; $P < 0.001$ for both grasslands and shrublands). Reductions in annual runoff in afforested grasslands and shrublands were similar in the first 5 years after tree establishment (–16% and –15%, respectively) but diverged as the plantations aged. Afforested grasslands reached a 50% reduction in runoff within a decade compared with a one-third decrease in afforested shrublands. Moreover, the data from grasslands show faster losses of runoff with eucalypt afforestation, sometimes within a decade (Fig. 19.2 and Farley et al. 2005).

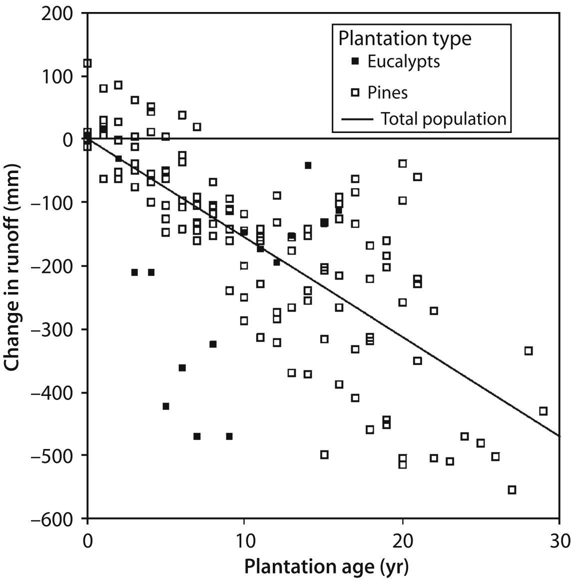

Fig. 19.2. Change in runoff with plantation age ($r^2 = 0.77$; $P < 0.001$). Data come from 26 catchment studies of afforestation globally and a database of 504 yearly observations (from Farley et al. 2005)

This synthesis clearly demonstrates that a loss of 100 to 500 mm (or one-third to three-quarters) of annual streamflow can be expected with afforestation at sites with mean annual precipitation >750 mm. Eucalypts tend to reduce streamflow more than pines do (Fig. 19.2 and Farley et al. 2005). Dye (1996) compared eucalypts and pines in South Africa and found that the rate of increase in evapotranspiration following afforestation was more rapid under eucalypts because of their faster growth and canopy closure; better data for poplar plantations would be helpful to compare with the more extensive pine and eucalypt datasets. While there is likely to be some variation in species effects by region, generalizations regarding the effects of different plantation species on runoff should be useful for planning afforestation projects and the tree species that will be used in them.

19.2.3 Afforestation: Potential Atmospheric Feedbacks

While afforestation typically increases evaporative water losses and reduces runoff locally, climate feedbacks at regional scales could also affect precipitation and water use. These regional effects on water availability depend on the location, extent, and patchiness of afforestation and operate through changes in albedo, roughness length, and water transport properties from soil to the atmosphere, including leaf area index, stomatal conductance, and rooting depth. These variables influence climate because they help determine the total amount of energy transferred between the vegetation and the atmosphere as well as the fraction of that energy driving evapotranspiration (latent heat) and warming of the air (sensible heat). Since little attention has been given to the direct climatic effects of afforestation, our understanding here must derive primarily from studies of deforestation.

Most simulations of tropical deforestation have concluded that the effect of the forest, relative to pasture, on precipitation is greater than its effect on evapotranspiration (Hahmann and Dickinson 1997; Hoffmann et al. 2003), such that runoff should be higher under forest than pasture. Similar effects of tree cover were observed in simulations of tropical savanna regions (Hoffmann and Jackson 2000, 2002; Clark et al. 2001). Analogously, at coarse scales the conversion of agricultural lands and grasslands to homogeneous forest cover might be predicted to increase precipitation slightly, in part because of increased water recycling through convective storms. Whether this increase is enough to offset completely the increased evapotranspiration of the forests is unclear.

In temperate regions, however, published simulations suggest otherwise. Although simulation studies have sometimes found that tree cover increases precipitation in temperate regions, this effect has been consistently smaller than the effect on ET, indicating that complete afforestation should result in reduced runoff (e.g., Xue et al. 1996; Bounoua et al. 2000). Furthermore, under some conditions, afforestation is likely to *reduce* precipitation, particularly near bodies of water, where actively transpiring vegetation might reduce the strength of the sea breeze and associated convection and cloud formation (Pielke and Avissar 1990). Simulations of land-use change in the US indicate that summer precipitation should decline with afforestation of the southern coastal plain, Florida, and the Great Lakes region (Copeland et al. 1996; but see Pielke et al. 1999). In such cases, the climate feedbacks resulting from afforestation should magnify the local effects of plantations on water yield, resulting in even lower water yield than predicted by catchment studies alone.

The pattern and scale of land-cover change in some cases may be as important as the switch between trees and herbaceous vegetation. Circulation patterns similar to a sea breeze can arise at the interface between forest and non-forest vegetation (Pielke and Avissar 1990; Pielke et al. 1997), which is particularly relevant over heterogeneous landscapes typical of afforestation. Where heterogeneity promotes these mesoscale circulations, convection cells develop where ET is lowest (Pielke and Avissar 1990; Pielke et al. 1997), leading to the rather counterintuitive observations that cloud formation can be greater over nonforest patches (Roy and Avissar 2002; Weaver et al. 2002). A patchwork of plantation and nonforest vegetation may therefore generate more precipitation than homogeneous forest vegetation, particularly under conditions of weak synoptic forcing, such as when prevailing winds are weak (Pielke et al. 1997).

19.3 Woody Encroachment and Agriculture

19.3.1 Grassland Conversions with Woody Plant Encroachment and Agriculture

Shifts among grasslands, woody communities, and croplands represent another form of vegetation change important for carbon cycling today. The conversion of croplands to perennial vegetation consistently leads to carbon stored in soil organic matter (Post and Kwon 2002; Guo and Gifford 2002). This carbon storage benefit is recognized in the U.S. Conservation Reserve Program (CRP), which has provided economic incentives for farmers to convert crops to perennials in ~15 million ha to date (Skold 1989; Jackson and Schlesinger 2004).

At the regional scale, potential carbon storage in croplands can be estimated by combining observed sequestration rates through programs like the CRP or no-till agriculture with the extent of agricultural lands in a region. Recent reviews of more than 100 observations show that SOC increased ~450 kg C $\text{ha}^{-1}\,\text{yr}^{-1}$ after croplands converted to pastures or no-till management (Post and Kwon 2000; West and Post 2002), peaking five to ten years after conversion and slowing considerably within two decades (West and Post 2002). Taking the U.S. as an example, if all ~132 000 000 ha of croplands in production in 2001 were converted to no-till agriculture or, less likely, were retired through the CRP, potential sequestration rates of 0.059 Pg C yr^{-1} might be possible for several decades. This amount would be ~4% of total U.S. fossil fuel emissions of ~1.6 Pg yr^{-1}. Currently, the ~15 million ha enrolled in the CRP store an order of magnitude less than this technical potential, ~0.005 Pg C yr^{-1} (Jackson and Schlesinger 2004).

Conversion of croplands back to perennial grassland is not the only change in land use likely to affect C pools in grasslands. Many regions of the world are currently undergoing woody plant encroachment, a process enhanced by management practices such as intensive grazing and fire suppression and possibly by interactions with climate change (Kucera 1960; Bragg and Hulbert 1976; Briggs et al. 2002). The soil C consequences of woody encroachment into native grasslands vary considerably, ranging from gains of soil C in some ecosystems (Archer et al. 2001) to no net change or losses in others (Kieft et al. 1998; Schlesinger and Pilmanis 1998; Gill and Burke 1999; Tilman et al. 2000; Smith and Johnson 2003). Recent work suggests that the changes in soil carbon storage are related to climate, with drier grasslands more likely to gain soil C and productive sub-humid/humid grasslands to lose it (Jackson et al. 2002).

From a soil C perspective, the primary difference between woody plant encroachment into native grasslands and into old agricultural fields is the quantity, quality, and distribution of soil C at the onset of woody plant

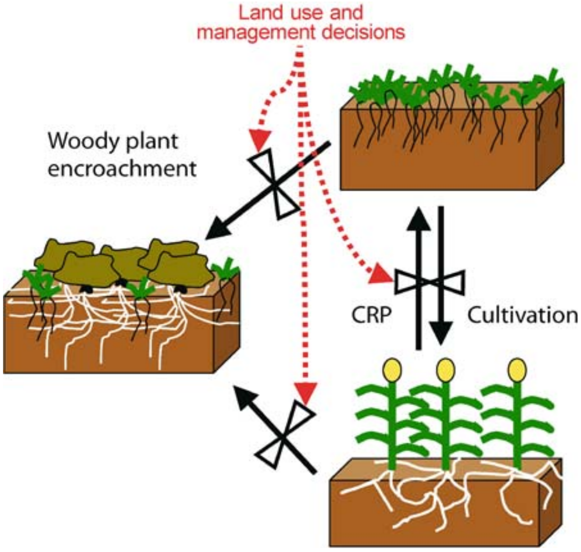

Fig. 19.3. Conceptual diagram of how land-use and management decisions alter the structure and function of grassland ecosystems (*CRP* = Conservation Reserve Program)

establishment (McCulley et al. 2005). In tallgrass prairie, for example, agricultural cultivation significantly reduces soil C pools (Burke et al. 1989; Huggins et al. 1998; Knops and Tilman 2000). Thus, unlike woody plant encroachment into native grasslands where the soil C response varies depending on the climate, land management, and species involved, woody plant establishment and dominance in many old agricultural fields should replenish soil C pools. Indeed, this hypothesis is supported by Guo and Gifford (2002) who found that converting cropland to secondary forest or plantations increased soil C pools by 53% and 18%, respectively.

19.3.2 Processes Controlling Soil C Storage: Grassland Vs. Woodland

The amount of C stored within the soil and the rate at which C accumulates and turns over is determined largely by the quantity and quality of C inputs, soil properties such as clay or sand content, and possibly the microbial community present. Edaphic properties such as texture are unlikely to change dramatically within the time-scale of plant establishment on abandoned cropland or conversion of grassland to woodland. However, major changes in other controlling variables, such as the quantity and quality of C inputs through net primary productivity as well as microbial community composition are likely.

In terms of carbon inputs to the soil, many differences between herbaceous and woody species exist. For example, grassland species tend to allocate a higher proportion of fixed C to belowground root systems than woody species do (Jackson et al. 1997). In addition, the two vegetation types differ in root morphologies and distributions, with grasses having a shallower, more densely fibrous root system and woody plants typically having deeper, coarser roots (Canadell et al. 1996; Schenk and Jackson 2002a,b). Thus, woody dominated systems may deliver more C than grasslands to the soil surface via litter while increasing C inputs deep within the soil profile. The quality of litter inputs, both above- and belowground, often differs significantly between the two types as well, with woody material containing more lignin and secondary compounds. All of these factors interact to alter the rate of decomposition, the soil microbial community, and ultimately the quantity, quality, and depth distribution of soil C storage.

Previous studies showing that differences in carbon inputs between grasslands and woodlands alter soil C storage come primarily from global analyses and woody encroachment studies in rangelands. Global analyses of root distributions and soil organic C contents suggest that converting croplands to grasslands or woodlands alters soil C profiles through changes in the amount and depth of root C inputs (Jackson et al. 1996; Jobbágy and Jackson 2000). More specifically, a comparison of grasslands and forests in sub-humid climates, such as tallgrass prairies experience, found that the proportion of total soil organic C stored in the top 20 cm of the soil profile was higher in forests; in contrast grasslands stored proportionally more soil C deeper within the profile (Jackson et al. 2000). Using the fact that woody and herbaceous plants often differ in photosynthetic pathways and produce organic matter with different ^{13}C signatures (Smith and Epstein 1971), woody plant encroachment studies have shown that C contributions to the soil are highest at the surface soil layers (Gill and Burke 1999; Smith and Johnson 2003), perhaps resulting from greater inputs of litter at the soil surface (Connin et al. 1997; Boutton et al. 1999; Hibbard et al. 2001). Moreover, in woodlands or brush, the presence of a thicker litter layer may result in a relatively high proportion of aboveground litter decomposing before entering the mineral soil. Alternatively, if such material had high C/N ratios, it might be slow to decompose and enhance longer-term soil C sequestration.

Besides altering the depth distribution of soil C storage, grasslands and woodlands differ in soil C quality, as measured by soil organic matter C/N ratios, organic C chemical constituents, and the relative percentage residing in active, slow, and passive soil C pools. In general, woody dominated areas have higher total soil C/N ratios, greater quantities of complex organic molecules within soil organic matter, higher percentages of slowly turning over soil C pools, and, consequently, longer mean residence times for C within the soil than grasslands have (Connin et al. 1997; Boutton et al. 1998; Gill and Burke 1999; Martens et al. 2003; Smith and Johnson 2003; McCulley et al. 2005).

19.3.3 Uncertainties in Water and Carbon Balances with Woody Plant Encroachment

The ecohydrological consequences of woody plant encroachment are much less clear than for afforestation (Wilcox 2002; Petheram et al. 2002; Huxman et al. 2005). Because the ratio of evaporation to transpiration increases with aridity, plants have a proportionally smaller role in regulating total water fluxes in arid systems. In addition, streamflow and evapotranspiration are differentially affected by woody encroachment, depending on the degree and seasonality of aridity and the availability of subsurface water (Huxman et al. 2005).

Despite uncertainties, a few generalizations are possible. Streamflow may decline with woody encroachment in semi-arid landscapes dominated by subsurface flow, including systems with available groundwater or karst systems where water flows quickly into the subsoil (Jackson et al. 1999; Seyfried et al. 2005). There, the deeper root systems of woody plants can capture water that is otherwise unavailable to herbs. Similarly, woody encroachment may increase bare soil evaporation in semiarid ecosystems, because of the increasingly patchy vegetation cover (Huxman et al. 2005). Explicitly considering the ecohydrology associated with vegetation change provides important information on the consequences of woody plant encroachment for carbon storage.

In addition to woody plant encroachment, woody plant or brush "thickening" is likely to decrease stream flow. Brush thickening is defined as an increase in woody plant density at sites where woody species were already present. Like woody encroachment into grasslands, thickening has occurred in many regions of the world, including the western U.S. and Australia (Van Auken 2000; Fensham and Fairfax 2003; Hicke et al. 2004). In practice, brush thickening will affect stream flow through similar mechanisms to those occurring with afforestation and woody encroachment. All three land-cover changes can increase leaf area, evapotranspiration, and rainfall interception, potentially decreasing stream flow. However, the more arid a system is, the more uncertain the outcome for water yield will be, as evapotranspiration from the soil plays an increasingly important role relative to plant transpiration at drier sites.

How much more carbon is stored in shrublands and woodlands compared to grasslands remains uncertain. Decades of research have described the formation of "islands of fertility" under single plants and plant clusters as woody species invade grasslands. This process increases heterogeneity in cover and net primary productivity, concentrating soil nutrients and carbon under the woody plants and depleting them by erosion and other processes in the interspaces. Using such shrub islands and herbaceous interspaces as endpoints to compare encroached and intact grassland systems may underestimate the carbon stored in the original grasslands and overestimate it in the expanding woodlands. This is especially true when the microsites first invaded by the woody plants are the deepest, most productive soils. When examined for entire ecosystems, data from 242 sites show increasingly more SOC for grasslands than for shrublands/woodlands as precipitation increases to 1 000 mm (Fig. 19.4).

Land-use history is a crucial lens for viewing the consequences of vegetation and land-use change. Degraded rangelands can be actively restored, and store carbon in turn, using any type of vegetation. Transformations in the opposite direction, however, from shrubland or woodlands to grasslands, are also enlightening. Recent meta-analysis of >100 studies emphasizes the potential for SOC gains at sites originally dominated by woodlands when converted to grasslands (Conant et al. 2001) and soil carbon losses when pastures are converted to plantations (Guo and Gifford 2002). Grasslands are deceptively productive ecosystems at both short and long time scales (e.g., Retallack 2001).

U.S. carbon budgets estimate the sequestration due to woody plant encroachment to be ~0.12 to 0.13 Pg C yr^{-1} but acknowledge large uncertainties in this estimate (e.g., Houghton et al. 1999). We believe the correct estimate will eventually be positive but smaller, both because of the relationship between soil carbon stor-

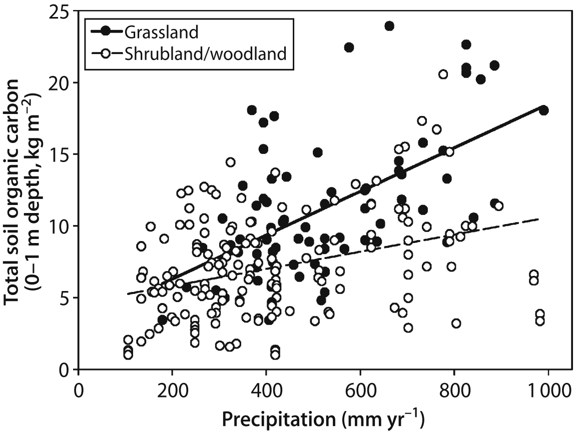

Fig. 19.4. An analysis of soil organic carbon (kg m^{-2}) vs. mean annual precipitation (mm) for the top meter of soil. The data are derived from the National Soil Characterization Database of the U.S. Department of Agriculture and the World Inventory of Soil Emission Potential Database of the International Soil Reference and Information Centre. Across the global dataset, the slope of the relationship of SOC vs. precipitation was 2.6 times higher for grassland vegetation than for shrublands/woodlands ($p = 0.001$). Whereas grassland SOC was statistically indistinguishable from values for woody plants at 200 mm MAP (Mean Annual Precipitation), woodlands had 43% less total SOC than grasslands at 1 000 mm ($p < 0.01$) (from Jackson et al. 2002)

age and precipitation described earlier (Jackson et al. 2002) and because the land area attributed to woody encroachment is over-estimated – 220 million ha, or two-thirds of the continental U.S. excluding forests and croplands (Houghton et al. 1999; Pacala et al. 2001). Better constraining the carbon sink for woody encroachment will entail a combination of field research, remote sensing, and spatially explicit modeling that takes into account precipitation (and climate in general), land-use history, erosion, and other disturbances. Patch-based comparisons of vegetation yield important ecological insight but must be scaled up appropriately for conclusions at ecosystem, landscape, and regional scales.

19.4 Summary and Conclusions

The environmental consequences of afforestation and other biologically based sequestration programs have received much less attention than their carbon sequestration potential (e.g., Herron et al. 2002; Jackson and Schlesinger 2004; Farley et al. 2005). Potential sequestration rates are high but will require managing enormous land areas. One of the most important issues in how to implement land-use change projects within the Clean Development Mechanism of the Kyoto Protocol is to understand their total effects on local livelihoods and environments (Pedroni 2003). For plantations, the synthesis described above clearly shows that a reduction in runoff can be expected after afforestation of grasslands and shrublands. In a few locations such as part of Australia where lower runoff can ameliorate salinity and groundwater upwelling, this may be a positive change. In other regions, the reduction in runoff could cause water shortages, a tradeoff that should be acknowledged before policies promoting afforestation are implemented. One challenge and opportunity to the research community is to help policy makers choose locations for afforestation that are as economical and environmentally beneficial as possible (Pimentel et al. 2004).

The ability to predict the likely effects of afforestation in specific places will be the biggest challenge to zoning and planning for these projects (Farley et al. 2005). Catchment data are collected over decades and are unavailable in most places. However, we can use indicators, such as the change in runoff as a percent of mean annual precipitation at a site, to gain insight into the likely severity of the loss of runoff. Synthesis data suggest that trees are able to use 15 to 20% more precipitation than grasses, so that in a region where natural runoff is less than 10% of mean annual precipitation, afforestation may result in a complete loss of runoff, whereas in places where natural runoff is 30% of precipitation, it may be cut in half when trees are planted (Farley et al. 2005). This information can be useful to land managers and policy makers in guiding the location of plantations with respect to other water demands. There are also many other changes that need to be examined through sequestration scenarios. For example, the potential effects on biodiversity would depend in part on the previous land use. If landowners choose to afforest agricultural lands, the effects on biodiversity would probably be minimal; if instead they choose to afforest native grasslands and rangelands, the consequences would be larger.

For woody plant encroachment in arid and semi-arid systems, the biggest uncertainties are the consequences for the water balance and groundwater recharge and its regional and global role in the carbon balance. Understanding the consequences for water yield is especially important because essentially all of the places where woody encroachment occurs are water limited for both plants and people.

Finally, this book summarizes some of the scientific progress in more than a decade of GCTE's existence (GCTE-Global Change and Terrestrial Ecosystems). As GCTE ends and the scientific community looks forward, the biggest need for global change research is to do a better job of combining research in the social and natural sciences. The natural science community cannot hope to predict the consequences of global change without input from economic and policy models. The plantation scenarios discussed above are a good example. In turn, economists and other social scientists need input on the environmental changes that are likely to affect people and economies in the future. This need is reflected in the next generation of GCTE, the Global Land Project (see Ojima et al. 2007, Chap. 25 of this volume). The Global Land Project is a joint effort of the International Geosphere-Biosphere Programme (IGBP) and the International Human Dimensions Programme (IHDP).

Fortunately, many good examples of such coordination are underway. One of these is the global desertification network, as presented in such projects as ARIDnet, a research network for studies of global desertification (Reynolds and Smith 2003; Reynolds et al. 2007, Chap. 20 of this volume; http://www.biology.duke.edu/aridnet/). ARIDnet and other related projects recognize the important dual effects of humans and the environment in understanding global change. Another example is SAHRA (Sustainability of semi-Arid Hydrology and Riparian Areas) based in Arizona (http://www.sahra.arizona.edu/). This project seeks to develop an integrated, multidisciplinary understanding of the hydrology of semi-arid regions, and to build partnerships with a broad spectrum of stakeholders (both public agencies and private organizations). With the multi-disciplinary philosophy that these and other projects display, we are well on our way to making our research stronger and more relevant to society.

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Chapter 20

Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences

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20.1 Introduction

Land degradation in drylands, which is referred to as desertification, is viewed by many as one of the most critically important issues facing many countries (e.g., Darkoh 1998; Dregne 1996; Kassas 1995). The United Nations portrays it as one of the "most important global change issues facing mankind" (UNCCD 1994). Land degradation is a vital societal concern because of its impacts on human populations (food security, economics, sustainability, etc.) and environment quality (dust storms, trace gas emissions to the atmosphere, soil erosion, etc.) (Vitousek et al. 1997). Like global climate change and biodiversity, desertification is the subject of an international framework convention, the Convention to Combat Desertification (CCD), the aim of which is to "target poverty, drought and food insecurity in dryland countries experiencing desertification, particularly those in Africa" (United Nations 1994). The CCD was established by the United Nations in order to facilitate the role of national governments in enacting policies to combat land degradation. The Convention provides for a large infrastructure (e.g., a Secretariat and the Global Mechanism), which is designed to mobilize and channel financial resources, including the transfer of technology to developing countries (details in Chasek and Corell 2002).

However, in spite of its high profile and acknowledged importance, desertification has remained stubbornly intractable. Part of the problem is that desertification tends to stir up more disagreement and controversy than consensus (e.g., Leach and Mearns 1996; Reynolds and Stafford Smith 2002a; Thomas and Middleton 1994). While the reasons underlying the uncertainty and confusion associated with this topic are numerous (see reviews by Grainger et al. 2000; Reynolds 2001; Reynolds and Stafford Smith 2002a), the bottom line is that desertification has proven to be a complex problem that is not amenable to simple solutions. A second aspect of the problem appears to reside with the CCD itself. The CCD model has been roundly criticized for its deficiency of directed research efforts, for lacking connections to "real-world" problems, and for serving solely as a mechanism for some countries to elicit funds from donor nations (Toulmin 2001). In spite of these criticisms, the CCD is the primary vehicle for addressing desertification and has inspired some successful spin-off activities that engage scientists and various stake-holders (see Corell 1999).

In this chapter we provide a brief overview of the most significant issues of land degradation in global drylands, with an emphasis on the interaction between human and natural dimensions of the problem. Despite considerable work on case studies of land degradation in individual regions of the globe, there is little integration between social and biophysical sciences, and there are great opportunities for comparative studies across the many different social and biophysical systems. We discuss some of the underlying causes of land degradation and their consequences. Further, we discuss a joint initiative on desertification of the Global Change and Terrestrial Ecosystems (GCTE) and Land-Use and Land-Cover Change (LUCC) programs, which provided a framework to facilitate directed research effort and progress on this important global environmental issue. Land degradation is an excellent topic for such an initiative given that LUCC is geared to improve the understanding of land-use and land-cover change dynamics, GCTE was focused on synthesis activities on critical topics in the terrestrial biosphere, and both programs are keen to engage both the physical and social science communities for the development of science relevant to global change.

20.2 Drylands, Desertification, Drivers, and Scales

20.2.1 Distribution of People and Land-Cover Types

In general, drylands are characterized by low and variable rainfall, extreme air temperatures, and seasonally high potential evaporation. Technically, drylands are defined as regions that have an index of aridity (ratio of mean annual precipitation to mean annual potential evapotranspiration) of 0.05 to 0.65 (see Middleton and Thomas 1997). Drylands can be further subdivided as arid (0.05–0.20 index of aridity; ca. 30% of drylands), semiarid (0.20–0.50 index of aridity, ca. 45% of drylands), and sub-humid (0.50–0.65 index of aridity, ca. 25% of drylands) and together cover approximately 5.2 billion hectares or about 40% of the land surface of the globe (Table 20.1a). Drylands have two primary types of human uses: the overwhelming majority serve as rangelands (>75% of drylands), while nearly 20% are rainfed or irrigated cropland. In terms of a land-cover classification, shrubland is the dominant cover type (24% of drylands), followed by cropland (20%), savanna (15%), grassland (13%), forest (8%) and urban (3%) (Table 20.1b).

Drylands are home to over two billion people: 42% of the Asian population, 41% of Africans, and 25 to 30% of the rest of the world (Table 20.1c). Combined, Asia and Africa contain 84% of all global drylands, dwarfing the amount of dryland area on other continents. In terms of importance, however, these numbers can be somewhat misleading. While Europe contains only ca. 6% of the world's drylands, this represents about 32% of its land mass and is home to 25% of its population. Similarly, Australia contains about 13% of the world's drylands but they cover over 75% of the continent and are home to 25% of its population. Hence in both Europe and Australia, drylands are crucial determinants of the economy, culture and climate. Some of the highest densities of human populations are in the dry sub-humid and semiarid areas of cropland, e.g., those in India, eastern China, and Europe, and in the savannas of Africa (White et al. 2003).

20.2.2 Defining Land Degradation and Desertification

Land degradation and desertification are composite phenomena that have no single, readily identifiable attribute. Perhaps this is why there are so many conflicting and confusing definitions (see reviews by Reynolds 2001;

Table 20.1. Distribution of global drylands, their major land cover types, and human populations

a Distribution of drylands (million ha)[a]	**Arid**	**Semiarid**	**Dry sub-humid**	**% of global drylands**	**% of continental land area**
Asia	625.7	693.4	352.7	32.3	39.3
Africa	503.5	513.8	268.7	24.9	43.4
Europe	11.0	105.2	183.5	5.8	31.5
South America	44.5	264.5	207.0	10.0	29.2
North America	81.5	419.4	231.5	14.2	33.4
Oceania	303.0	309.0	51.3	12.8	75.2
World totals	1 569 (30%)	2 305 (45%)	1 295 (25%)	100.0	39.7% of globe
b Distribution of land cover types (million ha)[b]	**Arid**	**Semiarid**	**Dry sub-humid**	**Total**	**% of continental land area**
Shrubland	683	534	50	1 268	24
Cropland	47	530	475	1 052	20
Savanna	83	402	303	788	15
Grassland	181	473	65	719	13
Forest	11	140	284	436	8
Urban/developed	26	82	66	173	3
Other[c]	559	213	149	922	17
World totals	1 591	2 374	1 391	5 356	100
c Distribution of human population (%)[b]	**Arid**	**Semiarid**	**Dry sub-humid**	**Percent of population living in drylands**	
Asia (Incl. Russia)	5	18	19	42	
Africa	6	18	17	41	
Europe	0	5	20	25	
South America	2	16	12	30	
North America	2	16	5	23	
Central America and Caribbean	6	11	8	25	
Oceania	1	5	19	25	
World totals	4	4	17	37	

[a] See Reynolds (2001) for citations.

[b] Based on GLCCD 1998; ESRI 1993; UNEP/GRID 1991; see White and Nackoney (2003) for citations.

[c] Includes barren or sparsely vegetated land; open water; permanent wetlands; snow and ice; and islands.

Thomas 1997). For example, a common misunderstanding among land managers and stakeholders is to equate land degradation solely with soil degradation. The definition of Stocking and Murnaghan (2001) emphasizes changes in biophysical variables and implies an impact on human populations: land degradation is how one or more land resources (soils, vegetation, water, landforms, etc.) has changed "for the worse," signifying a temporary or permanent decline in the productive capacity of the land. While heuristic, we favor the definitions used by the CCD (UN 1994), which go a step further by making it clear that while biophysical components of ecosystems and their properties are involved, the interpretation of change as 'loss' is dependent upon the integration of these components within the context of the *socio-economic* activities of human beings. The CCD's definition states that land degradation is the reduction or loss of the biological and economic productivity and complexity of terrestrial ecosystems, including soils, vegetation, other biota, and the ecological, biogeochemical, and hydrological processes that operate therein. In drylands, this involves soil erosion and sedimentation, shifts in natural fire cycles, the disruption of biogeochemical cycling, and a reduction of native perennial plants and associated microbial and animal populations. The CCD's definition of desertification explicitly focuses on the linkages between humans and their environments that affect human welfare in arid and semi-arid regions.

20.2.3 What Drives Land Degradation and Desertification?

Desertification is caused by a relatively large number of factors that vary from region to region, and that often act in concert with one another in varying degrees. Geist and Lambin (2004) carried out a worldwide review of the causes of desertification, and from 132 case studies identified four major categories of proximal causal agents: (1) increased aridity; (2) agricultural impacts, including livestock production and crop production; (3) wood extraction, and other economic plant removal; and (4) infrastructure extension, which could be separated into irrigation, roads, settlements, and extractive industry (e.g., mining, oil, gas). They concluded that only about 10% of the case studies were driven by a single cause (with about 5% due to increased aridity and 5% to agricultural impacts). About 30% of the case studies were attributable to a combination of two causes (primarily increased aridity and agricultural impacts), while the remaining cases were combinations of three or all four proximal causal factors.

A primary objective of Geist and Lambin's (2004) review was to identify general global patterns in causation of desertification. As such, the study identified specific agents as more or less important in particular regions, and indicated that these agents derive from underlying forces associated with particular combinations of socio-economic (including technology) and biophysical factors characteristic of particular regions. For example, two underlying forces, climate and technological factors (either new technologies or deficiencies in technology) were the key drivers of desertification in the majority (54%) of the case studies in southern Europe. In Africa, climate, alone or acting in concert with population demography, was a key driver in the 38% of the case studies. In the United States, 50% of the case studies were attributable to a combination of climate and technology drivers or these two factors interacting with economic forces. Desertification processes in Asia, Latin America, and Australia could only be attributed to more complex interactions among four or more underlying forces.

20.2.4 Estimating the Extent of Desertification

Not surprisingly, obtaining accurate estimates of the amount of drylands affected by desertification is a difficult task, fraught with numerous obstacles and complications. Nevertheless, the extent of global desertification is routinely reported as high as 70% of all drylands (UNCCD 2000)! Thomas and Middleton (1994) and others view such estimates as suspect because they are largely derived from the subjective judgments of scientists and laypersons, surveys completed by local governments, qualitative assessments, and data of varying authenticity and consistency. Unfortunately, the CCD definition of desertification (Sect. 20.2.2), which we consider most authoritative at present, is not amenable to easy quantification, especially as a single number or synthetic index.

A variety of problems confound estimates of the extent of desertification. For instance, observations made on short-term ecosystem dynamics are often cited as evidence of desertification ignoring the fact that drylands are highly variable over time (both intra- and inter-annually) and that a temporary loss of vegetation cover due to a short-term drought or to local land use (e.g., grazing) is distinct from – and not necessarily related to – a permanent loss of vegetation associated with desertification (Reynolds 2001). Inaccurate estimations are also fueled by technological barriers that preclude the monitoring of relevant variables, such as the cover of dry vegetation, that cannot be easily estimated using traditional approaches (Asner et al. 2003). Another crucial, but often overlooked, concern is that desertification is usually promoted by two or more causal agents (see Sect. 20.2.3). In spite of the CCD definition, most estimates of desertification are derived solely from either biophysical factors (e.g., soil erosion, loss of plant cover, change in albedo) or socio-economic factors (decreased production, economic loss, population movements, etc.), but rarely both types simultaneously (Stafford Smith and Reynolds 2002). When assessments are made without good knowledge of the underlying causes, it brings into question the validity of the variables or sets of variables being used in the assessment.

Over the years, in different arid and semiarid regions of the world, there has been a concerted effort to categorize and map various forms of land degradation at various scales, but these efforts have failed to include a careful, systematic identification of the critical variables that cause the observed dynamics (Stafford Smith and Reynolds 2002). This problem lies at the base of the confusion about how much 'desertification' there really is (see Batterbury et al. 2002). Stafford Smith and Reynolds (2002) argued that much of this confusion could be eliminated by focusing on a small number of critical variables that contribute to an understanding of the cause, rather than effect, of desertification. Of course, this is all the more problematic when we try to account for the causal factors driving desertification in different regions of the world and at different times: approaches developed to estimate desertification in one region may not be effective in others. The failure to recognize these issues has led to the disparities of estimates of desertification in the literature and is responsible for many of the disagreements alluded to above (Stafford Smith and Pickup 1993; Stafford Smith and Reynolds 2002).

20.2.5 Consequences of Desertification

There are few disagreements that desertification has a large number of biophysical and socio-economic consequences, which range across a wide spectrum of spatial and temporal scales. An in-depth treatment of the different consequences is beyond the scope of this chapter, but some relevant ones are presented in Table 20.2 (and see group reports in Reynolds and Stafford Smith 2002b). From the socio-economic point of view, most consequences (especially in pastoral systems) are a direct consequence of the decline in 'productivity' or the capacity of the land to support plant growth and animal production. During early stages of desertification such losses are compensated by the social resilience of the local human populations, especially in developing countries, or by economic inputs from government (Vogel and Smith 2002). However, when certain thresholds are crossed, social resilience or government subsidies may not be enough to compensate for the loss of productivity, and this fuels a battery of socio-economic changes that range from modifications in trade promoted by lower agricultural production to large population migrations (Fernández et al. 2002).

Virtually all of the biophysical consequences start with the loss of vegetation and soil (Table 20.2). These losses have a 'cascading' effect on other components and processes, leading to a progressive deterioration of the ecological structure and functioning of the system (Fernández et al.

Table 20.2. Some biophysical and socio-economic consequences of desertification in drylands and approximate spatial scales at which they are most relevant. The list is not exhaustive. See Sect. 20.2.5

Dimension	Consequence	Scale[a]	Examples
Socio-economic	Reduction in crop yield	F, C, D	Zaman (1997)
	Reduction in animal production	F, C, D	Fredrickson et al. (1998)
	Loss of economical important species	C, N	Latchininsky and Gapparov (1996)
	Migratory movements	C, D, N	Pamo (1998)
	Loss of local environmental knowledge	C, D, N	Bollig and Schulte (1999)
	Loss of traditional agricultural structures	D	Gallart et al. (1994)
	Changes in land use patterns	C, D, N	Zhao et al. (2005)
Biophysical	Loss of soil and nutrients	P, L	Schlesinger et al. (1999)
	Decreased infiltration	P	Sharma (1998)
	Modification of geomorphology	P, R	Lavee et al. (1998)
	Addition of sediments to water bodies	P, L, R	Kelley and Nater (2000)
	Reduction of plant cover	P, L, R	Asner et al. (2003)
	Shifts in species composition and richness	P, L, R	Gonzalez (2001)
	Changes in primary net productivity	P, L, R	Huenneke et al. (2002)
	Changes in the spatial pattern of resources	P, L, R	Schlesinger et al. (1990)
	Loss of biodiversity	R, G	Whitford (1993)
	Loss of biological soil crusts	P, L	Belnap and Eldridge (2001)
	Depletion of soil carbon stocks	P, L, R, G	Jackson et al. (2002)
	Depletion of soil nitrogen stocks	P, R	Asner et al. (2003)
	Reduction in ecosystem resilience	P, L, R	Von Handenberger et al. (2001)
	Modification of climate	R, G	Rosenfeld et al. (2001)

[a] Socio-economic: *F:* farm/household, *C:* community, *D:* district/provincial, *N:* national/international; biophysical: *P:* patch, *L:* landscape, *R:* regional, *G:* global.

2002). The specific biophysical consequences of desertification differ substantially between geographical areas of the globe as a function of the intensity and number of driving forces at work, the extent of the impacted area, the duration of the deterioration, and the resilience of the system components (especially vegetation). Even within a particular area we may find that there are different consequences depending upon the unique characteristics of the system. For instance, while Krogh et al. (2002) found that some keystone species associated with grasslands are negatively affected by shrub encroachment into former grasslands (a form of desertification, Schlesinger et al. 1990), recent studies in the southwestern United States have shown that shrub encroachment is associated with an increase in the species richness of birds (Pidgeon et al. 2001), mammals (Whitford 1997) and ants (Bestelmeyer 2005). Thus, some generalizations regarding biophysical consequences of desertification may be misleading or incorrect when applied to specific situations.

20.2.6 Scale and Hierarchy

The importance of scale is manifest in a number of ways when evaluating the extent and effects of desertification (Sect. 20.2.4). Obviously, humans are most concerned with the local subset of degradation that impacts them personally. Reynolds and Stafford Smith (2002a) use a hypothetical case-study of gully formation (overgrazing by cattle leads to loss of vegetative cover and, ultimately, soil erosion) to illustrate how different segments of society (the stake-holders) see such problems with differing degrees of concern. Whereas an ecologist might view erosion gullies as a breakdown in ecosystem function, this will resonate with a farmer only if the gullies have a demonstrable impact on his values, i.e., meat production by his cattle. If not, the farmer will not consider this as 'degradation'. Alternatively, other stake-holders, such as urban dwellers in a nearby town, may consider this localized soil erosion and gully formation a more serious problem because of the potential for silt runoff into the town's reservoir and its adverse effects on water quality.

Because local activities often have regional consequences (e.g., localized erosion gullies impacting regional water quality) and regional issues can, in turn, have local impacts, it behooves us to assume a multifactor, multiscale, hierarchical view of desertification. In Table 20.3, we illustrate representative scales of interest in desertification viewed from both socio-economic and biophysical perspectives. Coupled socio-economic and biophysical systems must be hierarchically nested in order to avoid errors that will undoubtedly occur if we attempt to extrapolate understanding over a range of scales that is too great, e.g., trying to predict what will happen at the

Table 20.3. Examples of various socio-economic and biophysical scales of concern in desertification and associated key variables. The socio-economic scales are from Stafford Smith and Reynolds (2002) and the biophysical scales approximate those used by Prince (2002). The list of key variables associated to each scale is not exhaustive and some are relevant at more than one scale

Socio-economic		Biophysical	
Scale	**Some key variables**	**Scale**	**Some key variables**
Farm/ household	Household size Labor attributes Characteristics of food supply (e.g. security, flexibility, etc.) Technological development Land management patterns	Patch	Plant cover Soil nutrients Soil infiltration and water holding capacity Abiotic attributes (e.g., slope, aspect)
Community or village	Land tenure and ownership Local government attributes Population size Flexibility of job market	Landscape	Sediment transport Species composition and richness Net primary productivity
District/ provincial	District land planning Decentralization of planning for communal land Land reform Conflicts between groups (ethnic, social and economical) Financial constraints (subsidies) Economic opportunities 'Natural' disasters (e.g., floods, drought, fire, pests, diseases)	Regional	Geomorphology Soil nutrient stocks (e.g. carbon and nitrogen) Ecosystem resilience
National/ international	Human population growth Macro-economic indicators National policies (e.g., resettlement programs, economic incentives) National and international conflicts (e.g., war)	Global	Climate (e.g., rainfall, radiation, albedo) Biodiversity Cover of vegetation types

household level based on observations made at the national scale. Sørbø (2003) describes examples from east Africa to show the importance of scale in pastoral herding communities. These pastoral communities are networked into various localized units, which function in a complex interplay of local and regional social, economic, and political factors, all of which have evolved over many years against a backdrop of severe environmental instability and unpredictable contingencies. It is not surprising that 'top-down' attempts to 'manage' these systems fall short of expectations. This is consistent with Batterbury et al.'s (2002) observations that, in arid and semiarid lands, the highest levels of the 'management hierarchy' are invariably quite remote from marginal lands and, consequently, have weak political and economic feedbacks. An important objective of institutions such as the CCD should be to provide a context within which levels in the hierarchy become more integrated and aware of the issues (Batterbury et al. 2002; Lambin et al. 2002).

20.3 Joint GCTE-LUCC Desertification Initiative

The simultaneous assessment of biophysical and socio-economic drivers (and consequences) of desertification has been recognized as one of the most challenging – but potentially rewarding – topics for further research (see review by Reynolds 2001). In an attempt to address this challenge, the GCTE and LUCC programs of the International Geosphere-Biosphere Programme joined forces to establish an initiative on desertification. The intent of this initiative was to bring together researchers from the various global change programs, representing both natural and human-influenced systems, with the objective of stimulating, developing, and refining a new paradigm to bear on this important global change concern.

One of the key, initial products of this GCTE-LUCC initiative was a book on global desertification (*Global Desertification. Do Humans Cause Deserts?*), which explicitly addresses many of the significant interactions and feedbacks between natural and human-influenced dryland systems. Focusing on the multitude of interrelationships within coupled human-environment systems that cause desertification, and drawing heavily from the chapters of this book, Stafford Smith and Reynolds (2002) proposed the *Dahlem Desertification Paradigm* (DDP). The DDP is a new synthetic framework that is unique in two ways:

- First, the DDP attempts to capture the multitude of interrelationships within human-environment systems that cause desertification, within a *single*, synthetic framework; and
- Second, the DDP is testable, which ensures that it can be revised and improved upon as a *dynamic* framework.

In this section we briefly present an outline of the key elements or assertions of the DDP and describe one method we are using for testing it. As is the case for many paradigms, the constituent ideas contained within the DDP themselves are generally not new, but rather, they bring together much of the previous work on this difficult topic in a way that reveals new insights.

20.3.1 Dahlem Desertification Paradigm

The DDP consists of nine assertions (Table 20.4), which embrace a hierarchical view of land degradation and highlight key linkages between socio-economic and biophysical systems at different scales. The first three assertions relate to the working framework of the DDP while the remaining ones focus on its implementation, limitations, and potentials. The main points of the DDP are:

1. that an integrated approach, which simultaneously considers both biophysical and socio-economic attributes in these systems, is absolutely essential to understand land degradation (assertions #1, #7);
2. that the biophysical and socio-economic attributes that govern or cause land degradation in any particular region are invariably 'slow' (e.g., soil nutrients) relative to those that are of immediate concern to human welfare – the 'fast' variables (e.g., crop yields). It is necessary to distinguish these in order to identify the causes of land degradation from its effects (assertion #2);
3. that socio-ecological systems in drylands of the world are not static (assertions #3, #6);
4. that while change is inevitable, there does exist a constrained set of ways in which these socio-ecological systems function, thereby allowing us to understand and manage them (assertion #9);
5. that restoring degraded socio-ecological systems to more productive, sustainable states requires outside intervention (assertion #4)
6. that socio-ecological systems in drylands of the world are hierarchical (assertion #8). Hence, scale-related concerns abound and desertification itself is a regionally-emergent property of localized degradation (assertion #5)

The strength of the Dahlem Desertification Paradigm is in its cross-scale conceptual holism. While the term desertification is only useful at the higher levels of aggregation, and degradation (appropriately refined) at the lower levels, the DDP framework embraces all these levels of concern. For example, at the international level, implementation of the CCD must be framed in terms of changes in coupled human-environment systems that matter to humans, which dramatically changes the meaning of the "extent of desertification" (Sect. 20.2.4) and both the timing and distribution of funding for inter-

Table 20.4. The nine assertions of the Dahlem Desertification Paradigm, and some of their implications. From Stafford Smith and Reynolds (2002)

	Assertion	Implications
1.	Desertification always involves human and environmental drivers	Always expect to include both socio-economic and biophysical variables in any monitoring or intervention scheme
2.	'Slow' variables are critical determinants of system dynamics	Identify and manage for the small set of 'slow' variables that drive the 'fast' ecological goods and services that matter at any given scale
3.	Thresholds are crucial, and may change over time	Identify thresholds in the change variables at which there are significant increases in the costs of recovery, and quantify these costs, seeking ways to manage the thresholds to increase resilience
4.	The costs of intervention rises non-linearly with increasing degradation	Intervene early where possible, and invest to reduce the transaction costs of increasing scales of intervention
5.	Desertification is a regionally emergent property of local degradation	Take care to define precisely the spatial and temporal extent of and processes resulting in any given measure of local degradation. But don't try to probe desertification beyond a measure of generalized impact at higher scales
6.	Coupled human-environment systems change over time	Understand and manage the circumstances in which the human and environmental sub-systems become 'de-coupled'
7.	The development of appropriate local environmental knowledge (LEK) must be accelerated	Create better partnerships between LEK development and conventional scientific research, employing good experimental design, effective adaptive feedback and monitoring
8.	Systems are hierarchically nested (manage the hierarchy!)	Recognize and manage the fact that changes at one level affect others; create flexible but linked institutions across the hierarchical levels, and ensure processes are managed through scale-matched institutions
9.	A limited suite of processes and variables at any scale makes the problem tractable	Analyze the types of syndromes at different scales, and seek the investment levers which will best control their effects – awareness and regulation where the drivers are natural, changed policy and institutions where the drivers are social

vention. Similarly, at the household or community level, where concern is on the specific type of land degradation that is occurring and its local socio-economic consequences, the DDP channels resources towards identifying those essential biophysical and socio-economic slow variables that really matter in terms of quantifying current and future risk.

20.3.2 Initiatives to Test the Dahlem Desertification Paradigm

The joint GCTE-LUCC initiative on desertification is embodied within the ARID*net*[1] research network (Reynolds et al. 2003). The general objectives of this network are to foster international cooperation, discussion, and exchange of ideas about global desertification (as summarized in the DDP), to conduct case studies, representing a range of biophysical/socio-economic land degradation types around the world, and to facilitate communication between researchers to foster more practical, field-level interactions with stakeholders in sustainable land management.

To accomplish these objectives, ARID*net* is organized into three nodes (North/South America; Asia/Australia; Europe/Africa) and is pursuing four specific tasks (Fig. 20.1):

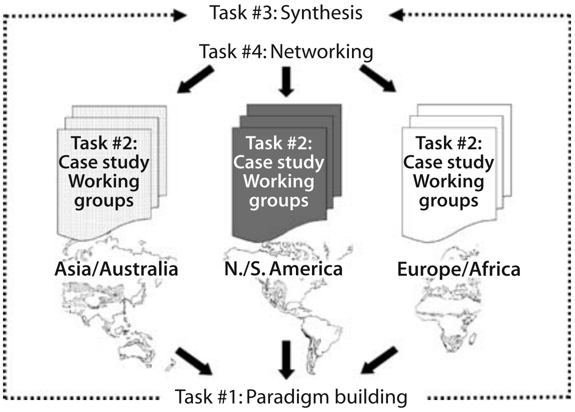

Fig. 20.1. ARID*net* is an international research network organized into three nodes (North/South America; Asia/Australia; Europe/Africa) and is pursuing four tasks (see text): paradigm-building, conducting case studies, developing a synthesis, and to facilitate participation via network-building

- *Paradigm-building*. Using workshops and symposia conducted in different parts of the world, ARID*net* will develop and refine the contents of the DDP through the joint participation of the international community of desertification researchers, stakeholders, and policy-makers;
- *Case studies*. Working Groups are specifically formed to develop case studies throughout the world in order to test the DDP in a well-stratified, comparative manner. These case studies are based on existing data and specific stakeholders, and represent a wide range of

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[1] Assessment, Research, and Integration of Desertification.

the biophysical and socio-economic conditions existing in drylands;
- *Synthesis*. The numerous case studies will feed into a quantitative assessment of what really matters in desertification. This synthesis will especially focus on those interactions between key biophysical and socio-economic variables; and
- *Network-building*. ARID*net* strives to recruit and foster the participation of a diversity of researchers from different fields and countries in the activities of the network.

20.4 Management of Desertified Drylands

In preceding sections we provided examples of the magnitude and importance of desertification as a major local and global environmental problem. In order to prevent further degradation and to restore degraded lands, a number of countries have enacted environmental policies to establish management actions to combat desertification. These actions are diverse but can be grouped under three headings: avoidance, monitoring, and restoration.

20.4.1 Avoidance

Management actions to avoid desertification are rarely proactive. If they exist, they normally are focused on the human drivers of desertification. Such actions vary widely according to the socio-economic conditions of a particular country, but often include the use of economic subsidies to promote changes in land use or crops (Harou 2002), the diversification of human activities in the areas affected (Pamo 1998), and the establishment of educational programs to improve education and social welfare (Vogel and Smith 2002). The latter activity is of crucial importance since one of the core causes of desertification in developing nations is the extreme pressure on the land resulting from high population growth (Geist and Lambin 2004; Le Houérou 1996). However, there are examples of success in reducing demographic growth and in implementing sustainable production systems in desertified areas worldwide (Arkutu 1995; Vogel and Smith 2002), indicating that with appropriate resources and political willingness, some of the most important desertification drivers can be controlled.

20.4.2 Monitoring

The monitoring of desertification is an increasingly important development in the management of dryland areas. The establishment of long-term and rigorous monitoring programs is an effective way to assess the status of natural resources and the evolution of desertification processes. Such programs could provide an "early warning" of pending concerns, e.g., the detection of changes in ecosystem attributes and processes at stages where management actions would be most cost-effective (see Fernández et al. 2002).

It is encouraging to see increased research dedicated to the development of easily accessible monitoring methods based on simple soil and vegetation indicators (e.g., Pyke et al. 2002; Tongway and Hindley 1995). These methods are based on the collection of basic information of those vegetation attributes and soil properties (e.g., cover, spatial pattern, resistance to penetration and texture) that largely determine the ecosystem's resilience to erosive forces and its ability to use water and nutrients. An important goal of these methods is to minimize the training and equipment required so as to increase their availability to nations with low economic resources. These ground-based methods are complemented with the use of remote sensing data, which have been successfully employed to monitor desertification processes in the U.S. (Asner and Heidebrecht 2005), South America (Asner and Heidebrecht 2003), Africa (Prince et al. 1998), Australia (Bastin et al. 2002) and Europe (Imeson and Prinsen 2004). Remote-sensing approaches are often based on measuring the same vegetation and soil attributes as ground-based methods, but they allow the establishment of monitoring programs at larger spatial scales. However, they often require the use of expensive equipment and appropriate training, two factors not available in many countries. Furthermore, recent studies suggest that traditional remote sensing measurements (e.g., NDVI measured during the growing season) do not provide an adequate indication of biophysical degradation (Asner et al. 2003). Further advancement in desertification monitoring depends upon a coordination between ground- and remote sensing-based research and the establishment of sound and cost-effective methodologies appropriate for particular regions.

20.4.3 Restoration

While we might hope that future actions of land owners, communities, regions, and nations will begin to adopt management practices and policies that minimize or avoid desertification, the sad fact is that vast areas of drylands are already in a wretched state, with varying degrees of reduced plant cover, impoverished species diversity, and depleted or eroded soils (Whisenant 1999). Restoration actions in these lands have traditionally focused on the biophysical variables, especially those aimed at increasing plant cover and halting soil erosion. Often, and irrespective of the underlying drivers of desertification, restoration efforts involve the establishment of woody plants (Whisenant 1999), which is deemed crucial to stop further degradation, and to foster recovery of ecosystem structure, composition, and functioning (Reynolds 2001). Such afforestation programs, which have been carried out since the 1800s, have resulted in millions of hectares of conifer trees (mainly) planted in drylands of Spain, Turkey, Morrocco, Algeria, Argentina, China, and many other countries (Richardson 1998; Pausas et al. 2004; Sánchez Martínez and Gallego Simón 1993; Gao et al. 2001). While some of these efforts have been effective in controlling desertification, many have failed (Odera 1996), and in some cases have exacerbated the degradation process (see review by Maestre and Cortina 2004).

In other instances, restoring desertified lands has involved instituting changes in land management practices (e.g., Pyke et al. 2002; Sørbø, 2003). Again, these may be undertaken without full understanding of the causal mechanisms involved, or without an appreciation of the socio-economic conditions (Sørbø, 2003), and again are prone to failure. This history of lack of success suggests a clear need to address fundamentals. First, as we have emphasized throughout this chapter, it is important to have a sound understanding of both the biophysical and human dimensions of causality. Second, we must incorporate as much of our knowledge of dryland structure and functioning as possible into our management actions. In this respect, important advances have been made in the application of conceptual and practical ecosystem models. Third, we must carefully evaluate and incorporate existing socio-economic attributes. Fourth, we must assess the potential for successful rehabilitation. Lastly, we must strive for improved restoration methodologies, including the use of new understanding of key ecosystem processes, e.g., plant-plant interactions (Maestre et al. 2001) and the role of soil heterogeneity in plant establishment (Maestre et al. 2003).

20.5 Summary and Conclusions

While conceptual, methodological and technological advances have been made during the past several decades to help land managers establish appropriate strategies for combating desertification, there have been relatively few successes in desertification abatement (Le Houérou 1996). As discussed in this chapter, desertification may have numerous underlying causes, which involve a complex interplay among biophysical and human dimensions. We propose that a key aspect of the prevention and remediation of desertification is the development of a integrative, theoretical framework in which biophysical and socioeconomic components are treated as coupled processes fostering desertification.

We further suggest that the Dahlem Desertification Paradigm provides the necessary theoretical framework for bringing researchers and policy-makers together for the purpose of developing testable hypotheses and methodologies regarding the monitoring, prevention and remediation of desertification. The DDP emphasizes the need to address all socio-economic levels (local, regional, national, international) in the development of effective desertification policy decisions. The DDP emphasizes moving beyond isolated studies of various parts of the desertification problem and toward establishing an integrated program of causal links of dryland degradation, from climate dynamics to ecological impacts to policy response strategies, which can be applied to a wide range of temporal and spatial scales. The challenges of building the necessary political and scientific bridges are enormous, but so is the need for urgent action to understand and manage desertified drylands worldwide.

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Part E

Regions under Stress

Chapter 21

Southeast Asian Fire Regimes and Land Development Policy

Daniel Murdiyarso · Louis Lebel

21.1 Introduction

Fires have long been an important tool for land development and management in tropical Southeast Asia. Fire disturbance regimes vary with forest structure, climate, topography and soils. These regimes have influenced, and been influenced by, the land-use systems of diverse cultures over centuries and millennia, producing diverse histories of fire and landscape dynamics. Low and moderate intensity fires are a regular event in the seasonally dry deciduous or savannah forests of Southeast Asia. These forests contain fire-adapted species and are frequently settled and used by swidden – cultivators. In contrast, fires in the moister evergreen forests of the humid tropics are much more irregular and typically associated with unusual events, for example droughts caused by dry phases of the El Niño – Southern Oscillation (ENSO). In the last 50–100 years the rate and extent of change in landscapes and disturbance regimes has increased substantially as societies throughout Southeast Asia have successfully grown in size, expanded and intensified the agricultural and forestry foundations of their economies, and adopted new management strategies to fire.

One of the side-effects of this success has been a more frequent incidence of synchronous fires, especially in very dry years, when deliberately lit and managed fires get out of control to become wildfires. Depending on wind and atmospheric conditions these events can lead to episodes of haze affecting major cities in other regions (Murdiyarso et al. 2004a; Tomich et al. 1998b). The most extreme episodes in Indonesia and Malaysia over the last 20 years have been associated with dry phases of ENSO and resulted in vast parts of Southeast Asia being covered in smoke for weeks at a time. In the northern parts of Thailand, Vietnam, Myanmar and Lao PDR, fires are an annual event associated with a predictable long dry season. There, the intensification of land-use practices and the creation of protected area networks in upland areas may now be reducing the frequency of fires.

At the simplest level fire regimes are affected by ecosystem conditions, land management practices and climate (Fig. 21.1). Agricultural and forest practices are, in turn, influenced by systems of incentives and constraints on land development, the most important of which are systems of local and state property rights to land and land-derived resources, and diverse sets of policies with strong impacts on land development (Fig. 21.1).

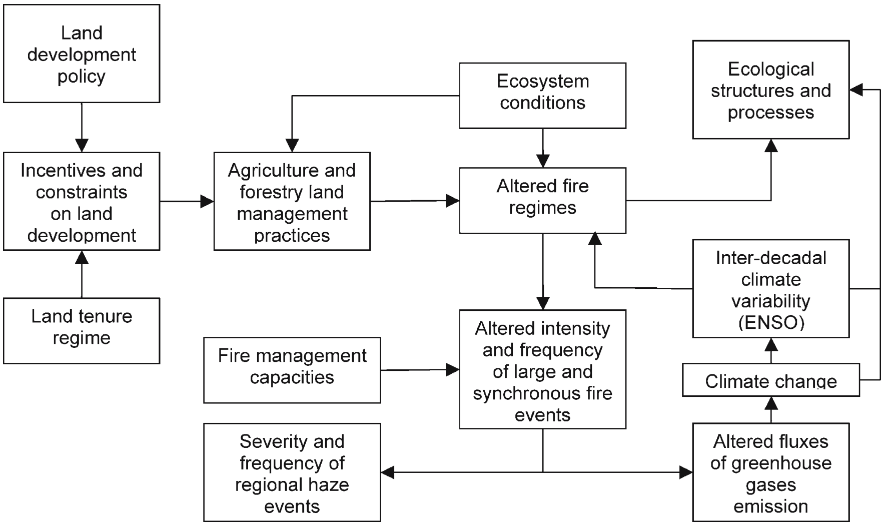

Fig. 21.1. Conceptual framework for how fire regimes are being altered in Southeast Asia

In this chapter we address two overarching questions about land development policies and vegetation fires in Southeast Asia, namely:

1. How have land development policies and changes in land management practices influenced fire disturbance regimes in Southeast Asia? What is the significance of recent changes in fire regimes for local ecosystems and livelihoods, regional air quality and global emissions?
2. How could insights from research about fire ecology, emissions and livelihood impacts be incorporated into development strategies and institutional responses that would reduce the risks of large-scale fire and haze episodes? Are there ways to mitigate undesirable feedbacks on the regional and global atmosphere which would not unfairly disrupt the aspirations of societies in the region to improve their well-being through land development?

The chapter is organized around the broad framework of how human activities are altering fire regimes in the region and the implications this has for ecosystems, livelihoods and feedbacks on the regional and global atmosphere (Fig. 21.1). First, we start with a consideration of what is known about the underlying causes of fires in the region. Second, we consider the immediate ecological and biogeochemical consequences at various scales. And third, we consider how fire has many positive and few negative implications for livelihoods. The chapter ends with a summary of our responses to the two questions.

21.2 Underlying Causes of Land Fires

21.2.1 Explaining Fire Occurrence

The likelihood of fires has been usefully conceptualized as an interplay between *pre-disposing conditions* and *human causes* (Stolle et al. 2003). A multi-factor analysis of factors associated with the distribution of fires from NOAA-AVHRR satellite imagery for 1992–1993 in Jambi province documented interactions between condition- or context-creating factors like climate, elevation, vegetation cover and suitability of land for rubber with more direct human factors like the presence of transmigration projects and timber concessions (Stolle et al. 2003). What is noteworthy from this study is that few fires were accidental. Land development policies and land-use practices were largely driving vegetation fires.

Repeated burning alters the nutrient balance of soils (Crutzen and Andreae 1990) and fires are frequently used as tools by farmers in nutrient-poor soils to take advantage of short-term nutrient releases from burned vegetation. Major fires as well as even more modest understorey fires in closed canopy forests generally increase the likelihood of subsequent fires both in Southeast Asia and the Amazon (Cochrane et al. 1999).

To this we add that past human practices, for example those which make ground conditions drier, alter fuel loads and fragment vegetation, over-time may themselves feedback to alter the "pre-disposing" conditions.

21.2.2 Land Development Policies

A wide range of land development policies have been important in choices of land use, in use of fire for land management, and in fire management practices. Some of the land policies with the most direct effects include forest timber concessions, re-zoning of land for human settlement and cultivation, subsidies for land improvements for specific crops, and irrigation infrastructure projects to stimulate expansion or intensification of production. In Indonesia, Myanmar and Lao PDR, in particular, but in all countries of the region at some stages, resettlement policies backed by varying degrees of coercion and force have been used against swidden farmers, in part, because of perceptions about the negative impacts of their land management practices using fire.

Several other policy areas are not so easy to label as "land development" per se, but their effects may be even larger than some of those listed above because, by altering economic incentives, these policies have much broader reach than rules and regulations that need to be backed by agency actions. In this set, those policies aimed at stimulating (or not) export-oriented agricultural development appear to be particularly important. These include rural credit schemes, trade tariffs, investments in and special deals for agribusiness, for forestry and for forest product enterprises, and monetary policies that influence foreign exchange rates and domestic interest rates.

Fire is often used in conversion of land from forest to agriculture. In Indonesia, much of this expansion has been driven by export-oriented agricultural development policies in recent decades, especially for pulpwood, palm oil and rice, but also by a need to open new land for growing rural populations. Fires may lead or follow other land-use activities like logging (Eva and Lambin 2000).

The history of major fires in Sumatra and Kalimantan, Indonesia, illustrate the interactions with land development policies well. In 1981 the Government of Indonesia released Decree No. 682/Kpts/Um/8/1981 that designated 20–30 Mha of forestland as Conversion Forests (World Bank 1999). Among others, 5 Mha of forest lands were allocated for timber plantations in Sumatra and Kalimantan. This policy sparked extensive fires mainly in those two islands as fire was used as a tool to clear land before plantation activities were established. In 1982 3.6 Mha were burned. The area of oil palm plantation more than tripled between 1981 and the fires of 1997. More than 2 Mha of new plantation was established in less than a decade.

At least as important as the policies on paper has been the rich history of *de facto* policies of the Suharto era that ensured land conversion permits, lucrative timber concessions, and deals for paper mills and associated tree plantations went to friends and family in the military, business and government (Dauvergne 2001; Pasong and Lebel 2000). Throughout this history, fire was often a tool for intentionally degrading land in insurance scams and a weapon of legitimization for land claims or of resistance by displaced people.

Another controversial policy-driven land development was the conversion of around 1.4 Mha of peat-swamp forests in Central Kalimantan (Murdiyarso and Adiningsih 2006; Tacconi 2003; World Bank 1999). The project, legalized by Presidential Decree No. 82/1995 and known as the Mega Rice Project, planned to create some 500 000 ha of rice fields and other tree crops. The construction of 700 km of primary canals (25 m wide and 6 m deep) and of numerous secondary canals has caused substantial drainage and peatland subsidence (Fig. 21.2). The drained area which was prepared to accommodate some 1.5 million transmigrants became susceptible to fire. Around 200 000 transmigrants who had settled there had to leave the area since it was no longer suitable to support their livelihood. Transmigration schemes which aimed to move people away from the densely populated island of Java often failed to live up to their original goals, but nevertheless, had important impacts on land use in many parts of Indonesia. In the strong 1997–1998 ENSO event, 11.6 Mha were burned.

Furthermore, in line with an attempt to decentralize authority, the government of Indonesia launched a new law in 1999 (Law No. 22/1999). As a result many regional regulations were enacted to boost revenues. Unfortunately, the human resources at regional levels could not meet the challenges when extraction of natural resources created new social and environmental problems.

21.2.3 Land Management Practices

In Fig. 21.1 we highlighted fire management capacities. This should be understood to mean not just technical capacities in terms of number of trucks or planes, but also understanding of farmers and local government agencies about how to handle fire regimes which have changed or with which, as new settlers, they may be unfamiliar (Colfer 2001).

Furthermore, at least six distinct interest groups have a stake in the trajectory of land-use change in Sumatra, but there are crucial differences among them in the weights they place on the various economic and environmental outcomes (Tomich et al. 1998a). These groups include the international community, hunter-gatherers, small-scale farmers, large-scale public and private estates, absentee farmers, and public policymakers.

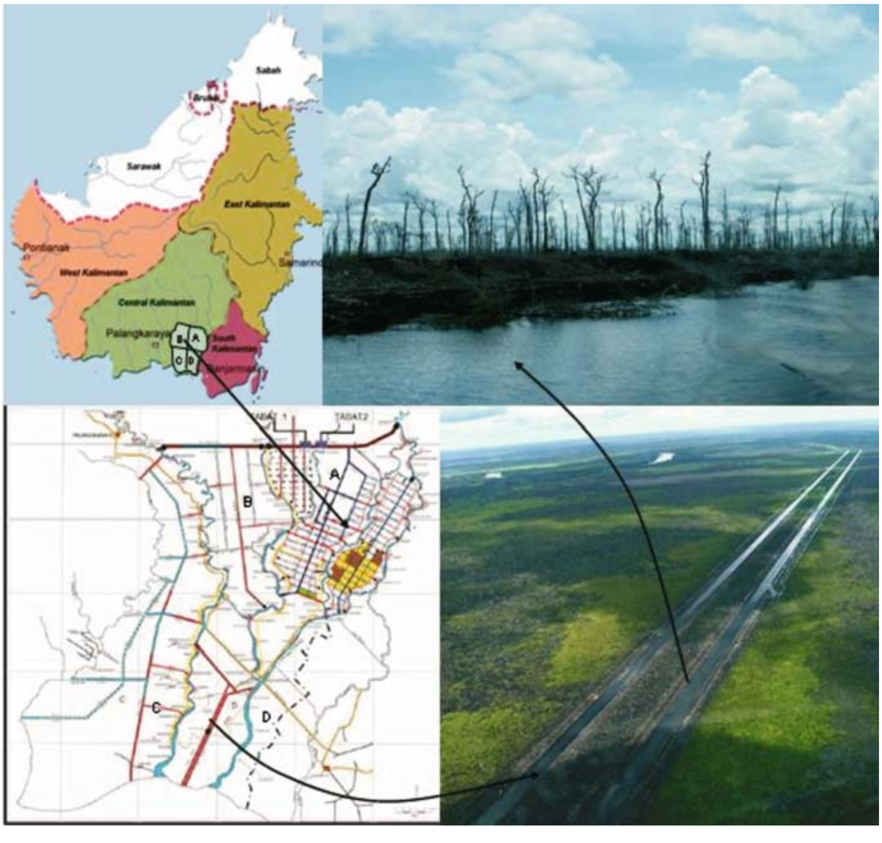

Fig. 21.2. Mega Rice Project in Central Kalimantan, Indonesia (photos: Wetland International-Indonesia Program 2002)

Small-Holder Farmers

Fire is often used as an effective tool for land clearing (Tomich et al. 1998a). Land management practices and the use of fires, however, fall into different categories depending on the intension of land-users. Wibowo et al. (1997) categorized four different types of Indonesian farmers practising shifting cultivation: (1) traditional communities with strong local institutions restricting the actions of individual farmers; (2) communities that are more integrated in the market economy, often combined with a loosening of traditional restrictions; (3) spontaneous settlers/migrants who may have skills but who are usually landless; and (4) government-sponsored transmigrants, who are granted land with titles. Except for the first category, these groups of farmers practice non-sustainable agriculture and bring no significant conservation skills to the management of their agricultural lands. Most of them viewed that burning is the cheapest and quickest way for land clearing.

Fires are used to provide space since they offer cheap and effective means to remove the debris before new plantations are established. Furthermore, fires also provide ash which contains readily available nutrients and controls pests and diseases. This may not be the case for large-scale plantations, especially as to the long-term economic advantages (Simorangkir 2006). In eastern Malaysia exclusion of fire and minimum soil disturbance during plantation forest establishment could double production of wood and strongly reduce environmental impacts (Nykvist et al. 1994). However, this has not automatically led to a reduced use of fire in the region. Slash-and-burn fires are still a common tool for halting or re-directing succession.

The practice is slightly different compared with that used in the peatlands. There, the fires burn much more below-ground biomass and, as the combustion is usually incomplete, they tend to produce a lot more haze over longer periods (Murdiyarso et al. 2004b). Fuller and Fulk estimated that during the 1997/1998 fires, 1.45 Mha of peatlands were burned involving 300 000 ha in Sumatra and 750 000 ha in Kalimantan. The most recent assessment shows that the total area of peatland burned was 2.12 Mha (Tacconi 2003). This is about 10% of Indonesia's total peatland area or 20% of the total area burned in the 1997/1998 fires.

Clearly, policy interventions are needed but, given the variety of fires, they cannot be generalized since each type requires a specific intervention. This confirms the earlier finding that quick fixes by banning fires will not be successful unless they properly address the underlying causes and provide alternatives (Tomich et al. 1998c).

21.2.3.1 *Logging*

Logging and tree plantation forestry have had a major impact on fire disturbance regimes. On the one hand logging has made much of the landscape susceptible to fire during periods of drought, and on the other, management for timber has often involved fire suppression policies. A history of unsustainable logging practises has been reinforced by state corruption that together have exacerbated fire management challenges (Dauvergne 2001).

Logging in closed canopy tropical forest creates canopy gaps and a pulse of leaf litter. The resulting drier conditions are likely to increases the risk of fires (Nepstad et al. 1999). Moreover, after fires occur in a concession the normal restriction on the 20-year cutting cycle is lifted for salvage harvesting, thus creating a perverse incentive for poor fire management (van Nieuwstadt et al. 2001). Logging in the logged-over forests appears to increase the risk of disastrous fires (Siegert et al. 2001).

21.2.3.2 *Forest Management*

Forestry departments in Southeast Asia have adopted models of "land management" based on moist, temperate forest ecologies. The key attitude is that fires are natural disasters and management is about fire suppression to protect property, especially valuable timber, from being burned. Although this may make sense in some forest ecosystems near urban areas, ecologically, and eventually economically, it doesn't make sense in many others. In seasonally dry tropical forests, fire suppression leads to higher fuel loads, more intense fires and the possibility of devastating fires, which take a long time for forest ecosystems to recover from because of massive mortality, destruction of seed banks, and alteration of soil structure (Stott 1988, 1996).

21.2.3.3 *Shifting Cultivation*

Fire is also an integral part of shifting cultivation practices that are diverse and in many ways qualitatively distinct from using fire to clear forests (Dove and Kammen 1997; Fox et al. 2000; Schmidt-Vogt 1998). Some practices, for instance, appear to be particularly effective in maintaining intermediate-level forest cover at landscape scales, with a very diverse spatial mosaic of landscape patches in different stages of succession. Whether or not swidden systems are viewed as destructive to forest biodiversity depends very much on what components are emphasized and to which land-uses such practices are compared (Forsyth 1998, 2003; Schmidt-Vogt 1998). The mosaic landscapes do not support many of the larger mammals needing intact tracts of forest, but on the other hand much other vegetation and small animals may persist in these landscapes and many other watershed functions may be maintained (Forsyth 1996; Thomas 2002). In comparison to plantations or conventional tillage agriculture such systems of course preserve a lot more of the original biodiversity (Schmidt-Vogt 1998; Thomas 2002).

This is brought home by comparing such practices to for example the impacts of conventional lowland agriculture which leads to largely irreversible conversion of land cover. In longer rotational systems there can be very intentional pre-burn preparation of land including lopping and stacking of branches and so on.

Intentional fires to prepare land for upland cultivation of rice and a diversity of other products is common in Lao PDR, in northern Vietnam, and in some scattered locations of northern Thailand, Borneo Indonesia, northern Myanmar and Yunnan province of China.

Lao PDR has pursued a policy of resettling ethnic minorities that utilize shifting cultivation practices from the uplands to the lowlands with the rationale that such practices cause deforestation and erosion. By 1997 the government had established 62 "sedentarisation" sites targeting some 320 000 people. In practice local officials have varied widely in their implementation efforts, and villagers may move to the lowlands for economic reasons rather than as a result of government intervention. Either way, the Akha in Muang Sing who moved to lower slopes were often not able to secure better livelihoods, received little or no government assistance, and instead became a cheap and exploited labor force for lowland Tai (Cohen 2000). In some locations the Akha remain under pressure to continue opium cultivation.

Government policies to limit or end shifting cultivation are found throughout montane mainland Southeast Asia. In combination with macro-economic changes accompanying improved road infrastructure and emerging markets for cash crops apart from opium, this has undoubtedly lead to major shifts in human use of fire in the uplands. After several decades of expansion of areas under shifting cultivation as a result of migration and population growth, there has been a large decline in areas with such practices over the past two decades. As far as we know, however, there has been no detailed study of fire regime changes and their ecological consequences. For example, is the occurrence of fires less frequent now, but when they occur are they more intense? Has the proportion of all fires that are accidental or lightning-lit increased?

21.2.4 Property Rights and Conflicts

The likelihood of destructive fires, both intentional and accidental, appears to be often related to investments in fire protection and management by communities, which in turn is affected by land tenure security and conflicts over land access rights. Insecure tenure and poor relations reduce the incentives for careful fire management. In serious conflicts fire may be used as a weapon, both by smallholders and larger commercial enterprises (Colfer 2001). Thus, in the 1997–1998 fires, estimates suggest that as many as 14% of the fires were related to social conflicts between plantation developers and local communities (Ganz 2003).

In most remote areas it is not the existence of formal state-recognized property rights that matters so much as whether the rights, customary or formal, are recognized by the various local actors. Upland swidden farmers throughout Southeast Asia typically have lacked formal title to the land they cultivate, but nevertheless have continued with well-defined land-use systems in which controlled fires are a crucial tool for food production.

In conflicts between large firms and small-holders, on the other hand, as has been the case frequently in Indonesia, clear systems of property rights appear to help reduce conflicts (Tomich et al. 1998b). Procedures also matter. Communities complain about unheard claims, unfair judicial systems, and non-transparent decision-making processes (Suyanto 2005). When push comes to shove, customary or "*adat*" rights are often not fully recognized by legal systems in the region. In the Philippines, fires in reforestation projects were also caused by conflicts between management (typically Department of Environment and Natural Resources, DENR) and field labourers (typically from local communities). It was not uncommon for newly planted trees to be burned because of some grievance, real or imagined (R. Lasco pers. comm. 2005).

21.3 Landscape, Regional and Global Interactions

21.3.1 Ecosystem Dynamics

Land fire regimes across Southeast Asia vary among locations because of differences in climate, types of vegetation and intensity and form of human activities. Some woody savannas burn very frequently, whereas other moist tropical communities are very rarely burned (van der Werf et al. 2003).

Knowledge about the ecological consequences of fires on tropical forests in Southeast Asia is modest, with most research coming from work on moist but ENSO-impacted forests in Indonesia. For many key processes influenced by humans activities the most detailed understanding so far is based on studies done in Central and South America (Cochrane et al. 1999; Nepstad et al. 2001), and more recently in northern Australia (Edwards et al. 2001; Horstman and Wightman 2001; Yibarbuk et al. 2001). This matters greatly for generalizations because the ecological impacts vary widely across different ecosystems (Eva and Lambin 2000) which is probably reflected by the cultural variation in land-use practices (see Sect. 21.2.1).

Nutrient losses due to volatilization during the burning of residual biomass are generally higher than the losses by leaching (Bruijnzeel 1998). This is not only for nitrogen, which comprises more than 90% of the lost biomass (Note: the sentence reads like if 90% of the biomass burned (presumably by weight) is nitrogen; I assume this is incorrect as N is a much smaller fraction of the biomass; please rewrite accordingly), but often also for mineral nutrients. These high atmospheric losses have been used to suggest the reduction of burning in land-clearing but very little reduction has been implemented. Burning also increases losses by leaching when compared to non-burning practices (Malmer et al. 1994).

As the carbon content of biomass fuels, apart from charcoal, varies over only a narrow range (37–54%) emission factors are largely determined by the combustion process. However, many other chemical species are emitted as trace gases and aerosols and these can vary substantially across both types of vegetation and fires (Andreae and Merlet 2001).

Southeast Asia is home to about 60% of the world's tropical peatlands. The impacts of fire and ecological change in this landscape are probably the area of greatest concern from the perspective of both regional haze episodes and global greenhouse gas emissions. The impacts of fires in Kalimantan were described in detail earlier in this chapter. Changing fire regimes in peat wetlands are an issue not only for Indonesia. Similar problems have arisen in the Melaleuca peat forests of U Minh in the Mekong delta of Vietnam, an area targeted for conservation but where new and enlarged canals have altered the water regime exacerbating the seasonal drying and facilitating the human access that increase the risks of ignition at critical times (Sanders 2002). Likewise, in peninsular southern Thailand road construction, as well as infrastructure for shrimp farms and agriculture, has contributed to some major peat forest fires by altering water regimes. Such fires produce relatively large amounts of smoke and greenhouse gas emissions per unit area.

Ecological interactions with fire are likely, but not well understood in Southeast Asia. Pest outbreaks by causing crown loss and tree dieback may increase susceptibility to fires. There are likely to be important interactions between fire, pest regimes, harvesting and other land management practices (Gower 2003). Post-fire undergrowth and seedbanks are sensitive to additional disturbances. Thus, the damage caused by conventional machinery used in "*salvage*" logging after fires reduces the forest's potential for recovery (van Nieuwstadt et al. 2001).

21.3.2 Regional Haze Episodes

Regional haze episodes are primarily a consequence of synchrony of fire events, strong winds and atmospheric inversions that expose large, sometimes distant, populations to hazardous levels of smoke and haze (Murdiyarso et al. 2004a). Trans-boundary haze episodes pose significant economic and public health burdens. For this reason they attract the attention of the international media and policy makers alike, at least until the next monsoonal rains clear the skies.

In the 1997–1998 fire events in Indonesia there were some indications that permits for clearing land had been held onto in the hope of drier, and thus easier to use, fire conditions eventuating and that these permits were then "used" simultaneously by many farmers when the dry ENSO phase unfolded.

Long-term fire histories in regions of Argentina and the US in which the climate is affected by the El Niño-Southern Oscillation have indicated that major fire years are those after a switch from wetter conditions that built up fuel loads to drier conditions that then rapidly dried out the forests (Kitzberger et al. 2001). In Southeast Asia human activities appear to be a more critical part of the causal fire cluster and to modify the pre-disposing conditions.

21.3.3 Greenhouse Gas Emissions

The 1997–1998 fire events in Indonesia were well studied and provide some of the better estimates of carbon fluxes (Table 21.1).

Default estimates of carbon released from deforestation could be based upon the decomposition of biomass over the lifetime of the wood products, but fire is the most effective and direct means to convert carbon stored in the biomass into the gaseous phase. Fire could also release the enormous below ground biomass stored in the peatlands. Page et al. (2002) made a detailed study of a 2.5 million hectare area in Central Kalimantan from which they estimated 0.81 to 2.57 Gt of carbon were released to the atmosphere in 1997 as a result of peat and vegetation fires in Indonesia. This represents 13–40% of total emissions in that year from fossil fuel burning. The contribution from peat fires was very significant.

The stability of wetlands overlying peat deposits is very important for the global carbon balance as they contain huge deposits. In 1990 Sumatran peatlands covered an area of 7.2 Mha, but this had reduced to 6.5 Mha in 2002. The estimated carbon released during that period was 3.47 Gt (Murdiyarso et al. 2004b). This is one of the more problematic aspects of land development and how it affects fires. Changes in these wetland peat landscapes which result in carbon emissions may be much harder to reverse. Due to the uniqueness of the ecosystems, car-

Table 21.1. Estimates of the carbon fluxes attributable to land fires in various locations during the 1997–98 dry phase of ENSO in Indonesia. Numbers in brackets indicate emissions just from fires in peatlands (Murdiyarso and Adiningsih 2006)

El Nino year	Area burned (Mha)	Estimated C-released (Gt)
1982	3.6	0.45
1987	0.1	0.01
1991	0.5	0.06
1997	11.6 (2.1)	1.45 (0.47)

bon sequestration elsewhere may not compensate the loss in their biological diversity.

Van der Werf et al. (2003) analysed a 4-year infrared satellite dataset from the TRMM (Tropical Rainfall Measuring Mission) and combined this with a large-scale biogeochemical model to estimate global carbon fluxes from fires in the tropics and sub-tropics. The model made estimates of emissions from combustion losses and decomposition due to fire-induced mortality. They estimated that overall the annual direct and indirect carbon losses from fires amounted to about 9% of net primary carbon production in the tropics and sub-tropics.

21.3.4 Interactions with Climate Variability and Change

How precipitation regimes across Southeast Asia will be affected by climate change is still highly uncertain at the spatial resolutions relevant for land management and vegetation community dynamics. Nevertheless, historical observations, experimental studies manipulating soil moisture and modeling, all suggest that climate changes could have major impacts on terrestrial ecosystems (Weltzin et al. 2003). Short-term changes in soil moisture can impact risks of ignition, and longer-term changes in rainfall may influence vegetation structure and litter densities that in turn influence fire regimes. Interactions between precipitation and temperature changes are likely.

Regional land-surface interactions that dominate weather patterns in the Amazon seem less likely to be important in most parts of Southeast Asia because of the predominance of ocean influences on climate in SEA.

21.4 Human Well-Being

21.4.1 Economic and Health Impacts

The regional economic impacts of fires have rarely been assessed, but the 1997–1998 event was so large and clear that several estimates were soon made (Bapenas 1999; Glover and Jessup 1998). These highlighted the importance of losses to the transport and tourism sectors within and outside Indonesia. The most worrisome impact in the public mind, however, was on health which can help explain the declines in tourist visits. The health impacts on inhabitants near fires were likely to have been much higher than on distant populations but longer-term health effects of recurrent episodes of haze and smoke are not well understood and most of the emphasis has been on the discrete transboundary episodes.

For example, in Singapore effective computerized patient information systems and air quality monitoring networks allowed researchers to analyze the association between air quality measurements and diagnoses for haze-related outpatient visits to hospital (Emmanuel 2000). They found that an increase in levels of fine particulate matter, PM_{10} from 50 $\mu g\, m^{-3}$ to 150 $\mu g\, m^{-3}$ was associated with increases of 12–26% in upper respiratory tract illness, asthma and rhinitis. No significant increases of admissions or mortality were noted. Emmanuel concluded that the health effects on Singapore of the 1997 smoke haze were generally mild. A thorough assessment in Malaysia, reporting at the same time as the Singapore study, acknowledged the significant economic costs of the transboundary haze, but concluded that the most serious sources of air pollution for human health were domestic, especially motor vehicles and oil and gas works (Awang et al. 2003).

21.4.2 Livelihoods

Fires have both positive and negative impacts on the livelihoods of people in affected and nearby areas. Most fires in Southeast Asia, as we have seen, are not accidental, but deliberately lit to achieve land conversion and management goals.

The drivers for land-use change, however, are often in part embedded in national development policies that are reinforced by preferential allocation of land for different activities. It is through these mechanisms that large negative impacts on the livelihoods of the poor are to be found, and fire is mostly a side-effect of these rather than a cause. In many remote areas, it cannot be ignored that fire is a tool for land improvements that help stake a land claim. In addition, it is not insignificant the involuntary risks that neighbouring and sometimes distant populations are placed under by smoke from vegetation fires, but neither are they unprecedented disasters – many of the citizens with the largest complaints are in cities filled with exhaust fumes of cars and the investments and consumption patterns of these citizens are driving some of the land-conversions in those distant places.

Road-building in remote areas is a controversial topic throughout the tropics. Obviously, improved infrastructure is important to market-integrated development and provision of basic services. Improved access can also accelerate land-conversion in un-intended places as well as the risks of accidental fires (Nepstad et al. 2001).

The importance of macro-economic conditions is underlined by the interactions between the 1997–1998 ENSO dry event and the Asian financial crisis which simultaneously impacted on livelihoods in the region. Sunderlin et al. (2001) found that dependence on forest resources increased markedly during the 1997–1999 economic and political crisis in Indonesia as unemployed city workers returned to their home villages.

One of the difficult ideas for policy and rural development advisors from developed countries is to understand that the conventional separation of agriculture and forestry activities so firmly embedded in their natural resource management bureaucracies is not the way many smallholder livelihoods have been organized in the tropical landscapes of Southeast Asia. Forestry, including collection, active management and cultivation of useful plants within forests, and farming activities that often include tree-crops, is much more integrated than the rural extension and new state-centric models of property rights can handle. On the other hand, people in the region are remarkably adaptable and willing to try new technologies given appropriate incentives. This often undermines the guiding, somewhat nostalgic, assumptions of non-government actors about aspirations for cash-crops of many smallholders. Much of the debate about alternative fire and related land management practices begins with assumptions about appropriateness of different livelihood and lifestyle activities, a debate which unfortunately is not always well-informed about or with representation of the interests of the farmers concerned. The appropriate use of fire in the tropics is ultimately a political issue to which research-based knowledge, about impacts and likely sustainability, can make a contribution, but not predetermine deliberation around trade-offs.

21.5 Informed Decision-Making and Better Governance

21.5.1 Role of Expertise

Research-based knowledge has been summarized several times as inputs into policy. Nevertheless, there appears to still be a large gap between the information which is needed to strengthen and re-design institutions at various scales to address changes in fire regimes and, in particular, large fire and haze episodes and the contributions which various expert communities have been able to deliver. In part this reflects the tendency for both science and policy to de-politicize issues by emphasizing the technical aspects of fire fighting and prevention or the alternative land preparation techniques, rather than by addressing directly the underlying causes which lie primarily in land development policies and investments. It also is an acknowledgment of some of the inherent complexities in an issue where the drivers, consequences and institutional responses are each significantly multi-scale (Fig. 21.3).

Multilateral and bilateral technical assistance by organizations and governments, such as the Asian Development Bank, the European Union, FAO, UNEP, The World Bank, Germany, Canada, Japan, USA, UK, and Australia has prepared global, regional, and national fire assessments. Capacities of national and local governments have been built up to suppress and mitigate fires. International and national NGOs, such as IUCN and WWF, have also been devoting increased attention to fires and highlighting the underlaying causes and impacts. Some 40 fire projects and missions costing well over US$30 million have worked in Indonesia over the last 20 years (Dennis 1999). Despite the money and effort spent on them, fires continue to burn every year. Thus it may appear to some that efforts to address the "fire problem" have not been effective (Tacconi et al. 2003).

Several other policy initiatives are possible and have in part been taken up. These include development of drought and fire information systems, medium-term forecasting of ENSO drought conditions, and reviews of

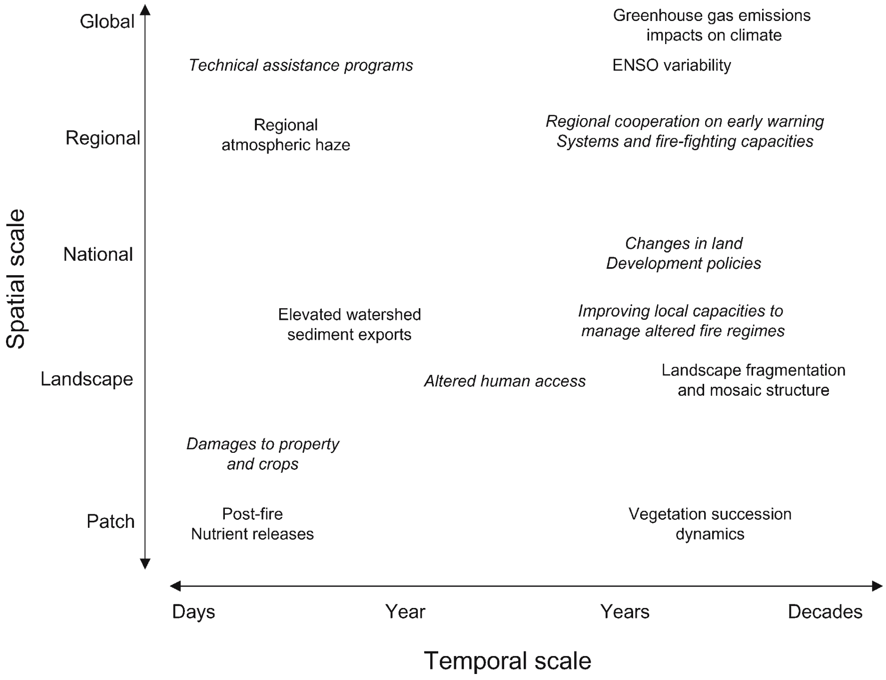

Fig. 21.3. Multi-scale view of the large-scale fire and haze events in Southeast Asia as an environmental and social "problem"

land-use zoning and clearing regulations (Applegate et al. 2001; Murdiyarso et al. 2004a). Proposed zero-burning options do not appear likely to be adopted widely (Murdiyarso et al. 2004a). There are also opportunities to improve the utilization of waste wood after logging by the removal of policies distorting prices (Murdiyarso et al. 2004a).

State capacities are in general limited, given the size of the areas of forest and cultivated lands under their jurisdictions. However, for communities to play an important role in fire management they must have control over forest resources (Ganz and Moore 2002). Where ownership is weak there is no incentive for communities to help. Incentives, however, can also act perversely: in parts of Indonesia communities are paid to fight fires, creating an incentive to light them (Karki 2002). On the other hand, without control of and rights to forest resources, pushes for "community-based" fire management may be seen by governments as a way to obtain "cheap labor" to protect their "forestry" resources. The private sector, in general, has not had responsibilities for fire management of forests commensurate with the benefits it has extracted.

In wetlands, greater attention to the impacts of infrastructure projects on hydrology could remove some of the underlying fire problems. In the provinces of Jambi, South Sumatra and Central Kalimantan, Wetlands International promotes canal blocking in the peatlands to prevent further peat dome subsidence, to improve hydrology and to avoid fires (Murdiyarso et al. 2004b). Controlling the water table is a key issue of peatland management in which local communities are heavily involved. Alternative livelihoods are also promoted by re-introducing local timber species with a high economic value and traditional fishery practices (*tabat*) wherever the water table is elevated.

21.5.2 Regional Cooperation

The Association of Southeast Asian Nations (ASEAN) has been at the forefront of mostly rhetorical attempts to promote regional cooperation on trans-boundary pollution issues, including those arising from vegetation fires. In 1999, after several years of discussions a Regional Haze Action Plan was developed by a Haze Technical Task Force with support from the Asian Development Bank. The widely accepted ASEAN response was expected to be revisited annually (Qadri 2001). The emphasis in implementation, as for example laid out in the Operationalized Regional Action Plan, remains firmly on fire suppression and mitigation. The underlying causes of fires are not addressed (Murdiyarso et al. 2004a).

The legally binding Agreement on Transboundary Haze Pollution (ATHP) adopted in 2002 entered into force in November 2003 following ratification by six member countries. However tension and pessimism with regards to the ATHP remain since Indonesia, the most likely source of such pollution, has not ratified the agreement. Indonesia faces tough institutional challenges in trying to bring together central and increasingly autonomous provincial governments for the implementation of international agreements of this type.

The ASEAN Peatland Management Initiative (APMI) with technical support from the Malaysia-based Global Environmental Centre (GEC) is a promising venture as it has been based on the concept of broad consultation with diverse stakeholders.

Improved fire-fighting capacities and preventative measures, especially with respect to "scaling-down-activities" in seasons with high risks of unintentional fire-spread, are both needed. Research has provided many new insights into the proximate causes of fires, their spread and the climactic and local conditions under which people prefer to light them. All this is useful background understanding to assist institutional and educational interventions. So far, however, this cumulative understanding has not had anywhere near enough impact. In the last few years, the transfers of responsibilities by central governments to local communities and local governments have risen but they have usually not being accompanied by the resources required to build the capacity to understand and manage new fire regime. While the barriers are not insurmountable the challenges are large and will require investments. These should be the focus of regional cooperation and broader technical assistance.

21.6 Summary and Conclusions

Forest and land fires in Southeast Asia are not the apocalyptic ecological and social disasters that are sometimes portrayed by the international media and some experts. However, fire regimes for most landscapes in the region have undoubtedly been altered by human activities, sometimes in ways detrimental to the ecosystems upon which livelihoods partly depend. In the past two decades the changes in Indonesia, in particular, have been rapid and associated with conversion of forest lands to agricultural crops and pulpwood plantations. In this latter context fire remains an important land-conversion and management tool for both larger corporations and small holders.

The challenge is largely one of governance. Alternative visions, objectives and paradigms for the development of the rural hinterlands of Southeast Asia persist (Lebel et al. 2004). Each adopts a narrow set of assumptions about the appropriateness of different ways to manage the complex agricultural and forested landscapes of the region, but without adequate regard for how the knowledge and interests of various stakeholders are to be considered nor how those vested with authorities are to be held accountable (Pasong and Lebel 2000).

At the same time other forces are making the institutional challenges even more difficult. Macro-economic and political changes are placing more of the critical drivers beyond the control of governments and societies in the developing countries within the region. The fire regimes in the tropics of Southeast Asia have been altered by human actions for millennia and undoubtedly will continue to be, but in the future these will increasingly be confounded by the short-term and cumulative impacts of the consumption behavior of distant actors on crop choices, land-use, atmospheric composition and climate change.

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Chapter 22

Global Change Impacts on Agroecosystems of Eastern China

Guangzhou Zhou · Shaoling Peng · Li Zhou · Yuhui Wang · Zhenzhu Xu

22.1 Introduction

Global environmental change and its direct impacts on the living environment and human societies have attracted the attention of international scientific bodies and governments of many countries (Zhang 1994; Ye and Chen 1992; Peng 1997; Peng and Ren 1998; Koch et al. 1995). Research shows that global change is already exerting a detectable influence on the structure and function of natural and agricultural ecosystems, including forest, grassland and farmland ecosystems in China (Liu 1993; Feng et al. 1999; Wang 1965; Xu et al. 1997). Some of the most relevant drivers of global change are the increase in atmospheric CO_2 which has a "fertilization effect" on net primary productivity. In addition, climate change resulting from increased greenhouse gases (GHGs) will also affect the energy balance of the regions, causing changes in water and heat exchanges which largely control the biotic zonation and productivity of ecosystems (Melillo et al. 1993; Zhang 1993; Martin 1990; Li and Wang 1997; Lorius et al. 1990). The resulting changes in the energy balance and biogeochemical cycles will also exert feedbacks on the climate system either enhancing or damping the changes due to increased GHGs (Parton et al. 1993; Neilson 1995; Peng and Ren 1996).

During the last fifty years, the rapid increase in mean annual temperature in China took place mainly in North China. The increasing temperature in the northern part of Northeast China, Inner Mongolia and west basin regions reached a maximum of 0.8 °C per decade. An observable increase in precipitation in China took place in the western basin regions, with a maximum of about 10–15% per decade. However, the precipitation has decreased in North China and the southern part of Northeast China. The projections of climate change in China for the next 100 years based on the China Regional Climate model (RCM) indicates that climate warming will continue, and the temperature will increase about 3.9–6.0 °C by the year of 2100. The maximal increase in temperature will happen in north China during winter season. The mean annual precipitation may increase 11–17% by the year of 2100, and 10–25% in the northwest, northeast and south regions of China (Qin et al. 2005).

Under climate and atmospheric change, agricultural systems will undergo major impacts which will influence the quantity and quality of regional food production. This will require the development of major adaptation strategies to diminish negative impacts and take advantage of changing climate conditions (Luo and Peng 1996). However, in some regions over-cultivation, over-tending, and deforestation have caused soil degradation to become the major obstacle to adaptation and sustainable development of agriculture in China. In addition, urbanization and industrialization in other regions have taken large areas of farmland, rangeland, forest, and water supplies, and increasing environmental pollution will further aggravate the future productivity and viability of agricultural ecosystems (Luo and Peng 1996). Therefore, the study of possible impacts of global change on the agricultural ecosystem of China can provide insights into the development of adaptation strategies under future environmental conditions. This is a prerequisite to ensure the continuous provision of food with sustainable production systems (Parton et al. 1993; Prentice et al. 1992; Running et al. 1993).

Research on the impacts of global change on terrestrial ecosystems has taken many forms and used a variety of experimental and modeling approaches. One such approach has been the use of a large transect expanding different vegetation types and management practices under gradients of climate and other environmental drivers. Transects bridge the gap between discrete observation in plots and comprehensive spatial analysis by fully coupling observations and modeling and forcing them through environmental gradients as test beds of their robustness and appropriateness for detecting non-linear and threshold-like behavior.

The International Geosphere-Biosphere Programme (IGBP) has a core project, Global Change and Terrestrial Ecosystem (GCTE) which emphasized the importance of the ecological transect as a method in the study of terrestrial ecosystem and global change. The principles of transect selection are that the gradient of a particular ecological factor significantly changes along the transect, and the other ecological factors remain almost constant or their changes are quite small, so that the possible process of global change could be revealed by way of temporal-spatial substitution (Zhang 1994; GCTE 1995).

GCTE supported the establishment of fifteen global change terrestrial transects distributed in different key regions of the Earth (Canadell et al. 2002). Two of these are located in China; the water-driven Northeast China Transect (NECT) and the heat-driven North-South Transect of Eastern China (NSTEC). This chapter will report on the highlights of more than 10 years' researches on the impacts of global change (climate, elevated CO_2, and land use) on productivity of agroecosystems, including crops and grasslands from these two Chinese transects.

This paper reports on (1) physiological and plant responses to multiple global change forcing, (2) productivity and its responses to global change, and (3) carbon budget and its responses to global change.

22.2 Chinese Terrestrial Transects

Both transects, NECT and NSTEC, cover one of the regions in China where there are the most people and most food is being produced to sustain an ever growing human population. The transects include diverse ecosystems ranging from remaining native forests to a large diversity of man-made agricultural systems under different management intensities. The region is also under the influence of the Monsoon climate and relies heavily on the rain it brings for food production. Thus, the region covered by the transects is among the most sensitive regions in China for food security reasons.

NECT was established in 1994 and is mainly a rainfall-driven transect centering at 43.5° N and extending 1 400 km from 132° E in the east to 108° E in the west (Fig. 22.1) (IGBP 1995). Annual precipitation decreased sharply from around 800 mm in the east to less than 100 mm in the west. Vegetation types along the transect are determined largely by rainfall gradient and shift from dark conifer forest, conifer-broadleaf mixed forest, deciduous broadleaf forest, woodlands and shrublands in the east, to meadow steppe and cropland in the middle, and to typical steppe, desert steppe in the west (Gao and Zhang 1997). Functional types of plant species, jointly determined by life forms and carbon pathways, are quite different due to the rainfall gradient (Jiang et al. 1999). As a result of increasing human population and fast economic development, the region covered by NECT has been subject to increasing human pressure, including cultivation and overgrazing. Progressive degradation has been reported in the semiarid and arid grassland along

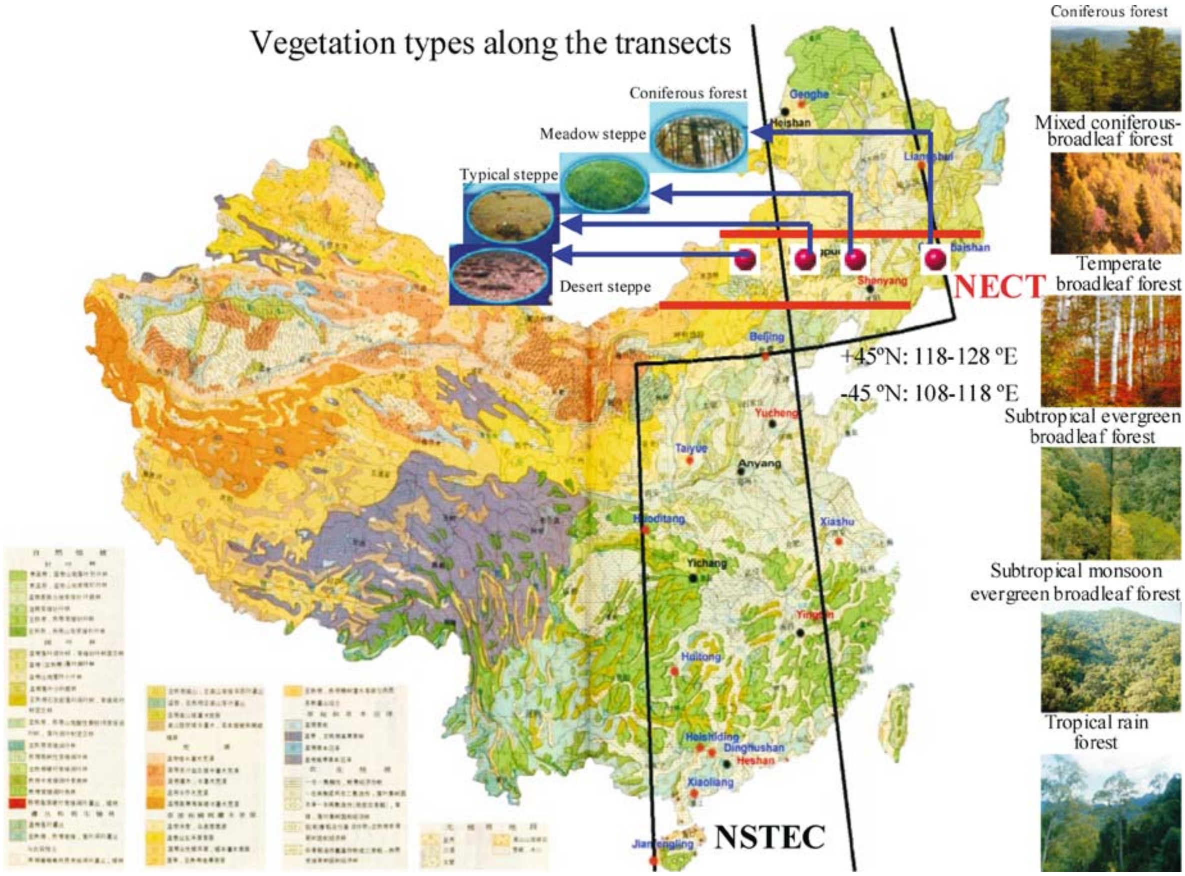

Fig. 22.1. Vegetation types along NECT and NSTEC

NECT during the past 30 years. A general question guiding the NECT is how does water availability influence the composition of plant functional types, soil organic matter, net primary production, trace gas flux, and land-use distribution?(Koch et al. 1995)

NSTEC is composed of two parts: 110–120° E, 15–40° N and 118–128° E, 40–57° N. It covers about 2 889 100 km^2, about 30.1% of the total land area in China. The geographical range covers 1 323 counties from 25 provinces, municipalities, and autonomous regions (Fig. 22.1). The main driving forces along NSTEC are temperature and land use (Teng et al. 2000). Eight vegetation types from south to north have been identified: mountain tropical rain forest, tropical seasonal rain forest, low subtropical monsoon evergreen broadleaf forest, mid-latitude subtropical evergreen broadleaf forest, high latitude subtropical evergreen-deciduous broadleaf forest, warm temperate broadleaf deciduous forest, temperate coniferous and broadleaf mixed forest, and cold temperate coniferous forest.

22.3 Physiological and Plant Responses to Multiple Global Change Forcing

Grasslands are one of the most widespread ecosystem types worldwide; they cover ca. 25% of the natural land surface and account for ca. 16% (18.9 Gt yr^{-1}) of the terrestrial global net annual primary production (Tieszen and Detling 1983). Thus they have a major influence on the functioning of the terrestrial biosphere. The *Leymus chinensis* grassland is a renewable resource to support livestock farming in the northern China. It is widely distributed in the east of the Euro-Asia continent grassland region, and more than half is located in China, especially in the Northeastern China plain and Inner Mongolia Plateau. The western and central portions of NECT are dominated by *Leymus chinensis* grassland. The physiological and whole-plant level responses of *Leymus chinensis* to multiple global change drivers were studied in order to understand how the ecosystem will respond to global change.

In laboratory cabinet experiments, the responses of *Leymus chinensis* to two different treatments: drought (30–45%, 45–60% and 60–80% of field water-holding capacity) and elevated CO_2 (350 ppm and 650–700 ppm) and their combinations were done from May 11 to October 15, 2001 (Zhou et al. 2002). The results indicated that doubling atmospheric CO_2 concentration resulted in increases of 40.9% in total biomass, 35.1% in root biomass, 27.5% in stem biomass and 57.7% in leaf biomass of *Leymus chinensis* during the whole growing season. Drought stress increased leaf water potential and stomatal resistance, and decreased transpiration and photosynthetic rates. However, when elevated CO_2 interacted simultaneously with drought stress, the "CO_2 fertilization" effect was suppressed and biomass production declined by 47.3% when compared with non drought treatments (Zhou et al. 2002). It is different from the more classic thinking that CO_2 fertilization effect will be proportionally bigger in water-stressed regions because of the increased water use efficiency of plants under elevated CO_2. This result implies that the effects of concurrent elevated CO_2 and water stress on water use efficiency of plants are interactive and that the beneficial CO_2 fertilization effects on water use efficiency will not be enough to compensate the negative effects of droughts in the region.

The responses of wheat, corn and soybean to two different treatments: temperature (Table 22.1) and elevated CO_2 (350 ppm and 650–700 ppm) and their combinations were done from November 4, 2000 to May 10, 2001 in laboratory cabinet experiments (Zhou et al. 2002). The results indicated that global warming and elevated atmospheric CO_2 concentration would accelerate crop growth and development and shorten the growth period, provided water is not limiting. The photosynthetic rate of crop and stomatal resistance would increase, and the transpiration rate decrease. During the same phase, the leaf area and biomass of leaf, root and stalk of the crop decreased because of insufficient growing time. Moreover, elevated atmospheric CO_2 and high temperature resulted in a decrease in trace elements (Zn, Fe, Mg, Ca, S) in wheat, soybean and corn (leaf, stalk and grain) with large differences among crops and crop parts, therefore lowering their nutritive values. Basically, the high temperature is a positive effect to the trace elements in wheat, but there is negative effect on soybean grain and positive effect on leaf and stalk (Zhou et al. 2002).

The combination of elevated CO_2, drought and warming will result in little gains despite the benefits of the CO_2 fertilization effect. In fact, results show decrease not only in the productivity of *Leymus chinensis* grassland and crop (wheat, corn and soybean) but also in trace elements (Zn, Fe, Mg, Ca, S) in wheat, soybean and corn.

The photosynthetic physiological characteristics of tree species will affect their ecological distribution and succession status. The photosynthesis light response curves of the potted seedlings of *Pinus koraiensis*, *Picea koraiensis*, and *Larix olgensis*, the dominant coniferous tree species in Changbai Mountains grown under doubled CO_2 (700 ppm) and ambient CO_2 (400 ppm) for two years were determined under a series of light intensities from 0 to 2 500 µmol m^{-2} s^{-1}. The comparison of dark respiration rate (DRR), maximum net photosyn-

Table 22.1. Temperature difference (°C) between treatment and CK

Crops	Nov	Dec	Jan	Feb	1st decade of Mar
Wheat and corn	2.5	4.8	5.8	5.2	0.9
Soybean	1.2	1.1	0.8	0.3	0.0

thetic rate ($A_{\max}$), quantum use efficiency (QUE), light compensation point (LCP), light saturation point (LSP) and photo inhibition point (PP) for those coniferous seedlings indicated that *Larix olgensis* is a sun-loving species with the most obvious response to elevated CO_2 concentration, followed by *Pinus koraiensis*, and the shade – tolerant species *Picea koraiensis* with the least response (Zhou et al. 2002). It implied that *Larix olgensis* might be apt to grow and develop from seeds in the course of ecosystem succession due to the sun-loving characteristics and high photosynthetic rate under elevated CO_2 concentration, followed by *Pinus koraiensis*. *Picea koraiensis* acclimatizes itself to shade environment. However, *Picea koraiensis* shows the most obvious sensitivity to the photosynthetic physiological characteristics of doubled CO_2 compared with those under the current situation, followed by *Pinus koraiensis* and *Larix olgensis*. Those changes will affect the capacity in the competition among tree species, and result in the change in ecosystem composition and tree diversity in temperate forest ecosystems.

We also examined the ecological responses of different tree species saplings (potted) to three soil moistures: 85%~100% (high water, CK), 65%~85% (Medium water, MW) and 45%~65% (low water, LW) of field water-holding capacity. The species selected were *Pinus koraienes*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Tilia amurensis*, and *Quercus mongolica* which are five dominant species in the korean pine-broadleaf forest at Changbai mountain located in the east end of NECT. The results showed that drought treatments significantly decreased the single-leaf area, number of fine root, root length, and individual biomass of seedlings. The root weight ratio was higher than the control. There were different responses to soil water stress for different species. The root weight ratios of *Tilia amurensis* and *Fraxinus mandshurica* increased with increasing soil water content, but the leaf weight ratio of *Juglans mandshurica* and *Quercus mongolica* were higher under MW compared with CK and LW. Biomass was significantly different among the 5 tree species. The biomass of *Tilia amurensis*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Pinus koraienes* decreased by 32.8%, 43.6%, 26.2%, 23.8%, 4.8% respectively, while *Quercus mongolica* showed an increase in 4.8%. It is suggested that *Quercus mongolica* had the highest drought-tolerance among the tested species. It implied that *Quercus mongolica* might replace *Pinus koraienes* to become the dominant species of the temperate forest ecosystems if this region becomes drier in the future because of climate change.

22.4 Productivity and Its Responses to Global Change

The productivity of terrestrial ecosystems is an important index for its health and its response to multiple global change forcing, and it also directly connects with carbon sequestration and its feedback on climatic change. Plant species number, soil C, soil N and aboveground biomass of grassland ecosystems along a precipitation gradient in the west part of NECT showed positive linear relationships with precipitation. In addition, plant species number, soil C and total soil N had strong positive linear relationships with above-ground biomass (Zhou et al. 2002). This suggests that global warming might result in the decrease in grassland productivity, affecting the development of stockbreeding in this area.

The responses of Northeast China Transect to global change were shown by a remote sensing driven regional vegetation model (Gao et al. 1997). It indicated that the potential vegetation of the transect was very sensitive to variation of temperature and CO_2 concentration. With a temperature increase of 4 °C, the induced increase in evapotranspiration could reduce the average biomass and net primary productivity (NPP) over the whole transect by 32.1% and 41.9% respectively. In contrast, a 20% increase in precipitation alone could lead to an increase of the average biomass and NPP by 8.1% and 13.4% respectively. Without changing the climatic conditions, CO_2 doubling could increase the average biomass and NPP by 12.2% and 17.1% respectively. Because of compensation between the positive effects of CO_2 and precipitation increase, and the negative effect of temperature increase, a doubling of atmospheric CO_2, a 20% increase in precipitation and a 4 °C increase of temperature would lead to a 2% reduction in the biomass and NPP of the natural vegetation over the transect.

Yu et al. (2002) modified the remote sensing driven regional vegetation model developed by Gao et al. (1997) to include land use as a constraint to spatio-temporal vegetation dynamics, and applied it to NSTEC in order to examine the combined effects of climate and land use on vegetation distribution, primary production, and nitrogen cycling. The responses of vegetation in NSTEC to global change, under different climatic scenarios, were obtained by subjecting the modified model to different climatic scenarios derived from 7 general circulation models (GCMs): GFDL, GISS, OSU, LLNL, MPI, UKML and UKMH. The simulated vegetation distributions and relative increases in areas of the 8 natural vegetation classes under the altered climate scenarios from 7 GCMs are given in Fig. 22.2 and Fig. 22.3, respectively. The simulations indicated that there were significant increases in the area of deciduous broadleaf forests but unchanged extent of evergreen broadleaf forests under all 7 GCM scenarios. The distributions of all other natural vegetation types decreased. CO_2 fertilization and increases in annual precipitation both enhanced assimilation and exerted positive effects on the competitive ability of broadleaf forests, exceeding the negative effects of increased temperature that increased the evapotranspiration and reduced water use efficiency. Under contemporary climate and present atmospheric CO_2 concentration, de-

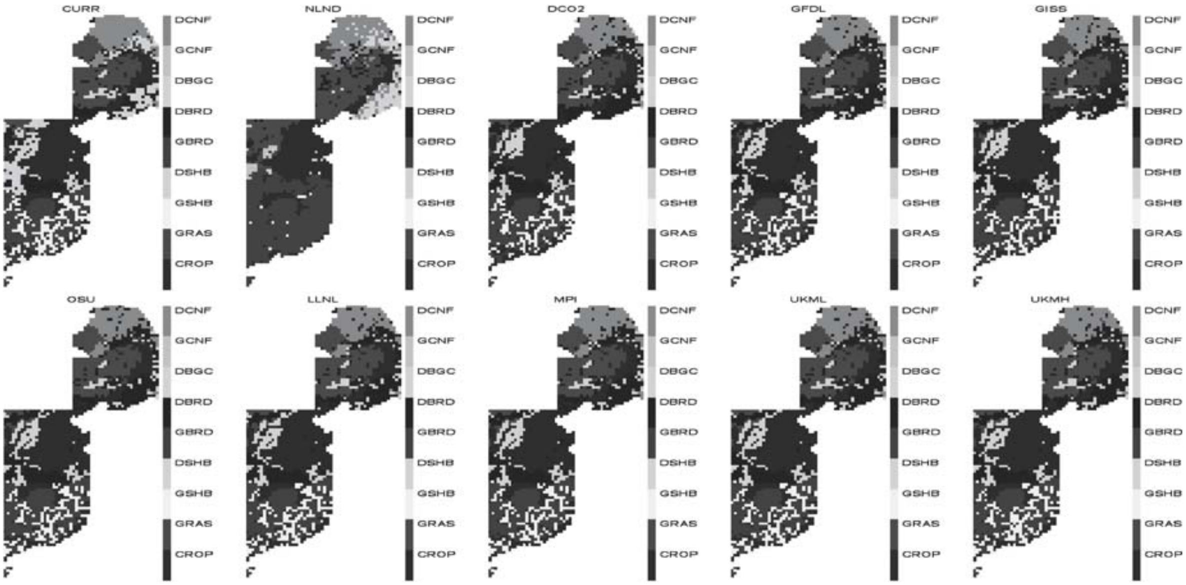

Fig. 22.2. Simulated vegetation distributions of NSTEC under contemporary climate with 350 ppm CO_2 with (CURR) and without (NLND) land-use constraint, with doubled CO_2 concentration but unchanged precipitation and temperature (DCO_2), and with doubled CO_2 concentration and altered precipitation and temperature as predicted by 7 GCMs (Yu et al. 2002)

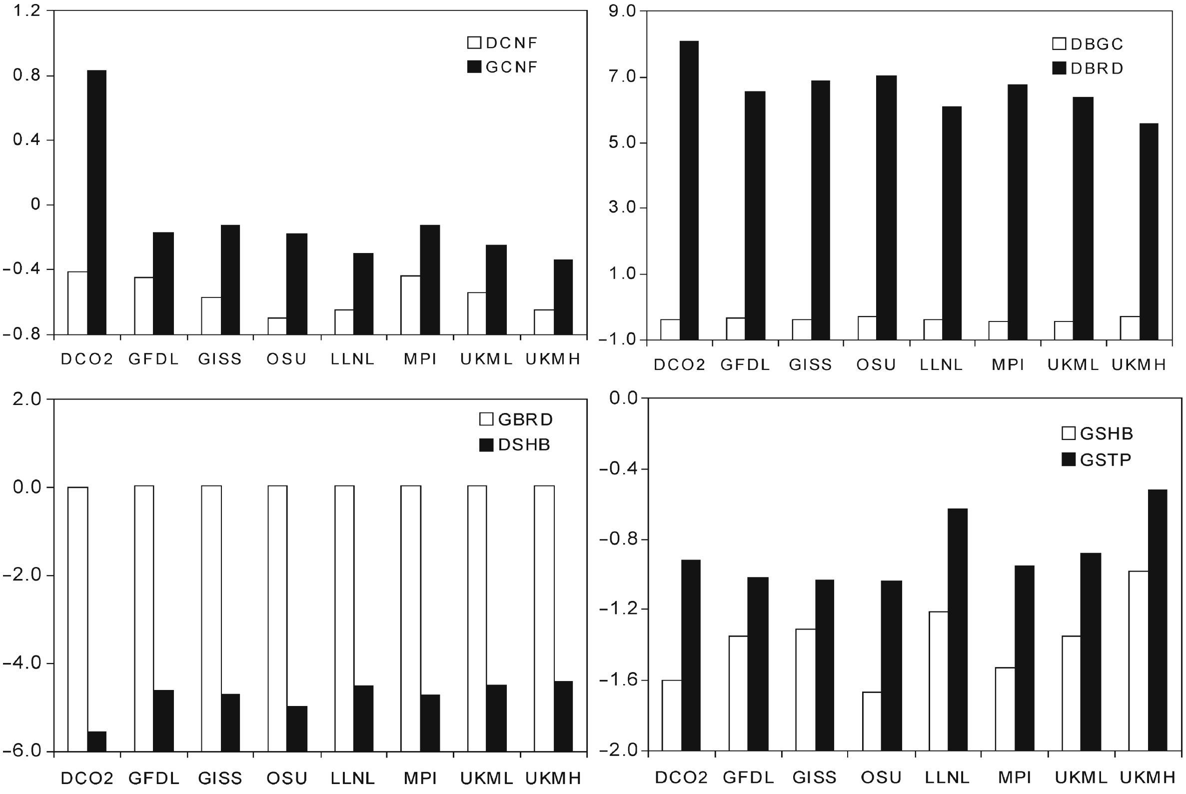

Fig. 22.3. Simulated distribution of 8 natural vegetation classes under doubled CO_2 concentration with unchanged precipitation and temperature (DCO_2) and altered precipitation and temperature as predicted by 7 GCMs (Yu et al. 2002)

ciduous broadleaf forests (DBRD) in the northern NSTEC are more likely to experience drought than evergreen broadleaf forests (GBRD) in southern China. Among the 7 GCMs, OSU and GFDL simulate the highest and lowest increases in precipitation respectively, but with approximately the same low temperature increases. UKMH and LLNL had the highest temperature increases among 7 GCMs, but with similar increases in precipitation. Figure 22.3 illustrates that deciduous broadleaf forests (DBRD) had the greatest increase in occupied area with the OSU scenario, whereas the increase for GFDL scenario was lower than that for the OSU scenario. Therefore, with similar increases in temperature, a higher precipitation increase would lead to a greater increase in area for DBRD because more water was available for assimilation at higher precipitation. The increases in area of DBRD were the lowest for the UKMH and LLNL scenarios because the large increases in temperature for these two scenarios increased evapo-transpiration and hence reduced water use efficiency. This effect of increasing precipitation and temperature on evergreen broadleaf forests (GBRD) is less evident because this vegetation type is mainly located in southern NSTEC where the baseline precipitation is much higher than in the north.

The agricultural climatic divisions of the NSTEC fall into the eastern monsoon agricultural climatic area. The suitability for growing winter wheat and maize based on sown-maturation temperature index were simulated in NSTEC. This was based on monthly and annual temperature and precipitation during 1961–1990 from 1 015 meteorological stations in and neighboring NSTEC (climatic baseline) and the future climatic scenarios given by the climatic baseline plus the change of climatic parameters (temperature and precipitation herein) between the 2030, and 2056 from the HADCM2 output (future climate projections) in Arc/Info GIS. The results show that at present 48.2% of the transect has a suitable temperature for growing winter wheat during winter wheat's sown-maturation phonological period. However, the suitability of wheat declines to 35.6% and 35.3% in 2030 and 2056, respectively, based on future climate projections from the HADCM2. Meanwhile, the proportion of unsuitable land will also be reduced. The land area for the moderately suitable class will increase greatly, from 23.7% at present to 44.28% in 2030 and 44.36% in 2056. If other production conditions could be met, there will be more land area suitable for growing winter wheat. The suitability assessment results for winter wheat production, if based on heading-maturation mean temperature index, are different from the above-mentioned results. The suitable class will drop from 84.5% at present to 67.9% in 2030 and to 61% in 2056. The area for the moderately suitable class will be doubled when the atmospheric CO_2 concentration is doubled. That is, it will increase from 15.2% at present to 32% in 2030 and 38.9% in 2056. Future warming will produce a negative effect on the production suitability of winter wheat in the NSTEC transect. Water is another important factor affecting winter wheat production. Based on the heading-maturation precipitation index, most of the land in the transect will not be very suitable for winter wheat production if there is no irrigation. Both of the classes of suitable and moderately suitable areas will decrease in the future, whereas unsuitable land will increase. This implies that the winter wheat production in the transect will increasingly become more depended on irrigation.

Based on the sown-maturation mean temperature index, the suitable land for maize production will decrease about 2.6% in 2030, and will increase to 72.5% in 2056. There will be little unsuitable land for maize production in the NSTEC transect in 2056. Negative effects of warming on maize production suitability will be less than that on winter wheat production. But, the heading-maturation mean temperature index tells a different story. Based on the index, the suitable land will increase from 12.5% at present to 13.8% in 2030 and to 16.2% in 2056. The unsuitable class land will decrease from 12.2% at present down to 10.5% in 2030, and it will increase to 23.5% in 2056. The moderately suitable class land will remain nearly unchanged to 2030, but it will decrease about 15% in 2056.

The above results show that global change impacts on winter wheat and maize production suitability are different. The direct reasons for this phenomenon are twofold: (1) maize has a wider distribution range than winter wheat, and hence is more adaptive to environmental change; (2) the growing seasons for winter wheat and maize are different. Winter wheat is usually sown in October and harvested in the next June, whereas maize grows in May–October. Studies show that the global warming effect in winter is stronger than in summer, which is why global change will greatly affect the growing suitability of winter wheat and will have less impact on the production suitability of maize in the future.

22.5 Carbon Budget and Its Responses to Global Change

Carbon fluxes from and into agroecosystems mainly include CO_2 and CH_4 emitted from cropland and grassland practices, ruminant animals and their waste treatment, biomass burning and carbon sequestration caused by corresponding land management activities. Of particular interest and importance is the role of soils in the global carbon cycle which affects the composition of the atmosphere and degree of climate change. Whether the soil acts as a source or sink of carbon gases depends greatly on the type and intensity of activities of human management on the land. Generally, intensive use of ecosystem leads to a net depletion of carbon storage compared with lightly exploited ecosystems. For example, conversion of grassland to cropland typically results in a decline in carbon stocks. Conversion of land to agricultural purposes often involves such a decline due to land clearing, draining, sod breaking, cultivating, and replacing perennial vegetation for annual vegetation. For agricultural systems, reduced tillage, reduced bare fallow, irrigation and fertilization are practices that are most likely to achieve substantial rates of carbon gain. Land-use changes, often conversion for agricultural development, accounts for an additional 14% decrease (Lin et al. 2002).

Based on CO_2 fluxes measured along the NSTEC and NECT during 1998–2000, the fluctuation of CO_2 emissions from soils showed obvious seasonal variation and was positively correlated with soil temperature at 5 cm soil depth (Lin et al. 2002; Zhou et al. 2002). The seasonal variation is mainly because the soil temperature is an important factor controlling the microbial activities in grassland soils. The highest emission rate happened in summer. Lin et al. (2002) pointed out that there was an exponential relationship between soil temperature and CO_2 fluxes of natural grasslands ($n = 95$, $y = 1.97e^{0.0681x}$, $P < 0.01$) and also maize fields at the depth of 5 cm during 1997 and 1998 in the Dalate Experimental Station. At Huangpuchuan Experimental Station, correlation coefficients between soil temperature and emission rates were 0.73 and 0.72 ($P < 0.01$, $n = 49$) for natural grassland and restoration grassland in 5 cm soil depth, respectively. For forest soils, CO_2 emission rate is also closely related to soil temperature. At the Dinghu Mountain Station, the CO_2 emission rate was higher in spring, autumn and winter than at Maoer Mountain Station because the soil temperature was lower in northern forests during these seasons than in southern forest area. In the summer season, however, CO_2 emission rates were lower at Dinghu Mountain than at Maoer Mountain because of lower soil temperatures. The variation range of CO_2 flux in north temperate forest soils were larger than in subtropical forest soils due to the wider temperature differences among seasons in northern areas. However, soil types, in addition to disturbance history, vegetation, and topography, modulate a great deal of the relative quantitative relationship between temperature and CO_2 emissions. Conversion of natural ecosystems to managed systems usually results in soil carbon emissions. Continuous observations of carbon fluxes were conducted in conversion lands from natural grassland to other land uses such as grazing land and cropland. In 1998 the data showed that conversion of natural grassland into farmland increased CO_2 emission. The average emission rate of CO_2 from natural grassland was 10.42 kg C ha^{-2} d^{-1} during the growing seasons for grasses, while it was 20.02 kg C ha^{-2} d^{-1} during the growing seasons for maize six years after conversion. The emission rate increased about 100% after the native grassland was converted to farmland. In 1999 and 2000, the CO_2 emission rates from the natural grassland were 10.0 and 9.12 kg C ha^{-2} d^{-1} respectively. In a maize field, the CO_2 emissions were 14.27 and 14.20 kg C ha^{-2} d^{-1}, respectively. Conversion of natural grassland to cropland increased CO_2 emission by 43–100% in sixth to eighth years since conversion. The conversion of natural grassland to cropland not only increased the CO_2 emissions, but also decreased the CH_4 oxidation rate. Measurements at the Yingtan Red Soil Experiment Station during the growing seasons showed that large CH_4 emissions occurred from rice producing flooded soils. Within the same experimental station these emissions show a striking contrast with those from uplands and forests (*Pinus massoniana*) which absorbed CH_4 from the atmosphere. Even upland and grassland acted as a CH_4 sink during the period of measurements, although uptake strength decreased by 41–56% when grassland was converted into farmland. The observations along NSTEC showed that sensitivity of soil carbon emission to temperature, water regime and direct human induced activities under current climate condition would continue in a warmer climate.

Terrestrial ecosystems can absorb large quantities of carbon dioxide from the atmosphere, but some observations suggest that land-use changes are greatly impairing this ability. When land is first converted into agricultural uses, such as conversion of grassland into cropland, conversion of forest into grassland or conversion of forest into cropland, the organic matter in the soil is oxidized quickly at the beginning, slowing over time. In addition, much of the originally existing vegetative biomass is released to the atmosphere as CO_2. Deforestation, biomass burning, drainage, plowing, cultivation, and overgrazing all promote the decomposition of organic matter and the release of CO_2 into atmosphere. Soil degrading processes, such as erosion, crusting and compaction, acidification, and salinification, further exacerbate the loss of soil carbon.

However, measurements from the national soil surveys during 1958–1961 and 1979–1982 as well as the continuous observational record from the observation network established after the mid-1980s by the former National Soil Survey Office of China, show that soil organic carbon (SOC) increased at a level of 11.6 g kg^{-1} in the plowing layer by appropriate management practices through 1985–1995 in cropland soils, an increase in 22% of the area in China (Lai et al. 1999). This suggests that appropriate management in cropland could indeed increase soil carbon stocks, particularly after SOC levels have been decided due to intense land use.

Lin et al. (2002) calculated the potential for agricultural and forest management activities to sequester carbon in the next fifty years in China (Table 22.2). They estimated that carbon sequestration potential is about 77.2 Mt C yr^{-1} (ranging from 26.1–128.3 Mt C yr^{-1}) for these activities during the next fifty years in China. The sustainability of carbon accumulated by management practices will strongly depend on the situation in which they are implemented and the duration of these activities. Due to the wide range of carbon aging rate and ini-

Table 22.2. Carbon sequestration potential of land use practices in China in the next fifty years (Lin et al. 2002)

Activities	Area (Mhm^2)	Feasibility (% of area)	Rate ($t\ C\ hm^{-2}\ yr^{-1}$)	Duration (yr)	C gain potential ($Mt\ C\ yr^{-1}$)	Other GHGs	Confidence
A	*B*	*C*	*D*	*E*	$F = B \cdot C \cdot D$	G	H
Cropland managenemt							
Boreal	18.2	30	0.3–0.6	40	1.6 – 3.3	$+N_2O$	M
Temp. dry	23.7	30	0.1–0.3	30	0.7 – 2.1	$+N_2O$	H
Temp wet	18.7	30	0.2–0.6	25	1.1 – 3.4	$+N_2O$	H
Tropical wet	9.4	30	0.2–0.8	15	0.6 – 2.3	$+N_2O$	M
Sub-total	70.1				4.0 – 11.1 (7.5)		
Rice paddy management	9.4	30	0.2–0.8	25	1.5 – 6.0 (3.7)	$+N_2O, ++CH_4$	L
All agroforest shelterbelt forest	10.0	30	0.1–2.5	50	0.3 – 7.5	$+N_2O$	M
Economic forest	14.9	30	0.1–1.3	8	0.4 – 5.8	$+N_2O$	M
Sub-total grassland management	24.9				0.7 – 13.3 (7.0)		
Temp. wet	35.5	15	0.4–2.0	50	2.1 – 10.7	$-N_2O-$	M
Temp. dry	257.7	15	0–0.3	50	0.0 – 11.6	CH_4	M
Tropical wet	66.6	15	0.3–3.0	40	2.0 – 30.0	$-N_2O-, CH_4$	M
Sub-total	360.0				4.1 – 52.3 (28.2)	$-N_2O-, CH_4$	M
Forest management							
Cold temperate	38.8	20	0.1–0.8	80	0.8 – 6.2		L
Warm temperate(wet)	8.2	20	0.1–3.0	50	0.2 – 4.9		L
Warm temperate(dry)	16.6	20	0.1–0.8	80	0.3 – 2.7	$-N_2O, -CH_4$	L
Tropic and sub-tropic	49.7	20	1.6–3.8	60	15.9 – 37.8		L
Sub-total	113.3				17.2 – 51.6 (34.4)		L
Total					26.1 – 128.3 (77.2)		

tial assumptions used to make these calculations, the uncertainty may be great (listed in the last column of Table 22.2). Most often, activities that decrease the loss or increase the stocks of carbon affect the emissions or removals of other greenhouse gases such as CH_4; relative influence of these activities on other greenhouse gases are also addressed in Table 22.2.

In the absence of disturbance, the simulated temporal dynamics of NPP and total soil carbon by the CENTURY model (Parton et al. 1993) were different at the three sites along NECT (Fig. 22.4). For each of the sites, inter-annual precipitation had a strong effect on NPP, which declined continuously due to decreased precipitation. The relationship between NPP and precipitation was linear (Fig. 22.5), suggesting that precipitation is a main limiting factor for plant growth along NECT. NPP was highest at the mixed coniferous-broadleaf forest ecosystem and lowest at the typical steppe ecosystem, following the mean annual precipitation gradient along NECT. Moreover, the mean annual carbon budgets also showed the same pattern. The value of the carbon budget was largest for the mixed coniferous broadleaf forest ecosystem (503.2 g C m^{-2} yr^{-1}), followed by the meadow steppe ecosystem (227.1 g C m^{-2} yr^{-1}), with the lowest being the typical steppe ecosystem (175.8 g C m^{-2} yr^{-1}). This also indicates that the precipitation gradient is a main driving force along NECT.

The simulated temporal dynamics of total soil carbon along NECT was independent of inter-annual precipitation (Fig. 22.4–22.5). This might be due to the smaller fluctuation of inter-annual precipitation during the simulation. However, the values of total soil carbon decreased from the mixed coniferous- broadleaf forest ecosystem, through the meadow steppe ecosystem, to the typical ecosystem, following the mean annual precipitation gradient along NECT. This suggests some control of mean annual precipitation on soil carbon along NECT implying that to some extent future carbon sequestration will be driven by future changes in precipitation for which large uncertainties still remain.

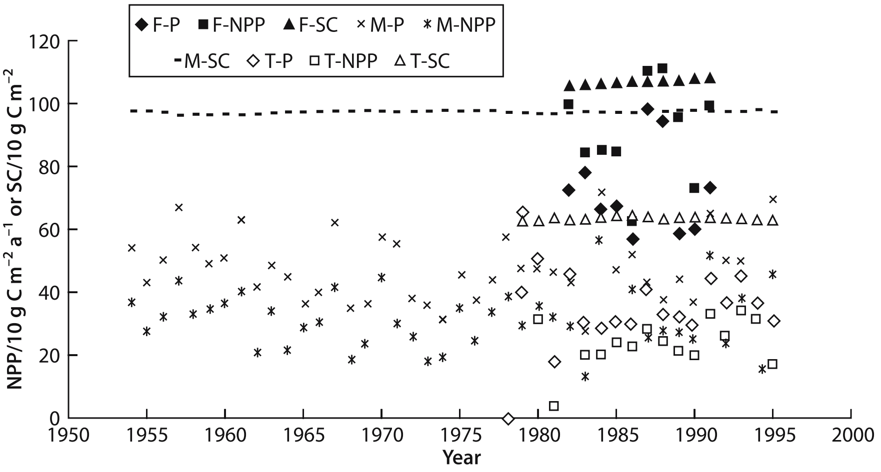

Fig. 22.4. Simulation of temporal dynamics of NPP and total soil carbon using actual weather records from 1982 to 1991 at Changbai Mountains Forest Ecosystem Research Station, from 1954 to 1995 at Changling Grassland Station, and from 1979 to 1998 at Inner Mongolia Grassland Ecosystem Research Station. *F:* Changbai Mountains Forest Ecosystem Research Station; *M:* Changling Grassland Station; *T:* Inner Mongolia Grassland Ecosystem Research Station; *NPP:* 10 g C m^{-2} yr^{-1}; *SC:* total soil carbon (10 g C m^{-2}) (Zhou et al. 2002)

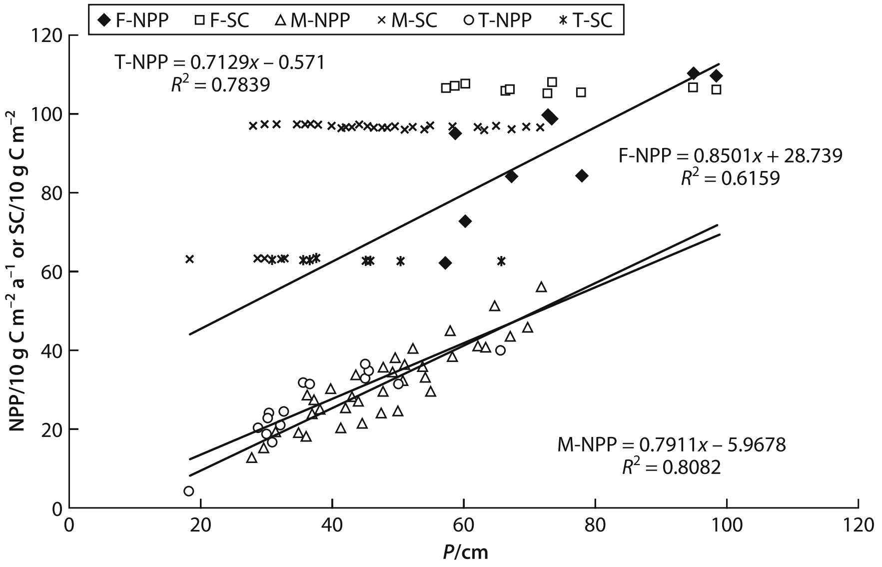

Fig. 22.5. Effects of precipitation (*P*) on NPP and total soil carbon at three simulated sites. *F:* Changbai Mountains Forest Ecosystem Research Station; *M:* Changling Grassland Station; *T:* Inner Mongolia Grassland Ecosystem Research Station; *P:* precipitation (cm); *NPP:* 10 g C m^{-2} yr^{-1}; *SC:* total soil carbon (10 g C m^{-2}) (Zhou et al. 2002)

22.6 Summary and Conclusions

Our limited knowledge on the dynamics of managed and unmanaged ecosystems has curtailed our ability to predict the effects of global change on the ecosystem goods and services that societies rely upon for their wealth and development. Global change terrestrial transects have proved to be an important and useful scientific approach to study the spatial and temporal dynamics of multiple drivers and complex responses. Although a number of studies on global change and terrestrial ecosystems have been done during the recent decade, much remains to be learned of the interactive effects of multiple drivers and their spatial and temporal dynamics which this chapter has presented. In addition, it is recognized that the study of global change not only needs fully effective cooperation of scientists in China, but also needs connection with relevant studies world-wide.

In order to improve integrative global change studies in China and develop the capability to predict the responses of terrestrial ecosystems to global change in China, the following research fields will require further development over the next decade: (1) mechanisms driving responses of terrestrial ecosystems to global change; (2) shifts and adaptation of vegetation and ecosystems to global change; (3) index system of plant functional types of China combined with remote sensing techniques; (4) soil responses to global change; (5) parameterization and scaling techniques in models to study ecosystem dynamics from landscape to regional scales; (6) development of coupled models of the carbon balance, and vegetation dynamics, and atmospheric circulation and climate in order to simulate responses and feedbacks of terrestrial ecosystems to atmosphere and climate changes; and (7) establishment of an information system of terrestrial ecosystems including continuous observations, databases, ecosystem models, and expert systems to observe and predicts changes in terrestrial ecosystems, and to inform policy makers.

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Chapter 23

Terrestrial Ecosystems in Monsoon Asia: Scaling up from Shoot Module to Watershed

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Jun Murase · Eitaro Wada

23.1 Introduction

We carried out research on "Global Change Impacts on Terrestrial Ecosystems in Monsoon Asia" (TEMA) as a GCTE core research project from 1995 to 2003. The purpose of TEMA was to predict the effects of elevated CO_2 and climate change on the distribution and structure of forest ecosystems in eastern Asia, and to determine the associated feedback effects to the global carbon cycle (Hirose et al. 1998). The target region is characterized by continuous forested biomes from tropic to sub-arctic zones under prevailing humid climates, and by the ongoing pressures of land use and pollution. The comparison between a latitudinal gradient where seasonality is amplified with latitude, and an altitudinal gradient in tropical mountains without seasonal thermal change enables us to analyze and describe the climate-vegetation linkage. We made detailed investigations mainly in such core sites as Mount Kinabalu (Malaysian Borneo), the Lake Biwa basin (central Japan), and the Tomakomai Forest (northern Japan), and in many satellite sites scatteed across the target region. The interim achievements of TEMA have been published in separate papers as well as special issues (Hirose and Walker 1996; Nakashizuka et al. 1999). The overall synthesis will be published as a journal special issue (Kohyama et al. 2005). We do not summarize these overall results here.

Our purpose in this chapter is to emphasize certain unique aspects of TEMA, which were not emphasized in other GCTE activities. We particularly focused on (1) the linkage of physiological processes of foliage canopies to landscape-scale processes of population demography and community dynamics, (2) integration of forest ecosystem processes into watershed-scale budgets, and (3) attention to lake ecosystems characterizing watershed-scale land systems. Other GCTE research has focused heavily on responses of physiological and ecosystem processes to global change. However, the prediction of the long-term response of forest systems to global change requires the coupling of ecosystem physiology and tree population demography. To interface the gap between them, TEMA focused on the branch-module-based reconstruction of tree foliage development at smaller scale, and the shift of vegetation zones determined by the dispersion of propagules and the suppression by resident vegetation at larger spatial scales.

Another aspect of TEMA was watershed-scale integration. Recently growing evidence shows that the majority of lotic and lentic waters are supersaturated in terms of CO_2 (Cole et al. 1994), suggesting that the inland aquatic systems function to return C that was fixed in the terrestrial ecosystems to the atmosphere through the biological activities. The inland aquatic systems also function to bury terrigenous organic carbon. According to Dean and Gorham (1998), lakes, reservoirs and wetlands bury organic carbon more than the oceans do, although these cover less than 2% of Earth's surface. Thus, the aquatic systems are likely "hot spots" for carbon processing in terrestrial ecosystems (Hanson et al. 2004).

We therefore focused on carbon flux along the atmosphere-forest-stream-lake continuum at a watershed scale. We found that the stream chemistry reflects biogeochemical metabolism at upstream forest ecosystems. In addition, we found that the carbon metabolism and biogeochemical cycling of inland aquatic systems are tightly linked with allochthonous organic matter input from the watershed and function to determine the fate of terrigenous carbon from the forests. These achievements from TEMA suggest that the effects of global and regional human impacts on terrestrial ecosystems should be examined at the scale of a watershed, as a unit of spatial integration.

23.2 Responses of Plant Communities to the Global Change: Scaling from Leaf to Landscape Through Individual Plant

In many natural plant communities, the local environment one individual experiences is different from that for others. Plants in a stand compete for resources with each other, and competition alters morphological and physiological traits of plants. These alterations in turn change the microclimate and resource acquisition of individuals in the stand, and consequently influence the growth of individuals (Hikosaka et al. 1999). However, studies on plant individuals growing in a stand are very few, which may make it difficult to predict responses of plants to CO_2 at a stand level.

One of the important foci of TEMA was a process-based analysis of environmental responses in population demography in plant communities. We adopted several approaches. We carried out an experimental study of monospecific stands as the simplest plant community. We also constructed a shoot-module-based simulation model, and an individual-plant-based model, to predict the response of plant communities to global change at different spatial scales.

23.2.1 Competition among Individual Plants in Even-Aged Monospecific Stands at Elevated CO_2

Competition among individuals in plant populations is categorized into two modes, i.e., symmetric and asymmetric competition (Weiner 1990). Symmetric competition indicates that individuals in a stand acquire resources in proportion to their sizes while in asymmetric competition large individuals acquire resources more than proportionately. For instance competition for light is asymmetric in dense stands (Ford and Diggle 1981; Weiner 1986; Jurik 1991; Nagashima 1999; Hikosaka et al. 1999), while that for nutrients is more symmetric (Wilson 1988; Weiner et al.1997; Hikosaka and Hirose 2001). The mode of competition is critical in development of size inequality in the stand. Size inequality is generally assessed with the coefficient of variation (Weiner 1990). Symmetric competition, where plant growth is proportional to the size, does not alter size inequality, while asymmetric competition increases size inequality in the stand.

Since diffusion of CO_2 within plant stands is very fast, competition for CO_2 is unlikely to occur among individuals (Jones 1992). Even though elevated CO_2 may benefit all individuals in the stand, the enhancement of growth by elevated CO_2 may indirectly alter the mode of competition (Wayne and Bazzaz 1997). There are two alternative hypotheses in this respect. One is that elevated CO_2 makes the competition more asymmetric and increases size inequality in the stand, because enhanced growth of larger individuals suppresses light acquisition of smaller individuals. The other is that elevated CO_2 reduces the degree of asymmetry in competition and consequently size inequality. This is because the end-product inhibition of photosynthesis due to elevated CO_2 (Stitt and Krapp 1999) may be stronger in larger plants exposed to high light, and because the reduction of the light compensation point of photosynthesis at elevated CO_2 may benefit smaller individuals growing in the shade (Osborne et al. 1997).

To test these hypotheses, we established even-aged monospecific stands of an annual, *Chenopodium album*, at ambient and doubled CO_2 with high and low nutrient availabilities in open top chambers (Nagashima et al. 2003). The growth of individual plants was monitored non-destructively every week until flowering. Elevated CO_2 significantly enhanced plant growth at high nutrients, but did not at low nutrients. The size inequality expressed as the coefficient of variation tended to increase at elevated CO_2. Size structure of the stands was analyzed by the cumulative frequency distribution of plant size (Fig. 23.1). At early stages of plant growth, CO_2 elevation benefited all individuals and shifted the whole size distribution of the stand to larger size classes. At later stages, dominant individuals were still larger at elevated than at ambient CO_2, but the difference in small subordinate individuals between two CO_2 levels became smaller. Although these tendencies were found at both nutrient availabilities, the difference in size distribution between CO_2 levels was larger at high nutrients. The CO_2 elevation did not significantly enhance the growth rate as a function of plant size except for the high nutrient stand at the earliest stage. This indicates that the higher biomass at elevated CO_2 at later stages in the high nutrient stand was caused by the larger size of individuals at the earliest stage. Therefore, the effects of elevated CO_2 on stand structure and size inequality are strongly depended on the growth stage and nutrient availability.

The emerging question is the ecophysiological basis of competition at elevated CO_2. As mentioned above, the difference in size structure results from different size-dependent growth rates of individuals within the stand. In a dense stand, large dominant individuals are better at capturing light. Small subordinate individuals, on the other hand, need less investment for biomass in support tissues because they maintain leaves at lower positions (Givnish 1982), and they can increase biomass allocation for leaf expansion, and partly ameliorate the limited light availability (Anten and Hirose 1998). To indicate the efficiency of biomass use to capture light, Hirose and Werger (1995) introduced the index Φ_{mass}, that is photon flux captured per unit aboveground mass. They suggested that Φ_{mass} might not differ between dominant and subordinate species in multispecies systems. However, plant growth is determined not only by the amount of acquired resources, but also by the efficiency of resource use (growth per unit amount of resource acquired). Hikosaka et al. (1999) defined light-use efficiency of photosynthesis (LUE) as photosynthesis per unit photon interception, and described the photosynthesis of individuals as the product of Φ_{mass} and LUE: $RPR = \Phi_{mass} \times LUE$, where RPR is the relative photosynthetic rate (photosynthetic rate per unit aboveground mass). Provided that plant growth is proportional to leaf photosynthesis, RPR is closely related to the relative growth rate. With a modification of the canopy photosynthesis model of Hirose and Werger (1987), Hikosaka et al. (1999) estimated the photosynthetic rate of individuals in a natural monospecific stand of an annual, *Xanthium canadense*. They found that Φ_{mass} was higher in larger individuals, while LUE was the highest in intermediate individuals. As a conse-

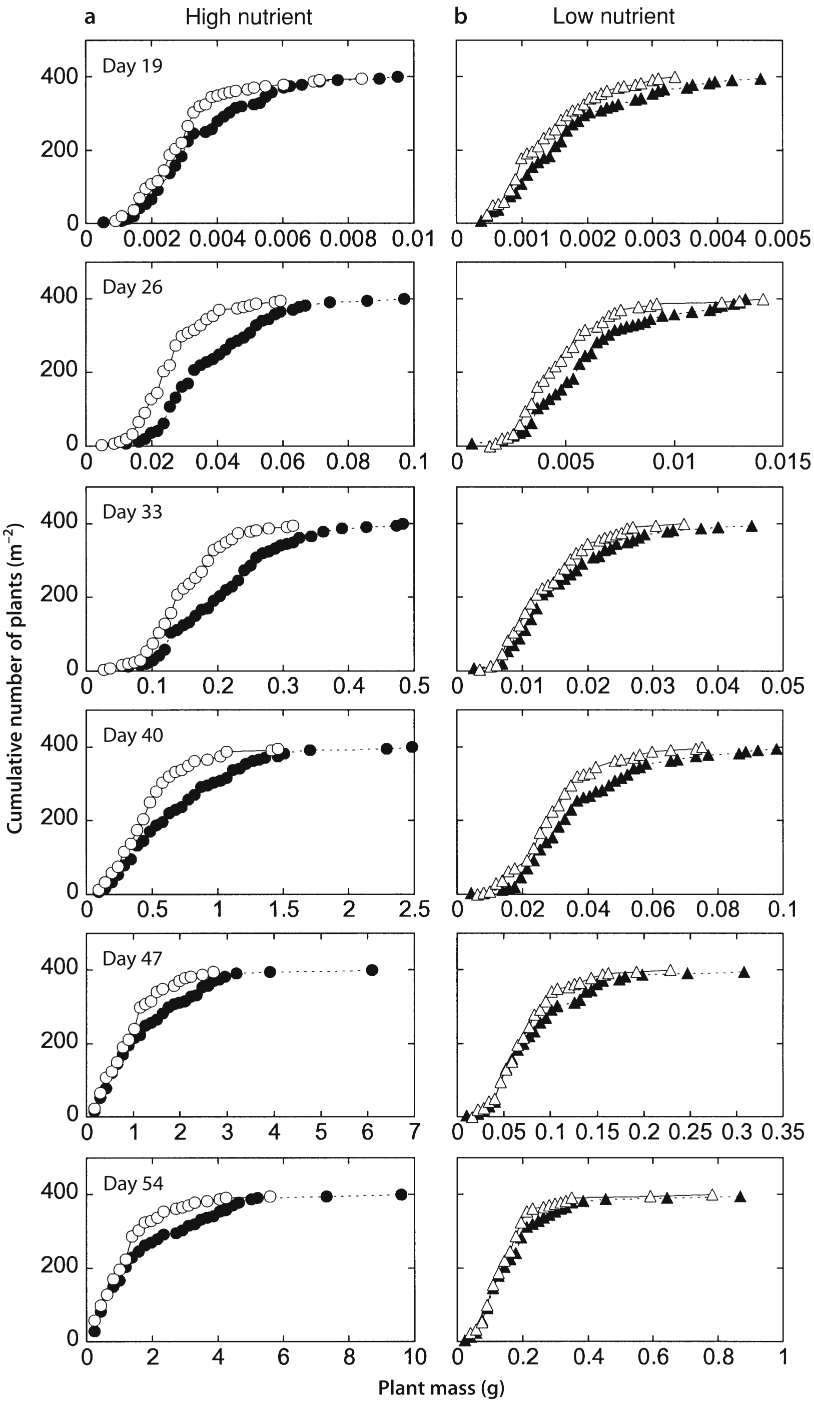

Fig. 23.1. Comparisons of cumulative frequency distributions of biomass in the *Chenopodium album* stands grown at ambient (360 μmol mol^{-1}, *open symbols*) and elevated (700 μmol mol^{-1}, *closed symbols*) CO$_2$ levels, at high (**a**) and low (**b**) nutrients (modified from Nagashima et al. 2003)

quence, RPR was high in intermediate and larger individuals, and lowest in smaller individuals.

We then applied the method of Hikosaka et al. (1999) to analyze acquisition and use of light in individuals in monospecific stands at elevated CO$_2$ (Hikosaka et al. 2003). As in the previous study, we established even-aged monospecific stands of an annual, *Chenopodium album*, at ambient and doubled CO$_2$ concentrations in open-top chambers (only high nutrient availability). The whole-plant photosynthesis of every individual in the stand was calculated from *(i)* the distribution of light and leaf nitrogen and *(ii)* the relationships between photosynthetic parameters and leaf nitrogen content per area. Elevated CO$_2$ increased light-saturated rates of photosynthesis by 10–15% and the initial slope of the light-response curve by 11%, but had no effect on the convexity of the light-response curve and dark respiration. The relative rate of photosynthesis (RPR) was analyzed as the product of

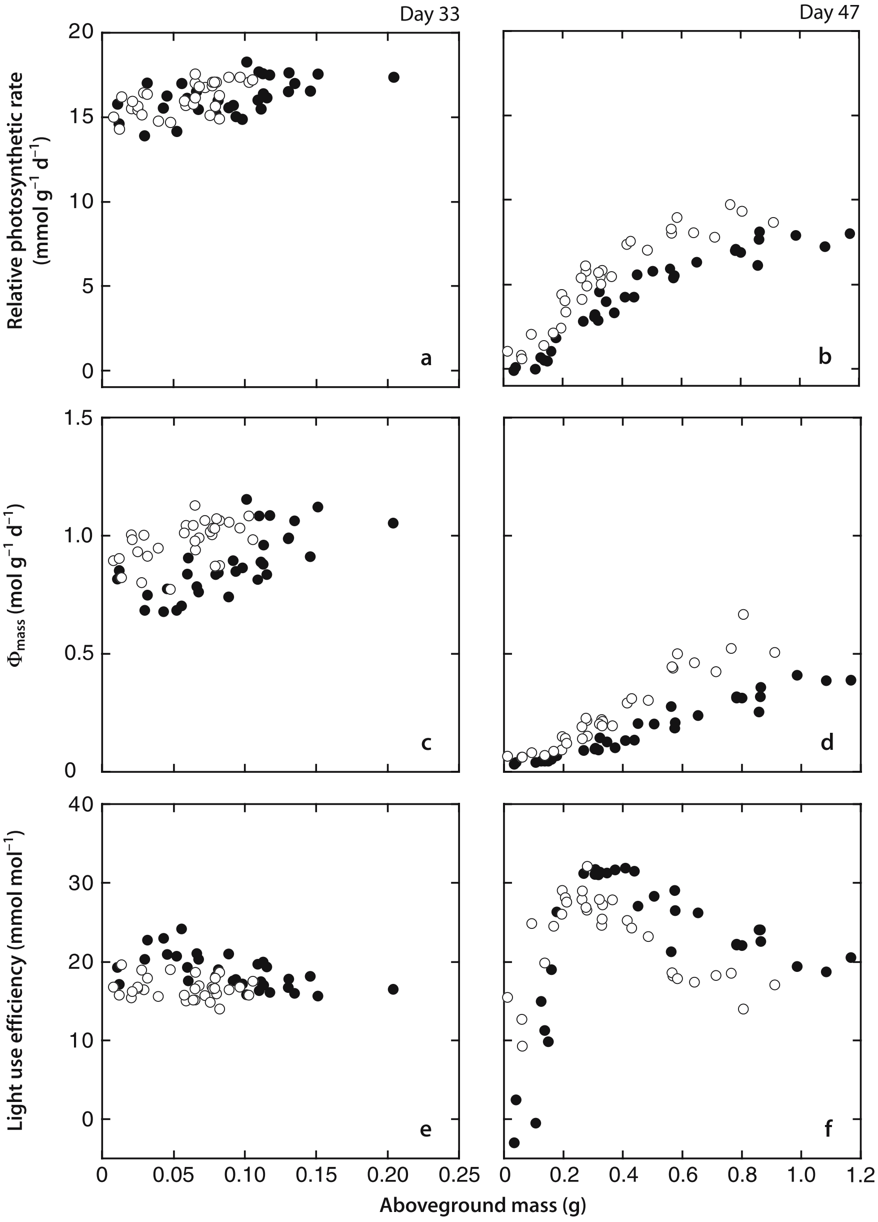

Fig. 23.2. Photosynthetic characteristics in *Chenopodium album* individuals competing in the stands grown at ambient and elevated CO_2 levels. **a, b** Relative photosynthetic rates (*RPR:* whole-plant photosynthetic rate per unit above-ground mass); **c, d** photon flux captured per unit above-ground mass (Φ_{mass}); and **e, f** light-use efficiency (*LUE:* photosynthesis per unit captured photon) as a function of above-ground dry mass at 33 (**a, c, e**) and 47 (**b, d, f**) days after emergence. $RPR = \Phi_{mass} \times LUE$. *Open circles*, ambient; *closed circles*, elevated CO_2

Φ_{mass} and LUE (Fig. 23.2). At an early stage of stand development (33 days after germination), RPR was nearly constant and no difference was found between ambient and elevated CO_2. However, CO_2 elevation influenced the components of RPR such that the reduction in Φ_{mass} at elevated CO_2 offsets the effect of the higher LUE. Later (47 days), RPR was positively correlated with plant mass at both CO_2 concentrations. When compared at an equal plant mass, RPR was lower at elevated CO_2, which was caused by a reduction in Φ_{mass} despite some compensation by higher LUE. We conclude that elevated CO_2 increases size inequality of a stand through enhanced photosynthesis and growth of dominants, which reduce the light availability for subordinates and consequently increase size inequality in the stand.

23.2.2 Shoot-Module-Based Simulator As a Tool of Individual Tree Response

The usual approach of individual-tree-based models is to employ species-specific allometry to relate size dimensions and allocate assimilates into parts (Bugmann 2001). This may not be appropriate because allometric properties change with environment due to plastic modular composition of tree branching architecture (Norby et al. 2001). To integrate physiological responses into an individual-level model of performance, more detailed simulators need to be developed. In the TEMA program, we invented a detailed functional tree simulator to simulate stand-level responses of forest ecosystems to environmental

Fig. 23.3. A 44 year old stand of Japanese subalpine fir forest, simulated by PipeTree. Tree individuals are explicitly described with a population of shoot modules with three-dimensional locations

change. This simulator, named PipeTree, describes current-year shoot growth in three-dimensional space (Kubo and Kohyama 2005). Light conditions that regulate photosynthesis are calculated at each shoot module by monitoring obstruction with in a hemispherical space. Allocation of assimilates into three-dimensional plant architecture is constrained by current-year shoot morphology including leaf/stem ratio, branching rules, and a so-called pipe-model relationship that sap wood area at any position of a stem is proportional to the cumulative leaf area above that position (Shinozaki et al. 1964).

Using observed data of a monospecific quasi-even-aged natural stand of subalpine fir (*Abies veitchii*) population in a subalpine forest of central Japan, Kubo and Kohyama (2005) revised the model structure and tuned physiological and morphological parameters. Figure 23.3 demonstrates a three-dimensional view of a fir stand simulated by PipeTree. The model quantitatively reproduced phenomena of amplified size hierarchy, self-thinning, and allometry shift with stand age. The model also showed that allometry shifts towards slenderer tree forms under elevated atmospheric CO_2.

Physiological-process-based detailed models like PipeTree can provide reasonable parameterization, and/or functional responses of parameters with environmental change, for coarse-scaled individual-based and other models of forest ecosystem dynamics.

23.2.3 Modeling the Shift of Forest Zonation

Available simulation tools of vegetation dynamics at larger scales up to the Earth do not explicitly examine the limit of seed dispersal, which is an essential feature of plants as sessile living organisms. The decline of species diversity is related to the dispersal limit coupled with habitat fragmentation; meanwhile the spread of alien species worldwide is caused by artificial dispersal. Therefore, reasonable models need to incorporate dispersal process.

In the TEMA program, we developed two models with dispersal processes to simulate vegetation shifts with global warming. Kohyama and Shigesada (1995) and Kohyama (2005) extended a tree-size-structure-based model into a geographic landscape. In the model, a tree species population is distributed in geographic space (distribution range) and at each location (size distribution and patch age structure). Dispersal capacity is expressed by a coefficient of dispersal at the smallest size. The dispersal coefficient (with units of squared distance) is similar to a diffusion coefficient but is defined not for a unit time but for a unit seeding event. When run for a scenario of a century-long warming followed by fixed warm climate, the model projected that extant forests would respond to warming without remarkable time lags by changing size structure and biomass. However for the boundaries between forest zones there were extreme time lags. It took thousands of years to attain new steady-state boundaries, and a tenfold increase of dispersal coefficients increased the movement of boundaries less than two-fold. This delay of boundary shifts was brought about by the 'mass effect' of existent forests (adapted to cooler conditions) that prevented the invasion of more-adapted forests in warmer conditions. Because species have broader potential niches than realized niches, and because established trees are long lived, such competitive depression of boundary shifts by resident forest zones resulted. If there were no neighbor forest types, a forest species could readily shift its distribution without an obvious time lag.

Takenaka (2005) proposed another type of vegetation dispersal simulator, based on a lattice model where one cell of the lattice corresponds to an individual tree. Dispersal probability is expressed there by an exponential function from the mother-tree cell. Establishment occurs only when seeds are dispersed to vacant cells, or canopy gaps. The model similarly simulated the millennial delay of forest boundary shifts. It also suggested that species diversity declines at the range of forest type shift due to random drift, and one species that happened to establish in a new site eventually dominated the landscape.

The framework of these models needs to be incorporated into dynamic global vegetation models (DGVMs) to predict changes in biome zones, or the failure of adaptive distribution of biomes, in response to global change.

23.3 Carbon Budget at the Forest Watershed Scale

Carbon biogeochemistry in forest watersheds consists of photosynthesis, autotrophic and heterotrophic respiration, changes in biomass above and below the ground, litterfall, decomposition of organic matter, changes in the storage of soil organic matter, and leaching of dissolved and particulate carbon to groundwater

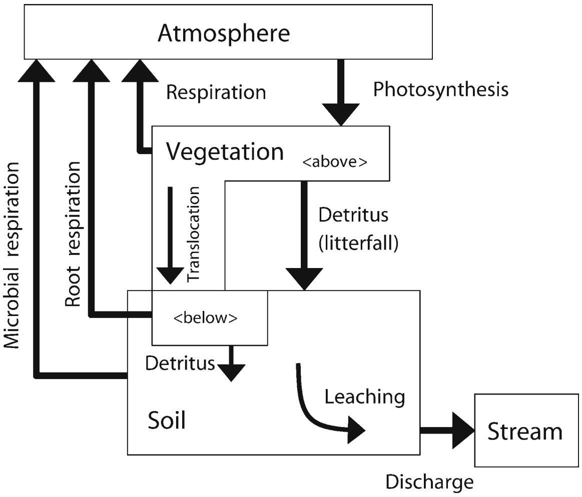

Fig. 23.4. Compartment model of carbon flow in a forested watershed

and streams (Fig. 23.4). Here, we focus on current results and a synthesis of the biogeochemical processes of carbon in forest watersheds based mainly on work conducted during TEMA.

23.3.1 Carbon Exchange between Atmosphere-Forest-Stream Boundaries

Eddy-correlation techniques for assessing CO_2 flux in the forest canopy provide quantitative information on net photosynthesis and respiration (for both vegetation and microorganisms), also referred to as net ecosystem exchange (NEE). NEE is a critical index for the quantitative assessment of the extent to which atmospheric carbon dioxide has been sequestrated by the ecosystem. In the Horonai River basin located in northern Japan, the NEE flux observed using the eddy correlation method (1999–2001) was 258 g C m^{-2} yr^{-1} (SD = 36), with atmospheric carbon dioxide sequestrated mainly during the growing season from June to September (Tanaka and Tanaka 2002; Shibata et al. 2005). Yamamoto et al. (1999) reported that NEE flux ranged from 65 to 136 g C m^{-2} yr^{-1} (mean = 106) in a temperate forest located in central Japan, which suggests that the inter-annual variation in regional climate is reflected in the inter-annual variation in NEE flux. Carbon exchange between forests and the atmosphere is driven by biotic factors such as photosynthesis, respiration, and nutrient conditions, and abiotic factors like solar radiation, temperature, air stability and others. While the expected increase in anthropogenic nitrogen pollution in the Asian region over the next few decades (Galloway and Cowling 2002) is likely to affect the future dynamics of NEE in this region, the effect of nitrogen deposition on carbon sequestration is still under discussion (Lloyd 1999; Nadelhoffer et al. 1999).

Table 23.1. The annual carbon budget of a cool-temperate forest basin (1999–2001; Horonai River in Tomakomai Experimental Forest, Hokkaido University, northern Japan)

	g C m^{-2} yr^{-1}
Net ecosystem exchange (NEE) = *a*	258
Increment of biomass = *b*	108
Leaching to stream = *c*	4
Net storage of carbon in the ground (= *a* – *b* – *c*)	146

In the NEE budget analyses, increases in above-ground biomass and leaching in streams are useful measures that can be employed to better understand the role of vegetation and soil in the carbon sequestration from a quantitative perspective. Since the budget for NEE (input) and leaching in streams (output) is indicative of the net storage or release of carbon (so called net ecosystem production (NEP)) in the watershed, respectively, the difference between NEP and the carbon accumulated in the vegetation corresponds to the net carbon storage (or release) for the soil system. In the Horonai River basin, the annual rate of increase of carbon in vegetation, the extent of leaching to streams, and the net carbon storage in the soil were 108, 4 and 146 g C m^{-2} yr^{-1}, respectively (Table 23.1, Hiura 2005; Shibata et al. 2001; Shibata et al. 2005). Furthermore, it was found that 41% and 57% of the NEE were retained in vegetation and soil, respectively. Since the mean residence time of carbon is markedly different for vegetation and soil, the relative partitioning of sequestrated carbon in the ecosystem is a very important consideration when predicting the effect of carbon dynamics on environmental change. However, the cumulative effect of possible sampling errors means that budget analyses are inherently difficult. These include: *(i)* difficulties in measuring eddies during periods of high atmospheric stability and the irregularity of the canopy surface, *(ii)* the large spatial heterogeneity in the vegetation of the watershed, *(iii)* the large temporal and spatial variation in residence times associated with the leaching of carbon into streams. Consequently, indirect or direct estimates of the carbon contributions from above and below-ground biomass, combined with the quantification of fine root production and mortality, will be one of the most effective means of ameliorating the effect of the aforementioned uncertainties associated with assaying carbon storage in the ground (Shutou and Nakane 2004; Satomura et al. 2003).

23.3.2 Transport of Dissolved Organic Carbon Associated with Dissolved Nitrogen from Terrestrial to Aquatic Ecosystems

Although the annual flux of dissolved carbon into streams was generally very small when compared with that associated with gas exchange between the terrestrial ecosys-

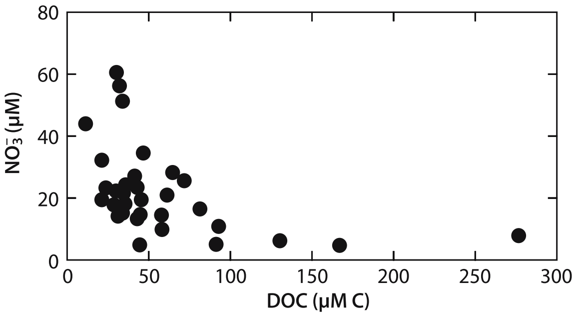

Fig. 23.5. The relationship between dissolved organic carbon (DOC) and nitrate (NO_3^-) concentrations in 35 natural streams in the Lake Biwa watershed, central Japan (modified from Konohira and Yoshioka 2005)

tem and the atmosphere, the supply of dissolved organic carbon to lotic and lentic ecosystems is an important source of energy for aquatic biota and as a source of secondary emissions of carbon dioxide from water surfaces. The quantitative and qualitative fate of dissolved organic carbon was different for each watershed. This is due to the heterogeneity expressed in terms of microbiological activities, reaction to the solid phase, hydrological flowpass in the ground, and the interrelationship between carbon and nitrogen cycling in forest ecosystems (Shibata et al. 2001; Neff and Asner 2001; Katsuyama and Ohte 2002; Konohira and Yoshioka 2005). Consequently, the flux and concentration of dissolved organic carbon in stream water can be a useful biogeochemical signature of carbon cycling in catchment ecosystems. Nitrate (NO_3^-) concentrations in streams are also important biogeochemical signatures of nitrogen cycling. In the Lake Biwa watershed in central Japan, an inverse relationship was observed between dissolved organic carbon (DOC) and NO_3^- concentrations in 35 natural streams (Fig. 23.5; Konohira and Yoshioka 2005). In a regional analysis of the variability in DOC and NO_3^- concentrations in stream water collected from two regions outside the Lake Biwa watershed, it was found that forest streams have high and variable NO_3^- concentrations with low DOC concentrations near Tokyo (an urban area in central Japan), while in northern Hokkaido (a cold, rural area in northern Japan) streams had high and variable DOC, and low NO_3^- concentrations, respectively (Konohira and Yoshioka 2005). These results suggested that the forest biogeochemical processes that affect DOC and NO_3^- concentrations are closely related to each other.

The relationship between DOC and nitrates in forest streams has also been reported in England (Harriman et al. 1998). Since the inorganic nitrogen in the soil is produced by the decomposition of organic nitrogen and then consumed by nitrogen immobilization, the decrease in nitrogen immobilization that arose as a consequence of a decrease in available carbon explains the increase of NO_3^- in soil (Hart et al. 1994). A carbon (energy) deficit with an excess of nitrogen available in the soil will result in low DOC and high NO_3^- in streams. Conversely, a nitrogen deficit in the presence of excess carbon will result in leachate that has high DOC and low NO_3^- concentrations being transported to streams. Stream DOC and NO_3^- concentrations will therefore be useful indices of carbon and nitrogen availability in forest catchments.

The transport of carbon and nitrogen from terrestrial ecosystems to streams also tends to fluctuate seasonally depending on each watershed environment. Shibata et al. (2001) indicated that direct input of litterfall as POC from riparian forest to stream was strongly affected by the phenology of the riparian canopy, while the DOC and DIC in the stream was influenced by the water infiltration rate the ground, with a longer retention time in Horonai River watershed, northern Japan. Seasonality of the climate and biological productivity are important drivers for the leaching of the dissolved nitrogen and carbon to the stream. Ohte et al. (2001) revealed that high temperature and precipitation during summer increase stream NO_3^- concentrations in central Japan, while higher discharge during snowmelt was important for NO_3^- leaching in snow-dominated regions of northern Japan. They emphasized the importance of the seasonal interrelation between hydrological processes in the ground and biogeochemical production of dissolved nitrogen (mainly nitrate) in soil for the temporal fluctuation of dissolved nitrogen in stream water in monsoon regions. Typhoons, which are episodic hydrological events, also enhance export of DOC to stream, especially in subtropical to tropical regions in Monsoon Asia (Kao and Liu et al. 1997).

23.3.3 Dynamics of Dissolved Organic Carbon at the Interface of Stream and Lake Ecosystems

Riverine export and watershed processes are important for modifying the terrestrial sink of anthropogenic CO_2 emission (Kling et al. 1991; Ludwig et al. 1996). The DOC concentration in rivers is usually higher than that of particulate organic carbon (POC) (Ludwig et al. 1996; Webster and Meyer 1997). Furthermore, DOC is an important component in stream and lake waters not only as an energy source, but also as a mediator of optical properties of waters. Since humic substances, which are major parts of DOC being exported from forest ecosystems, absorb sunlight, DOC controls the penetration of sunlight in rivers and lakes, and filters UV-B radiation for aquatic organisms (Schindler et al. 1996). Dynamics of DOC are, thus, important for understanding the biogeochemistry in watershed-scale land ecosystems.

Stream DOC concentrations exhibited a linear correlation with humus-like fluorescence intensity in the lake watersheds of Lakes Hovsgol, Baikal, Biwa and Shumarinai, although the slopes of these regressions differed slightly between the different watersheds (Hayakawa et al. 2003; Yoshioka 2000). The results suggest that humic substances were predominant in stream DOC, and the chemical composition of the stream dissolved organic matter was relatively homogeneous among watersheds. However, such a correlation was not found in the pelagic areas of these lakes. The surface DOC concentrations of Lake Biwa mainly fluctuated during the period at which stratification occurred (from March to November), with a concomitant gradual decrease being observed in the humus-like fluorescence intensity. These findings indicate the production of autochthonous DOC and that the humic substances were derived from the watershed (allochthonous) and subsequently decomposed in the lake. The increase in the protein-like fluorescence observed in the surface layers of Lake Biwa also suggested the autochthonous production of dissolved organic matter (Mostofa et al. in review). Since humic substances are highly resistant to biological degradation, the change in the humus-like fluorescence intensity observed in the lake may instead be attributed to photodegradation. The change in the position of the peak humus-like fluorescence, determined using a three-dimensional excitation emission matrix, suggested that the alteration of the humic substances could be attributed to solar irradiation (Hayakawa et al. 2003; Mostofa et al. in review).

23.4 Carbon Budget and Functions of the Lake Biwa Ecosystem

To understand key processes determining the function of aquatic habitats in terrestrial carbon balance, we measured and analyzed the budget and the fate of C in a lake ecosystem in the TEMA program. We chose Lake Biwa for this model study. Lake Biwa is the largest lake in Japan and one of the ancient lakes, with a surface area of 674 km^2, a mean depth of 41 m, a watershed of 3 848 km^2 and a water retention time of ca. 5.5 years. The lake was originally oligotrophic. However, due to development in the watershed for the past 40 years, the lake has become moderately eutrophic. At present, the lake is mesotrophic and supplies water resources for 14 million peoples living in the Kinki District of Japan. The following estimates were made in the north basin, which accounts for 99% of the water volume of this lake.

23.4.1 Carbon Budget in the Lake

The concentration of particulate organic C (POC) in Lake Biwa ranged from 0.2 to 1.1 g C m^{-3} in the surface mixing layer (0–15 m deep), but was less than 0.3 g C m^{-3} in the hypolimnion (>15–20 m deep). The pattern coincided with seasonal and vertical changes in phytoplankton abundance (Yoshida et al. 2001). Similarly, the concentration of dissolved organic C (DOC) was high in summer in the surface layer (1.4 g C m^{-3}) but became vertically homogeneous in winter (~1.0 g C m^{-3}). Based on monitoring data, the annual input of allochthonous organic C (POC + DOC) per unit area of Lake Biwa was 9.6 g C m^{-2} yr^{-1}. The net primary production rate in the surface layer in the Lake Biwa ranged from 0.3 to 2.7 g C m^{-2} d^{-1} and algae fixed 323 g C m^{-2} annually (Urabe et al.1999; Yoshimizu et al. 2001). Thus, autochthonous input of organic C is 30 times higher than the allochthonous input (Fig. 23.6). Nonetheless, the share of allochthonous C was <40% of DOC in the surface mixing layer and 50–60% in the hypolimnion (Yoshioka 2000), implying that allochthonous organic C is less respired compared with autochthonous organic C. Interestingly, organic C corresponding to 90% of the allochthonous input flowed out annually from the north basin of Lake Biwa (Yoshimizu et al. 2002). Since most organic C from the inflow rivers was humic substance and since its concentration was seasonally stable in the lake water (Yoshioka 2000), a substantial fraction of allochthonous organic matter seemed to flow out from the lake without being consumed efficiently within the lake.

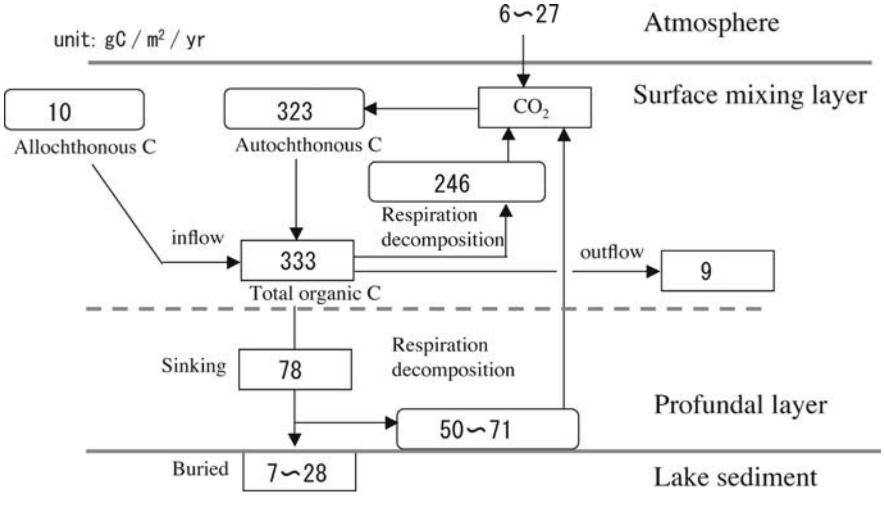

Fig. 23.6.
Carbon budget at an offshore site of Lake Biwa

Of the organic C in the surface water, 78 g C m^{-2} yr^{-1} was transported annually to the profundal layer (Yoshimizu et al. 2001), implying that 75% of the organic C was respired within the surface layer. From the age of lake sediments determined by ^{210}Pb and ^{137}Cs and the abundance of organic C at the lake bottom (Murase and Sakamoto 2000; Urabe et al. 2005), the annual rate of organic C burial at the lake bottom was estimated to be 7–28 g C m^{-2} yr^{-1}. This implies that 64–90% of the organic C exported from the surface layer is respired or decomposed at the profundal layer and/or the lake sediments. This number is smaller than burial rates in lakes with surface areas < 500 km^2 but larger than those in larger lakes such as Lake Micigana and Lake Bikal (e.g., Dean and Gorham 1998). In addition, it is in accordance with the oxygen consumption rate (~180 g O_2 m^{-2}) during the stagnant period in the hypolimnion of the Lake Biwa (Kumagai and Fushimi 1995). According to its $\delta^{15}N$ signature, 40% of organic matter in the lake sediments was estimated to be terrestrial in origin (Murase and Sakamoto 2000). This suggests that allochthonous organic matter is selectively stored in the lake sediments due to less efficient utilization by living organisms.

These estimates show that the *P*/*R* ratio of Lake Biwa is 1.02~1.09, implying that C fixation slightly exceeds CO_2 production. This is because the allochthonous organic matter is much less discharged compared with primary production and less efficiently utilized by organisms. Note that the present C budgets did not consider horizontal transports of organic matters within the lake. In this lake, pCO_2 at the surface water was less than saturation level from spring to fall, but its annual mean was 397 ppmv because CO_2 in the water was supersaturated in winter (Urabe et al. 2005). Thus, as a whole, the Lake Biwa ecosystem functions as a C source. Indeed, there are estimates that the community respiration rate of heterotrophs exceeds the net primary production at an offshore site. The slight discrepancy between the C budgets of the biological community and the pCO_2 observations may be due to decomposition of organic matter produced at the littoral area.

23.4.2 Metabolism in the Lake Sediments

The lake sediments are characterized by the concentrated accumulation of organic carbon. Standing stocks of organic carbon in the upper most layer (2 cm) of the sediment were estimated to be 9.2×10^{10} g C for the whole lake (Murase and Sakamoto 2000). This value is 2.5 times higher than the estimated amount of carbon in the whole lake water (3.6×10^{10} g C). The littoral sediments and the deeper layer of the profundal sediments showed higher contribution of terrestrial organic matter than the surface layer of the profundal sediments (Murase and Sakamoto 2000).

Except for the top few millimeters, the bottom sediments of the lake are anoxic and methanogenesis is the major terminal carbon metabolism. Potential methane production rates of the profundal sediment (0–25 cm in depth) ranged from 2.4–24 mg C m^{-2} d^{-1} (Murase and Sugimoto 2002). Carbon isotopic data for methane and CO_2 in the sediment suggested that hydrogenotrophic methanogenesis was the major pathway (Murase and Sugimoto 2001). A part of the produced methane was stored in adsorbed form in the lake sediment (Sugimoto et al. 2003), but some was diffused up to the surface, where 80–90% of diffused methane was oxidized (Murase et al. 2005). The methane oxidation rates at the sediment surface are comparable to the rate of oxic carbon mineralization (17–20 mg C m^{-2} d^{-1}) and these rates accounted for 50–160% of the estimated carbon sedimentation rate (Murase, unpublished). Our estimates suggested that the increase in oxygen consumption rate by 50% potentially makes the surface sediment anoxic causing the catastrophic change in gas metabolism of the sediment. In addition to eutrophication, an increase in temperature of the bottom water due to the global warming (Hayami and Fujiwara 1999), which caused enhancement of microbial activities, prolonged stagnant periods, and lower solubility of oxygen, would accelerate the oxygen depletion in the sediment.

The potential methane production rate in the littoral sediments was approximately 5 to 10 times higher than that in the profundal sediments (Murase and Sugimoto 2002). At the littoral area, substantial methane diffused from the sediment across the oxic-anoxic boundary into the lake water during the stagnant period (Murase et al. 2003). Disturbance of the surface sediment by internal waves of the lake seemed to accentuate transportation of methane from the sediment to the lake (Sakai et al. 2002), which can be major sources of dissolved methane in the whole lake water (Murase et al. 2003).

23.4.3 Terrestrial Environment and Function of Lake Ecosystems

Considering the watershed and lake surface areas, the discharge rate of allochthonous organic carbon to, and carbon burial rate in, lake Biwa are two orders of magnitude lower than the NEE in the temperate forests in Japan, but almost comparative to the outflow rate of organic carbon to streams from the forests (Sect. 23.3.1 and Table 23.1). Thus, standing water is a potentially important arena determining the fate of organic carbon leaching to streams from the forests. This suggests that even slight changes in the carbon budget in the forests may have serious impacts on lake ecosystems.

According to del Giorgio et al. (1994), the *P*/*R* ratio of lake ecosystems becomes > 1 with increasing the trophic condition. This implies that the function of lake ecosys-

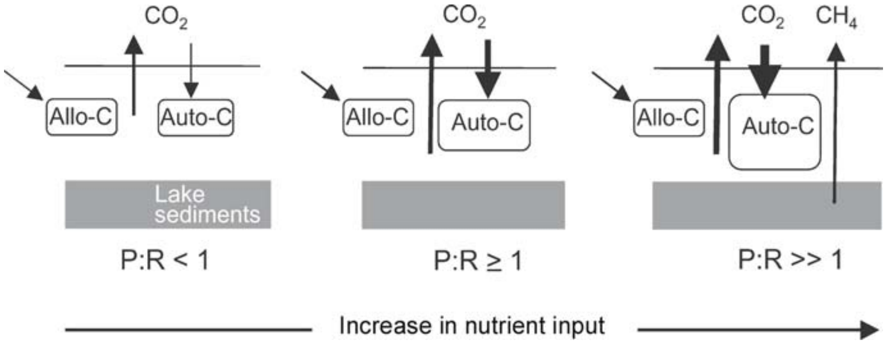

Fig. 23.7. Changes in lake ecosystem functions in terms of C sinks/sources as a function of increases in nutrient loadings. *Auto-C:* autochthonous organic carbon, and *Allo-C:* allochthonous organic carbon

tems is changed from C sink to C source with increasing nutrient loading from the watershed. In Lake Biwa, the primary production rate is nutrient limited (Urabe et al. 1999). Therefore, increase in nutrient loadings would increase C sequestration from the atmosphere through increased C fixation rate and push this lake toward a C sink. Progress of further eutrophication due to anthropogenic activities in the watershed, however, may turn the lake ecosystem to vent gasses that are more efficient for warming (Fig. 23.7). An increase in the sinking flux of organic C due to increased primary production promotes oxygen consumption in the profundal layer and lake sediments. Global warming would accelerate the oxygen consumption at the lake bottom by increasing water temperature at the profundal zone and reducing vertical mixing in winter. This may, in turn, promote the emission of methane, a more efficient gas for global warming than CO$_2$, from the lake sediments to the atmosphere.

As such, it is most likely that the function of lake ecosystems in terms of being a C sink or a C source depends on the land cover and land use, and thus the anthropogenic activities, in the watershed. Unfortunately, only a few studies have included aquatic habitats when carbon balance of terrestrial ecosystems is examined in Asian area (Kao and Liu 1997; Ludwig et al. 1996; Sarin et al. 2002; Shibata et al. 2001). Considering future anthropogenic development in Monsoon Asia and the potential importance of inland aquatic systems as a hot spot where terrigenous carbon is processed, studies at a watershed scale are essential to assess impacts of changes in carbon budgets in terrestrial ecosystems under elevated CO$_2$ and climate change.

23.5 Summary and Conclusions

A GCTE core project "Global change impacts on terrestrial ecosystems in Monsoon Asia" (TEMA) has been carried out from 1995 to 2003. This chapter overviews the TEMA-employed unique approach of integrating across different scales, i.e., from a plant leaf to watershed budgets, targeting on the eastern Asian region. We particularly focused on the linkage between physiological processes of foliage canopy and landscape-scale processes of plant demography and plant community dynamics, where individual plant processes were integrated from physiology, and we projected the change in geographic pattern from individual plant processes. We evaluated the watershed unit where freshwater chemistry provides a signature of biogeochemical characteristics of terrestrial ecosystems. Stream chemistry controls the trophic condition of lake ecosystems, which can contribute to global change particularly through methane emission. Integration at the scale of watersheds will contribute, within the scope of the new GLP in relation to LOICZ, to the validation of the impact of environmental change on human society, and the impact of human activities on watershed-scale environments.

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Chapter 24

Responses of High Latitude Ecosystems to Global Change: Potential Consequences for the Climate System

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24.1 Introduction

Terrestrial ecosystems of high latitudes occupy approximately one-fourth of the Earth's vegetated surface. Substantial climatic warming has occurred in many high latitude areas during the latter half of the 20th Century (Serreze et al. 2000), and evidence continues to mount that this warming has been affecting the structure and function of terrestrial ecosystems in this region (Stow et al. 2004; Hinzman et al. 2005). It is important to understand these changes because they may have consequences for the functioning of the climate system, particularly in the way that *(a)* radiatively active gases are exchanged with the atmosphere, *(b)* water and energy are exchanged with the atmosphere, and *(c)* fresh water is delivered to the Arctic Ocean (Chapin et al. 2000a; McGuire et al. 2003). The exchange of water and energy has implications for regional climate that may influence global climate, while the exchange of radiatively active gases and the delivery of fresh water to the Arctic Ocean are processes that could directly influence climate at the global scale.

Over the past decade the IGBP-GCTE high latitude transects have become important foci for research on responses of high latitude terrestrial regions to global change (Steffen and Shvidenko 1996; McGuire et al. 2002). This network of transects (Fig. 24.1) includes two in Siberia, the Far East Siberian Transect (FEST) and the East Siberian Transect (EST); one in Scandinavia (SCANTRAN/SCANNET), which has been augmented by carbon storage studies along a transect in Finland; one in Canada, the Boreal Forest Transect Case Study (BFTCS); and one in Alaska.

The high latitude transects generally span substantial temperature gradients (mean annual temperature of 5° to –15°C) both within and among transects (McGuire et al. 2002). Temperature along each transect co-varies with precipitation and photosynthetically active radiation. Disturbance regimes including fire and insects are also variable among the high latitude transects. For example, fire is essentially non-existent in much of Scandinavia, but burns annually an average of approximately 1% of the boreal forest along the EST (McGuire et al. 2002; Fig. 24.2). Similarly, land-use and land-cover change also varies among the high latitude transects (Kurz and Apps 1999; McGuire et al. 2002, 2004).

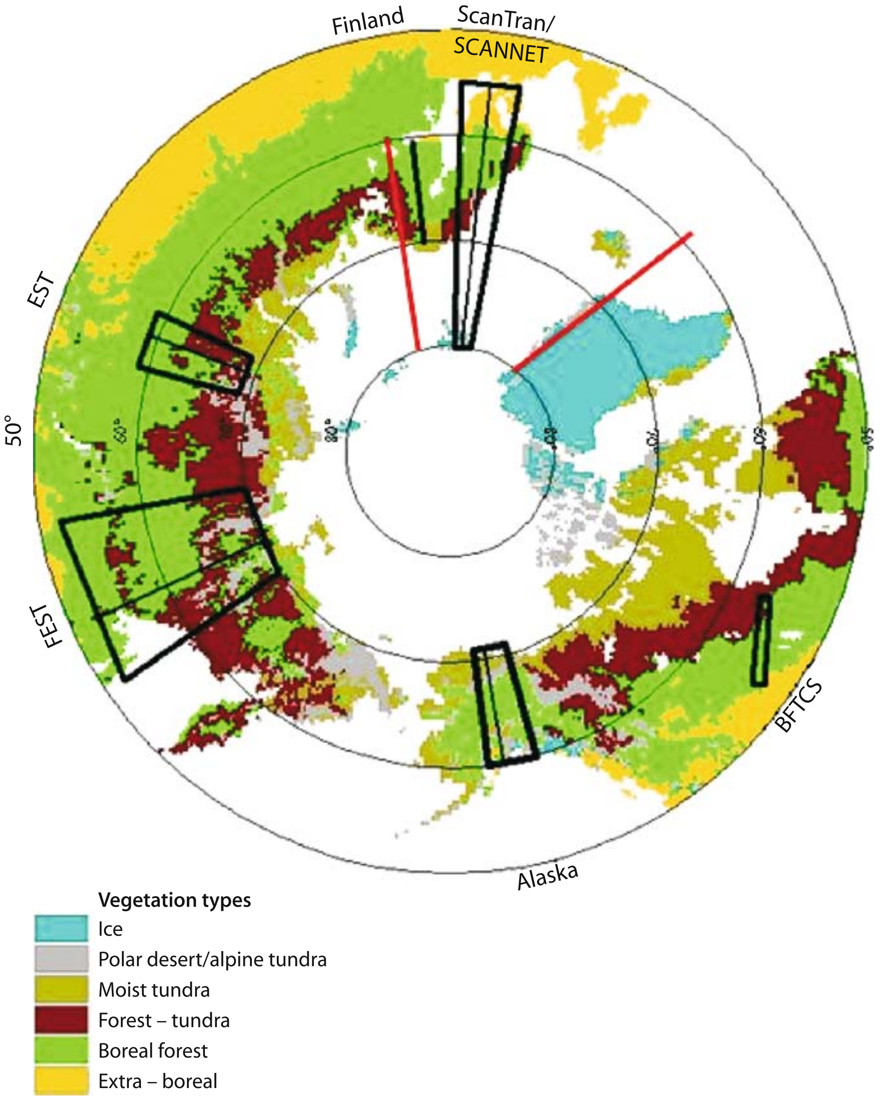
Each of the transects provides a different perspective into the responses of high latitude ecosystems to global change. In this chapter we first summarize how climate, disturbance regimes, and land cover in high latitudes have changed during the last several decades. We then summarize the results of ecological research along these transects that have contributed towards a richer understanding of high latitude terrestrial responses to these changes. We conclude with a discussion of challenges and opportunities for integration.

24.2 Recent Changes in Climate, Disturbance Regimes, and Land Cover

Temperature. While temperature has changed substantially in high latitudes during recent decades (Serreze et al. 2000), changes have not been uniform. Warming has been most pronounced in continental Siberia and in Alaska, with most of the warming occurring in winter (December–February) and spring (March–May) (Serreze et al. 2000; McBean et al. 2005). During the last century, northern Scandinavia experienced warming during the 1920s and 1930s, cooling from the 1940s until the 1960s, and warming since the 1970s; this pattern mirrors the global mean temperature trend over the last century (IPCC 2001). In recent decades, air temperatures have increased substantially in western Canada (Serreze et al. 2000). While eastern Canada generally cooled since the 1970s (Serreze et al. 2000), the cooling appears to have ceased since the late 1990s (McBean et al. 2005).

Precipitation. The increase in the hydrological discharge of northern Eurasian rivers into the Arctic Ocean over the last century, as documented by Peterson et al. (2002), is largely explained by increased moisture transport into high latitudes (McClelland et al. 2004). Consistent with this observation, Vaganov et al. (1999) documented increased winter precipitation along the FEST during the last century. While precipitation has remained stable in Alaska, several lines of evidence indicate that Alaska is

Fig. 24.1. Polar projection vegetation map indicating the location of high latitude transects. This network of transects includes two in Siberia, the Far East Siberian Transect (*FEST*) and the East Siberian Transect (*EST*); one in Scandanvia (*SCANNET*), which has been augmented by carbon storage studies along a transect in Finland; one in Canada, the Boreal Forest Transect Case Study (*BFTCS*), and one in Alaska



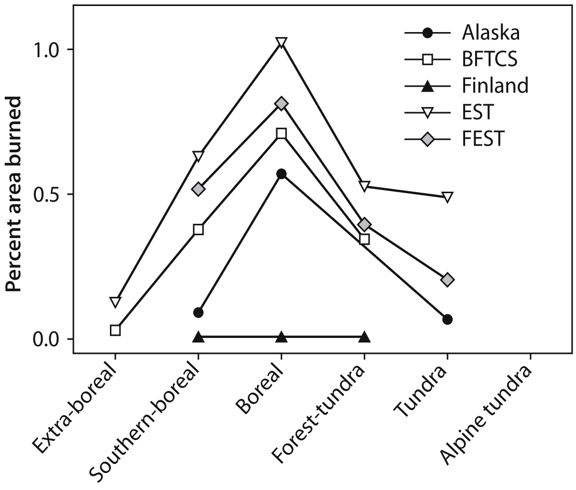


Fig. 24.2. Patterns of historical area burned along each of the high latitude transects as a function of vegetation distribution (reprinted with permission from McGuire et al. 2002)

experiencing increased drought stress because of increased summer water deficits (Oechel et al. 2000; Barber et al. 2000). There is also increased variability in climate in Siberia, and long periods of warm dry weather have become more frequent.

Permafrost. A wealth of evidence indicates that permafrost is warming in the FEST (Hinzman et al. 2005), Canada (Vitt et al. 2000), Alaska (Fig. 24.3; Romanovsky and Osterkamp 1997; Osterkamp and Romanovsky 1999; Hinzman et al. 2005), and Fennoscandia (Christensen et al. 2004; Luoto et al. 2004). While permafrost warming is consistent with regional increases in air temperature, deeper snow cover also plays a roll (Osterkamp and Romanovsky 1999; Stieglitz et al. 2003). In Alaska, warming of permafrost may be causing a significant loss of open water across the landscape, as thawing of permafrost connects closed watersheds with groundwater (Yoshikawa and Hinzman 2003). However, the reduction

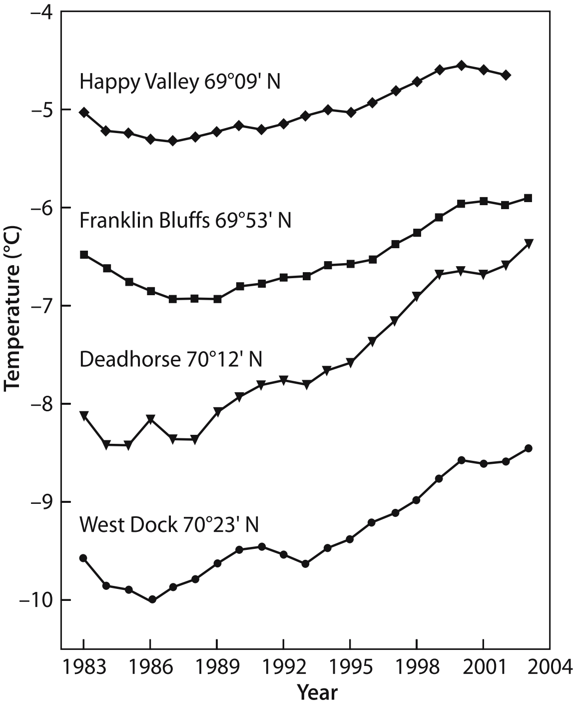


Fig. 24.3. Changes in soil temperature at 20 m depth for several northern sites of the Alaska transect (data courtesy of Tom Osterkamp; see also Romanovsky and Osterkamp 1997)

of open water bodies may also reflect increased evaporation under a warmer and effectively drier climate in Alaska as the loss of open water has also been observed in permafrost-free areas (Klein 2005).

Growing Season. Several studies based on remote sensing indicate that growing seasons are changing in high latitudes regions (Dye 2002; McDonald et al. 2004; McGuire et al. 2004; Smith et al. 2004). These studies identify earlier onset of thaw in both northern North America and northern Eurasia, but the magnitude depends on the study. Putting together the trends in the onset of both thaw and freeze, Smith et al. (2004) indicate that the trend for longer growing seasons in northern North America (3 days per decade) is primarily because of later freezing, while the trend in northern Eurasia (1 day per decade) is because the trend for earlier thaw is slightly greater than the trend for earlier freezing. However, in the EST Vaganov et al. (1999) found delays in the onset of the growing season associated with increases in winter precipitation. Data from the Scandinavian transect also indicate that that growing season changes may be complex at the regional scale (Callaghan et al. 2004).

Fire Disturbance. Important changes in land cover that have occurred in high latitudes include changes associated with disturbance (e.g., fire, insect outbreaks, timber harvest, cropland establishment/abandonment, and industrial activities like oil and gas extraction) and large-scale changes in the distribution of vegetation (e.g., the advance of tree line in regions now occupied by tundra). During the 1970s and 1980s, the area burned annually in northwest Canada increased substantially (Kurz and Apps 1999; Stocks et al. 2000, 2003). There is also evidence that fire frequency in Northern Eurasia has increased in recent decades. Analyses of fire frequency data from Russia suggest a long-term average of annual area burned of about 10 million ha yr^{-1} including low-severity surface fires (Conard and Ivanova 1997; Wirth 2004). Satellite-based analyses also suggest increased area burned with an average exceeding 10 million ha yr^{-1} from 1998 through 2003, with a peak of 22 million ha in 2003 (Soja et al. 2004). After fire, soil temperatures typically warm and the active layer becomes deeper, but soils cool again as mosses grow back during succession. However, severe fires or more frequent fires can lead to the degradation of permafrost, which may result in substantial mortality of forests.

Insect Disturbance. On average insect infestations annually affect an area almost as large as does fire in the forests in Canada (Kurz and Apps 1999) and Alaska (Werner et al. 2006). Since approximately 1920, between 1–2 million ha yr^{-1} of forests in Canada have annually experienced insect-induced stand mortality (Kurz and Apps 1999), while the long-term annual fire area in Canada averages 2 million ha yr^{-1} (Stocks et al. 2003). Large outbreaks seem to occur at intervals of approximately thirty years. In Russia, the area affected by insect disturbance is about 2 million ha yr^{-1} (Shvidenko and Nilsson 2003), which is less than the area affected by fire. Similarly, northern Fennoscandia experiences outbreaks approximately every decade during which thousands of square kilometers of mountain birch forests are defoliated (Tenow 1996). There is concern that some of the recent large outbreaks that have been observed in Siberia (Siberian gypsy moth), Canada (Mountain pine beetle), and Alaska (Spruce bark beetle, Larch sawfly, Eastern spruce budworm; Werner et al. 2006) are associated with warm dry weather in the summer. For example, the Siberian gypsy moth is estimated to have affected 10 to 11 million ha of forests in the taiga of Siberia in 2001 and 2002, which is much higher than previously observed rates of infestation. Thus, insect outbreaks that are linked to climate change appear to be increasing in a number of areas spanned by the high latitude transects.

Forest Harvest. Annual forest harvest in Canada approximately doubled from ~0.5 million ha in 1970 to ~1 million ha in 1990 (Kurz and Apps 1999). More dramatically, timber harvest in Alaska increased over six-fold from 1952 to 1992 (McGuire et al. 2004). Recent trends of forest harvest rates in Canada and Alaska are substantially influenced by economics of the global forest sector, as much of the harvested wood is exported out of the region to markets in Asia and the conterminous United States. Concern over conservation issues and the collapse of Asian economies in the 1990s have had substantial impacts in decreasing forest harvest in Alaska and the U.S. Pacific northwest during the 1990s. In Russia, forest harvest between 1950 and 1990 was relatively steady at about 2 million ha yr^{-1}. The harvested areas were mostly concentrated in the European North (about two-thirds of the total) and in the most populated regions of Siberia. With the breakup of the Soviet Union, forest harvest during the last 15 years decreased substantially to around 1 million ha yr^{-1} for the years 2000–2002. This estimate of recent harvest rates should probably be increased by 15 to 20% because of illegal harvest in the Russian Far East.

Agricultural Land Use. In the prairie provinces of Canada, there was an estimated net deforestation of 12.5 million ha between 1860 and 1992 (based on Ramankutty and Foley 1999). Since 1950, Canadian forests have had a net gain of 3.0 million ha at the expense of agriculture. While this is a small proportion of the total forest base (<1%), it is important to recognize that most of the afforestation has occurred in eastern Canada and deforestation continues to occur in western Canada. In Russia, abandonment of arable lands between 1988 and 2001 was approximately 30 million ha. Abandonment is most pronounced in the zone of the boreal forest because the low productivity lands were unprofitable in the transition to a market economy. Recent land-use changes in Fennoscandia primarily include expansion of some of the larger towns in the region, but at the cost of the rural areas where depopulation is at an advanced stage as 32 000 Norwegian northern coastal farms have been abandoned since 1955 (Eilertsen 2002). Habitat fragmentation as a result of increased infrastructure and transport route development has proceeded rapidly since the 1940s and is expected to accelerate.

Treeline responses. The transects differ in the presence or absence of barriers to coniferous forest movement northward into areas occupied by tundra. The Brooks Range separates boreal forest in interior Alaska from arctic tundra on the north slope of Alaska, and there are ocean barriers to vegetation shifts in the SCANNET region. In contrast, geography is not a significant barrier to treeline migration along the Siberian and Canadian transects. The replacement of tundra with boreal forest occurred in earlier warm periods of the Holocene in northern Eurasia (MacDonald et al. 2000) and western Canada (Spear 1993). Over the last half century, treeline advances into tundra have been documented in Russia (Esper and Schweingruber 2004), Canada (Scott et al. 1987; Lavoie and Payette 1994), and Alaska (Suarez et al. 1999; Lloyd et al. 2003; Lloyd and Fastie 2003). However, fire and human activities in Russia have moved treeline to the south (Vlassova 2002). In Fennoscandia, treeline advanced at some sites during the first half of the 20th Century (Hustich 1958; Kullman 1986), but changed tree growth form at treeline at other sites (e.g., shifts from stunted krummholz trees to upright trees) without substantial changes in position of the tree species' limit (Kullman 1995). In mountainous areas of Scandinavia, several studies documented that elevational treeline has moved upslope during the last half of the 20th century in association with increases in temperature (Juntunen et al. 2002). However, in Scandinavia there are other issues besides climate affecting the position of treeline such as land use and browsing by reindeer and moose (Callaghan et al. 2004).

24.3 Responses of Radiatively Active Gases

24.3.1 General Issues

High latitude ecosystems contain approximately 30% of the world's vegetation carbon (McGuire et al. 1995) and about 40% of the world's soil carbon (Melillo et al. 1995). Much of the soil carbon in high latitude ecosystems is highly labile and has accumulated simply because of cold and/or anaerobic soils conditions. Thus, high latitude ecosystems could substantially affect atmospheric concentrations of CO_2 and CH_4. Likely changes in the fluxes of CO_2 and CH_4 could both enhance warming (positive feedbacks) and mitigate warming (negative feedbacks) (Smith and Shugart 1993; Chapin et al. 2000a; Clein et al. 2002; Zhuang et al. 2004). As summarized below, studies of carbon and methane dynamics along the high latitude transects have provided new insights on how CO_2 and CH_4 exchange respond to changes in climate and disturbance.

24.3.2 Responses of CO_2 Exchange to Climatic Change

Aerobic vs. Anaerobic Decomposition. Warming could cause release of carbon as CO_2 from aerobic boreal soils, i.e., soils that are not saturated with water, through enhanced decomposition (McGuire et al. 1995, Arneth et al. 2002). In anaerobic boreal soils, warming could affect carbon storage by altering soil drainage patterns. Although soil drainage may be especially vulnerable to the response of permafrost to climatic warming, the net effect on CO_2 exchange is not clear because drainage can either be enhanced or retarded by permafrost degradation. For example, the release of CO_2 from aerobic decomposition is likely to be enhanced if permafrost warming results in a drop of the water table (Oechel et al. 1995; Christensen et al. 1998) or thaws soil in areas of discontinuous permafrost (Goulden et al. 1998). In contrast, CO_2 emissions from soils are likely to be reduced if permafrost thaws in situations where drainage is impeded and decomposition is diminished because of aneorobic conditions (Christensen et al. 1998, 2004) and moss production is increased (Turetsky et al. 2000).

Experimental Warming of Aerobic Soils. In general, the warming of aerobic soils is expected to increase decomposition in high latitude ecosystems. This warming effect may be constrained by increases in leaf area index, which shade the soil surface. For this reason summer soil temperatures in arctic sites can be higher than those in the shade of subarctic birch forests (Callaghan et al. 2005). Although the warming of aerobic soils will tend to increase the release of CO_2 from high latitude ecosystems, the net effect of warming depends on the balance between production and decomposition. A recent meta-analysis of experimental warming studies indicates that an increase in productivity is approximately compensated by an increase in decomposition rates (Rustad et al. 2001).

Responses to Extension of the Growing Season. Climate warming is lengthening the growing season throughout much of the region occupied by high latitude ecosystems (Dye 2002; McDonald et al. 2004; Smith et al. 2004; Euskirchen et al. 2006). In temperate forests, annual carbon storage is enhanced by approximately 6 g C m^{-2} for every day that the growing season is lengthened (Baldocchi et al. 2001), and modeling analyses suggest that carbon storage in high latitude ecosystems may have a similar level of sensitivity to changes in growing season length (Euskirchen et al. 2006). The start of the growing season, as defined by photosynthetic activity of the canopy, is tightly coupled to the thawing of the soil in conifer stands of the BFTCS in Canada because frozen soil prevents transpiration (Frolking et al. 1999). Eddy covariance studies of Scots pine stands in the EST indicate that photosynthetic capacity at the beginning of the growing season is less than expected from relationships of assimilation vs. light and temperature during the peak of the growing season (Lloyd et al. 2002). One possible cause is a high respiration cost in needles for restructuring the photosynthetic apparatus (Shibistova et al. 2002) and for repairing damage of early season photoinhibition (Ensminger et al. 2004). Deciduous stands begin net carbon uptake following leafout, which is also sensitive to the timing of snowmelt. Studies in Siberia and Alaska indicate that deciduous forests become net CO_2 sinks much later in the season than coniferous stands, but that the delay is compensated for by higher assimilation rates and results in annual carbon balances that are similar between deciduous and coniferous stands (Röser et al. 2002; Lui et al. 2005).

Evidence from Inventory and Remote Sensing Studies. While site-specific studies do not clearly show whether experimental warming or lengthening of the growing season augments carbon storage, analyses of forest inventory data for Russia suggest that Russian forests are generally sinks for carbon (Schulze et al. 1999, 2002; Shvidenko and Nilsson 2002, 2003). Analyses based on satellite data suggest that both production and vegetation carbon storage have generally been enhanced in high latitude ecosystems during recent decades (Myneni et al. 1997, 2001; Randerson et al. 1999; Zhou et al. 2001; Nemani et al. 2003; Jia et al. 2003), although there are extensive areas in high latitudes that exhibit decreases in production (Goetz et al. 2005).

The Role of Soil Nitrogen Cycling. One hypothesis for the mechanism of increased production is that warming increases decomposition of soil organic matter to release nitrogen in forms that can be taken up by plants. Since production is often limited by plant nitrogen supply in boreal forests (Van Cleve and Zasada 1976; Van Cleve et al. 1981; Chapin et al. 1986; Vitousek and Howarth 1991; Schulze et al. 1995; Wirth et al. 2002a), an increase in nitrogen availability to plants should increase production. Several warming experiments and modeling studies have provided support for this mechanism (Van Cleve et al. 1990; Bonan and Van Cleve 1992; Bergh et al. 1999; Stromgrem and Linder 2002; Clein et al. 2002). One hypothesis is that the transfer of soil nitrogen released by decomposition to plants should result in greater carbon storage in plants because plants have a higher carbon to nitrogen ratio than soils (Shaver et al. 1992). Whether the capacity for increased plant growth can offset decomposition losses largely depends on the degree to which nitrogen released through enhanced decomposition is transferred to plants vs. immobilized in soil organic matter or lost from the terrestrial ecosystems in aquatic or gaseous pathways (McGuire et al. 1992; Stieglitz et al. 2000). If warming enhances production of high latitude ecosystems, soil carbon storage could increase if the transfer of carbon from vegetation to the soil is greater than the enhancement in decomposition from warming. If this condition occurs, then the long-term rate of soil carbon storage depends on whether the carbon that is transferred to the soil decomposes quickly or slowly (Hobbie et al. 2000; Clein et al. 2000). Our understanding of soil carbon and nitrogen transformations in response to warming is incomplete and is a key gap that limits our ability to make projections of the long-term response of soil carbon to warming in high latitude ecosystems (Clein et al. 2000).

Drought Stress. Warming-induced increases in production may not occur if other factors limit production. For example, forests on coarse-textured soils are among the most severely nitrogen-limited boreal ecosystems, but are also frequently subject to drought stress because of low water retention in the soil and superficial root systems (Kelliher et al. 1999). Warming has reduced growth in old white spruce trees growing on south-facing aspects in interior Alaska because of drought stress (Barber et al.

2000), and remote sensing analyses suggest that drought stress may be affecting a substantial portion of the North America boreal forest (Goetz et al. 2005). At treeline in Alaska, the growth of trees located in warm dry sites below the forest margin declined in response to recent warming, whereas the growth of trees located at treeline, particularly in wet regions, increased (Lloyd and Fastie 2002). Thus, there appears to be substantial spatial variability in the response of white spruce growth to recent warming in Alaska, and studies conducted elsewhere on other species throughout the boreal forest suggest that growth responses of warming depend on interactions between temperature and the timing and amount of precipitation (Briffa et al. 1998; D'Arrigo and Jacoby 1993; Jacoby and D'Arrigo 1995; Linderholm et al. 2003).

Winter Decomposition. Warming can also promote the loss of carbon as CO_2 from high latitude terrestrial ecosystems through higher rates of winter decomposition and through the increased decomposition of terrestrially derived carbon in aquatic ecosystems. A number of studies, which have primarily been conducted in the vicinity of the FEST and Alaska transects, have concluded that winter decomposition represents an important component of the annual budget of CO_2 exchange between high latitude ecosystems and the atmosphere (Coyne and Kelley 1974; Waelbroeck and Louis 1995; Hobbie and Chapin 1996; Zimov et al. 1993, 1996; Oechel et al. 1997; Fahnestock et al. 1999; Grogan and Chapin 1999; Shibistova et al. 2002; Michaelson and Ping, 2003). In general, winter decomposition is expected to increase with increases in soil temperature. One particularly interesting hypothesis involves the degree to which the heat of microbial activity might further enhance decomposition from high latitude soils (Zimov et al. 1993, 1996). The nitrogen released by winter decomposition may be less accessible to plants than nitrogen released in summer because of plant dormancy in winter, immobilization of nitrogen by soil microbes during winter, and loss of nitrogen from terrestrial ecosystems in spring runoff.

Terrestrial-Aquatic Linkages. High latitude streams and lakes can act as conduits for CO_2 via the decomposition of dissolved and particulate carbon derived from terrestrial ecosystems (Kling et al. 1991). After spring runoff, concentrations of dissolved and particulate organic carbon in high latitude aquatic ecosystems are highly correlated with precipitation as water is flushed through the organic layer (Prokushkin et al. 2005). There is also a significant increase in the carbon concentrations of streams after fire. Therefore, increases in precipitation or increases in the frequency of fire disturbance in high latitudes might enhance delivery of soil organic carbon to and subsequent decomposition in aquatic ecosystems. Arctic rivers also deliver a substantial amount of organic carbon to the Arctic Ocean (Romankevich and Vetrov 2001). A key uncertainty about increases in this flux is whether this will increase the release of CO_2 from immediate decomposition in coastal ecosystems or whether the carbon will be sequestered in marine sediments. About half of the carbon entering the Arctic Ocean from terrestrial ecosystems is from river inputs and about half from the erosion of coastal soils along the Arctic Ocean. While some of this carbon may become buried in ocean sediments, some of this material will likely be immediately decomposed in coastal Arctic ecosystems. Coastal erosion has increased in recent decades (Are 1999) associated with reduced summer cover of sea ice on the Arctic Ocean. It is expected that erosion of organic matter from soils along the coast of the Arctic Ocean will increase over the next century if sea ice continues to retreat and that this will enhance the CO_2 flux to the atmosphere from the Arctic.

24.3.3 Responses of CH_4 Exchange to Climatic Change

In general, CH_4 emissions of wetlands are expected to increase dramatically in response to warming (Zhuang et al. 2004). A study of CH_4 emissions from wetlands in Greenland, Iceland, Scandinavia and Siberia showed that annual mean emissions were strongly dependent on temperature (Fig. 24.4; Christensen et al. 2003), which indicates that high latitude CH_4 emissions could increase in response to climate warming. Emissions of CH_4 will also depend on changes in the water table. For example, while the release of CO_2 from aerobic decomposition is likely to be enhanced if permafrost warming results in a drop of the water table (Oechel et al. 1995; Christensen et al. 1998), emissions of CH_4 are likely to decrease because methanogenesis is an anaerobic process (Roulet 2000). In contrast, if the thawing of permafrost results in the expansion of lakes and wetlands, then releases of CH_4 are likely to be enhanced (Zimov et al. 1997; Christensen et al. 2004).

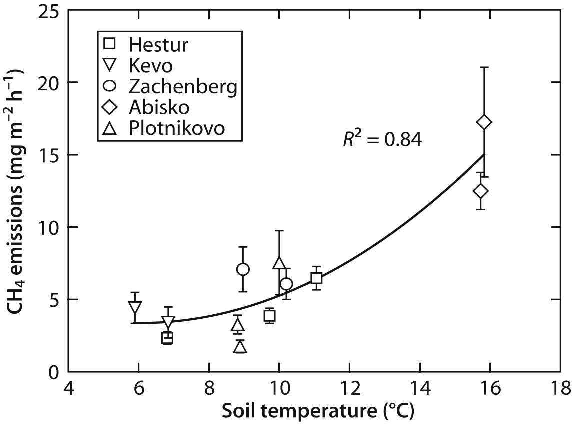


Fig. 24.4. The sensitivity of tundra CH_4 emissions in Greenland and Eurasia to soil temperature (reprinted with permission from Christensen et al. 2003)

The balance of changes in CO_2 exchanges vs. CH_4 emissions in terms of their radiative forcing is, however, complicated and difficult to assess. The current emissions of CH_4 from high latitude ecosystems, which are in the range 20–60 Tg CH_4 yr^{-1} (Zhuang et al. 2004), play a significant role in the global methane budget. In eastern Canadian peatlands, the enhanced CH_4 emissions associated with the creation of wetlands will likely result in a positive feedback to warming for up to 500 years until the enhanced storage of carbon in the wetlands (i.e., uptake of CO_2 from the atmosphere) offsets the enhanced radiative forcing associated with CH_4 emissions (Roulet 2000). In the southern end of the EST, recent studies of wetland trace gas exchange have shown that the radiative forcing of the CH_4 emissions are stronger than the substantial uptake of CO_2 (Friborg et al. 2003). For tundra regions of the high latitude transects, the balance of evidence suggests that tundra is currently a source of greenhouse warming due to substantial CH_4 emissions (Callaghan et al. 2005; Zhuang et al. 2004) that represent a radiative forcing effect that is much greater than small source/sink activity associated with the exchange CO_2 (Sitch et al. 2006). It is also likely that this source strength will increase in the future due to enhanced CH_4 emissions regardless of the strength of the carbon sink in tundra regions (Callaghan et al. 2005).

24.3.4 Responses to Changes in Disturbance and Land Cover

General Issues. A number of regional analyses suggest that carbon storage in high latitude forests is largely determined by how stand-age distribution changes at the regional scale. For stand-replacing disturbance, the temporal course of carbon storage in forests is largely controlled by wood increment and decomposition of coarse woody debris. Disturbance is generally characterized by a period of ecosystem carbon loss, during which production is less than decomposition, followed by a period of ecosystem carbon gain once production exceeds decomposition. If disturbances in high latitude regions become more frequent or more severe, carbon could be released from some ecosystem carbon pools (Kasischke et al. 1995; Wirth et al. 2002b), although the carbon stored in dead wood initially increases after disturbance (Shvidenko and Nilsson 2002).

Changes in Fire and Insect Disturbance Regimes. Together, both fire and insect disturbance have likely released substantial amounts of carbon into the atmosphere from forests in Canada (Kurz and Apps 1999; Chen et al. 2000; Amiro et al. 2001) and Russia (Shvidenko and Nilsson 2000a,b; Kajii et al. 2003). The degree to which increased fire frequency could release carbon from high latitude ecosystems depends, in part, on fire severity. Fires in most of the southern Eurasian boreal forest, which is dominated by Scots pine and Sibierian larch, tend to be surface fires in which most trees survive because of thick bark. In contrast, fires in the permafrost zone of far eastern Russia (Gmelin's larch), in Siberian dark taiga forests (spruce, fir, stone pine) and in boreal North America (mainly spruce), tend to be stand-replacing fires (Wirth et al. 1999; Shvindenko and Nilsson 2000a; McGuire et al. 2002; Wirth 2004; Csiszar et al. 2004). Analyses of the effects of climate change projections on fire weather suggest that climate change could increase fire frequency in Canada (Flannigan et al. 2001; Csiszar et al. 2004). In contrast, palaeoecological work in Canada revealed that colder and wetter periods were associated with higher fire frequencies (Lesieur et al. 2002). Nevertheless, of disturbance regime responses to climate change, fire is the disturbance agent that has the greatest potential to quickly release large amounts of carbon from high latitude regions.

The Influence of Disturbance Severity. Disturbance severity may substantially affect the temporal dynamics of carbon release and storage of high latitude ecosystems. For example, severe fires can lead to a complete destruction of organic soils. In these cases there is a large loss of up to 60 t C ha^{-1} CO_2 in fire emissions, but the ecosystem could come into positive carbon balance sooner if post-fire decomposition rates are low and vegetation recovery is high. The severity of fire disturbance also could affect the trajectory of vegetation succession after fire. Insect disturbance that causes partial or complete stand mortality leads to immediate post-fire carbon loss because of lowered production. In stands that have suffered substantial mortality, subsequent additional loss of carbon may occur if stands are then salvage logged. Also, stands affected by insect disturbance may be more vulnerable to fire because tree mortality generally increases the flammability of forest stands.

Changes in Forest Harvest Regimes. Forests of high latitude regions represent a wood resource of global significance. In general, forest harvest and management results in lower vegetation and soil carbon stocks than equivalent unmanaged forests. In the Russian Far East, carbon loss from illegal logging in the transboundary areas (Rosencranz and Scott 1992) results in the export of wood to China and other Asian countries, but this activity has not offset the drop in legal commercial logging associated with the breakup of the Soviet Union. Thus, it is expected that the change in the degree of forest harvest in the Russian boreal forest will result in net carbon storage over the next few decades unless harvest rates return to previous levels.

Changes in Treeline. Although rapid tree migration rates of up to 25 km yr^{-1} (Ritchie and MacDonald 1986) have been suggested for warming periods in the early Holocene, there are major uncertainties concerning the future rate of forest movement and the extent of range expansion that can take place. It is estimated that the potential increase in ecosystem carbon storage by replacing tundra with boreal forest is likely to proceed at a very slow pace because of inertia associated with the ability of boreal forests to migrate into regions of arctic tundra (Starfield and Chapin 1996; Chapin and Starfield 1997; Lloyd et al. 2003). The replacement of arctic tundra with boreal forest could increase ecosystem carbon storage substantially (Smith and Shugart 1993; Betts 2000).

24.4 Responses of Water and Energy Exchange

24.4.1 General Issues

Most of the energy that heats Earth's atmosphere is first absorbed by the land surface and then transferred to the atmosphere. The energy exchange properties of the land surface therefore have a strong direct influence on climate. High latitude ecosystems differ from more southerly biomes in having a long period of snow cover, when white surfaces might be expected to reflect incoming radiation (high albedo) and therefore absorb less energy for transfer to the atmosphere. Observed winter albedo in the boreal forest varies between 0.11 (conifer stands) and 0.21 (deciduous stands) (Betts and Ball 1997). This is much closer to summer albedo (0.08–0.15) than to the winter albedo of tundra (0.6–0.8), which weather models had previously assumed to be appropriate for boreal forests. The incorporation of true boreal albedo into climate models led to substantial improvements in medium-range weather forecasting and in climate re-analyses (Viterbo and Betts 1999). There is substantial spatial variability in winter albedo within high latitude ecosystems due to the spatial mosaic of conifer forests, deciduous forests, non-forested wetlands, burn scars, and tundra (Chapin et al. 2000a). The latter three have an albedo of approximately 0.6 when the short-statured vegetation is snow covered.

During summer, albedo of boreal vegetation is lower than in winter, with deciduous stands and boreal non-forested wetlands having approximately twice the albedo of conifer forests (Chapin et al. 2000a; Chambers and Chapin 2003). This difference in albedo leads to fluxes of sensible heat in conifer stands that are 2 to 3 times those of deciduous stands, whereas the latent energy fluxes (i.e., evapotranspiration) of deciduous forest stands in the boreal forest are 1.5 to 1.8 times greater than those of conifer forest stands (Schulze et al. 1999; Baldocchi et al. 2000; Chapin et al. 2000a). Because transpiration is tightly linked to photosynthesis, latent heat exchange tends to be dominated by transpiration in boreal forest stands with high productivity (e.g., deciduous forests). In contrast, evaporation plays a more important role than transpiration in the latent energy exchange of forest stands with low productivity (e.g., black spruce and pine forests), where surface evaporation from mosses or lichens can account for up to half of total evaporation (Baldocchi et al. 2000; Kelliher et al. 1999). The substantial sensible heating over conifer stands leads to thermal convection and may contribute to the frequency of thunderstorms and lightning (Dissing and Verbyla 2003), which plays an important role in the fire regime of the boreal forest as a source of ignition.

24.4.2 Responses to Changes in Climate, Disturbance, and Land Cover

Responses to Changing Growing Seasons. Responses of high-latitude ecosystems to global change could influence water and energy exchange with the atmosphere in several ways. Because there are substantial seasonal and spatial differences in sensible and latent energy exchange in high latitude ecosystems, climate warming could affect regional climate by altering both positive and negative feedbacks. One positive feedback associated with climate warming may result from lengthening of the growing season, which leads to earlier snowmelt and later snow cover. This effectively reduces annual albedo and should lead to substantial heating of the atmosphere (Chapin et al. 2005). Besides the extension of the snow-free period, the extension of ice-free periods on lake surfaces and the reduction in the area occupied by glaciers and continental ice sheets may also enhance atmospheric warming.

Responses to Changes in Vegetation. Positive feedbacks that involve changes in vegetation include more shrubs in tundra (Sturm et al. 2001; Silapswan et al. 2001), expansion of boreal forest into regions now occupied by tundra (Chapin et al. 2005), and replacement of summer-green conifers (larch) with evergreen conifers (pine; Kharuk et al. 2005). These changes would lead to substantial heating of the atmosphere, a response that could possibly accelerate the replacement of tundra by boreal forest (Table 24.1; Bonan et al. 1995; McFadden et al. 1998; Chapin et al. 2000a,b). Studies conducted with general circulation models indicate that the position of northern treeline has a substantial influence on global climate, with effects extending to the tropics (Bonan et al. 1992; Thomas and Rowntree 1992; Foley et al. 1994).

Table 24.1. Energy budget feedbacks to regional summer climate

Energy feedbacks	W m^{-2}
Feedback from vegetation change: tussock to shrub transition	3.9
Feedback from vegetation change: tundra to forest transition	5.0
2% change in solar constant	4.6
Doubling atmospheric CO$_2$	4.4

Responses to Changes in Disturbance Regimes. Disturbance and logging may also affect energy exchange with the atmosphere. For example, while fire disturbance often reduces albedo shortly after the fire, it also provides the opportunity for herbs, shrubs, and eventually deciduous broadleaf trees to develop, which will generally raise albedo. Thus, disturbance regimes that increase the proportion of non-forested lands and deciduous forests could reduce energy absorption and represent a negative feedback to atmospheric warming (Chapin et al. 2000a). In Siberia, self-replacing pine and larch in light taiga forests occur on dry upland soils and on permafrost, respectively (Furyaev et al. 2001). After these vegetation types are disturbed by fire or logging, a sometimes sparse post-fire vegetation and the lack of a deciduous pioneer phase result in a high and sustained production of sensible heat (Schulze et al. 1999). Severe fires in the Russian Far East can cause the collapse of permafrost and prevent the recovery of trees, effectively increasing albedo by converting conifer forests into ecosystems dominated by deciduous herbs and shrubs for hundreds of years. In general, post-fire deciduous broadleaf stands have a higher summer albedo (0.14) than do conifer stands (0.09) which they replace and therefore transfer less energy to the atmosphere (Chambers et al. 2003), as described above. Thus, the degree to which the response of vegetation dynamics to climate warming influences regional climate depends on the interaction of factors that may both enhance and mitigate warming.

24.5 Delivery of Freshwater to the Arctic Ocean

24.5.1 General Issues

The delivery of freshwater from high latitude ecosystems is of special importance because the Arctic Ocean, which contains only about 1% of the world's ocean water and receives about 11% of world river runoff (Forman et al. 2000; Shiklomanov et al. 2000), is the most river-influenced and land-locked of all oceans. Changes in freshwater inflow, which currently contribute as much as 10% to the upper 100 meters of the water column for the entire Arctic Ocean (Barry and Serreze 2000), could alter salinity and sea ice formation to affect the strength of the North Atlantic Deep Water Formation (Aagaard and Carmack 1989; Broecker 1997). Modeling studies suggest that maintenance of thermohaline circulation is sensitive to fresh-water inputs to the North Atlantic (Manabe and Stouffer 1995).

High latitude ecosystems play a significant role in the hydrology of the circumpolar north because they dominate the land-mass that contributes to the delivery of freshwater to the Arctic Ocean. Over the past 70 years there has been a 7% increase in the delivery of freshwater from the major Russian rivers to the Arctic Ocean (Peterson et al. 2002; Serreze et al. 2003). The analysis of McClelland et al. (2004) evaluated three mechanisms for these changes: (1) the construction of dams on the major Siberian rivers, (2) the thawing of permafrost, and (3) an acceleration of the fire regime. Of these possible explanations, an increase in fire frequency during the 20th century has the greatest potential to influence trends in runoff. However, the changes in the fire regime cannot fully explain the magnitude of increase in the delivery of freshwater to the Arctic Ocean, and therefore it appears that a poorly detected increase in precipitation may be the primary cause of the increased discharge. Nevertheless, a major challenge is to better understand and quantify the role of disturbance regime dynamics in the discharge dynamics of freshwater into the Arctic Ocean.

24.6 Summary and Conclusions

While it is clear that changes in high latitude regions have consequences for the climate system via a number of possible pathways (Fig. 24.5), we do not completely understand whether the net effect of changes will enhance or mitigate warming. Responses of water, energy, and trace gas exchange may result in either positive or nega-

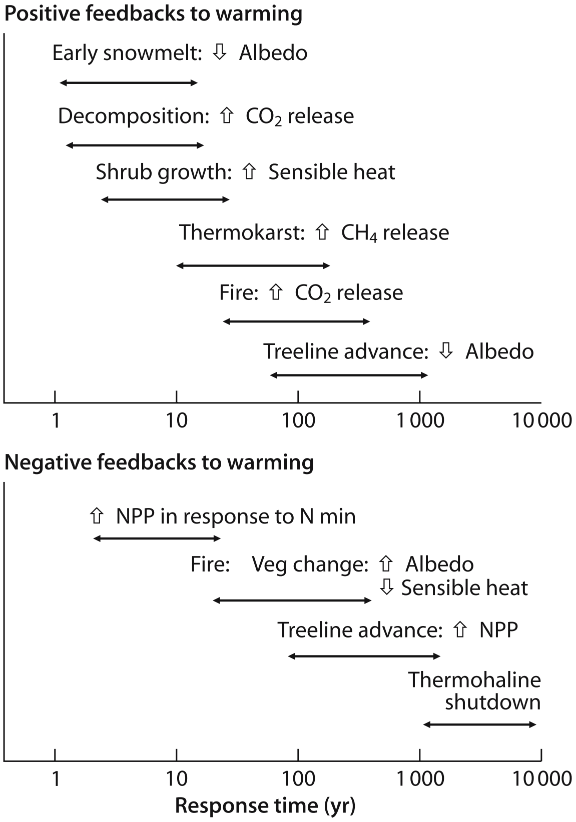


Fig. 24.5. The response times over which different positive and negative feedbacks to climate are most pronounced (reprinted with permission from Chapin et al. 2000a)

tive feedbacks to both regional and global warming. Of particular concern is whether the net response of high latitude ecosystems could lead to positive feedbacks that greatly enhance the rate of regional and global warming. While the responses of carbon storage in high latitude ecosystems have important implications for the rate of CO_2 accumulation in the atmosphere and international efforts to stabilize the atmospheric concentration of CO_2 (Smith and Shugart 1993; Betts 2000), it is important to understand how simultaneous changes in other trace gas exchanges and albedo of high latitude ecosystems also influence regional and global energy balance. For example, the reduction in radiative forcing associated with enhanced carbon storage from an expansion of the boreal forest may be exceeded by the warming effects of lower albedo (Betts 2000). Also, current responses of fire regimes to climate change suggest that fire is likely to increase in frequency and severity in the future, which has implications for both carbon storage and albedo of high latitude ecosystems. Increased delivery of freshwater from the high latitudes to the Arctic Ocean also has substantial implications for climate if it disrupts thermohaline circulation by weakening the formation of North Atlantic Deep Water, a response to warming that could ironically launch the Earth into another ice age (Manabe and Stouffer 1995). The exchange of water, energy, and trace gases among high latitude ecosystems, the atmosphere and the ocean are linked. Therefore, analyses of the response of high latitude ecosystems to global change will require an integrated understanding of how the response of these linkages will manifest themselves at a spectrum of spatial and temporal scales. The studies that have been conducted within and among the high latitude transects have laid the foundation for integration of ecological research with climate system research. Further development of this integrated understanding is relevant to identifying the implications for how the responses of high latitude ecosystems will influence the climate system. These insights are important for the development of mitigation and adaptation strategies in high latitude regions and in regions outside of the high latitudes.

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Part F

Future Directions: the Global Land Project

Chapter 25

The Future Research Challenge: the Global Land Project

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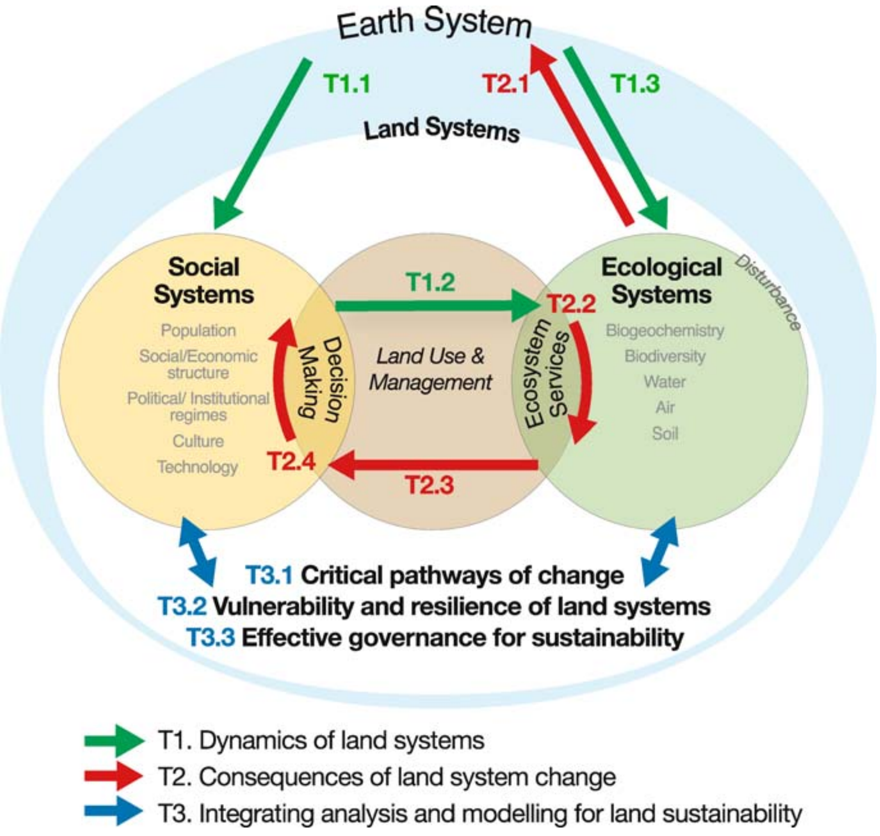
25.1 Introduction

Human transformations of ecosystems and landscapes are the largest source of environmental change on Earth, affecting the ability of the biosphere to sustain life (Steffen et al. 2004; Vitousek et al. 1997). As a species, humankind has become ever more adept at appropriating and altering the Earth's resources for human needs. Intensification and diversification of land use and advances in technology have led to rapid changes in biogeochemical cycles, hydrologic processes, and landscape dynamics (Melillo et al. 2003). Changes in land use and management affect the states, properties, and functions of ecosystems. In turn, these consequences affect human well-being. There is a need for improved understanding of how human actions affect natural processes of the terrestrial biosphere, and an even greater need to evaluate the consequences of these changes (Kates et al. 2001; NRC 1999). The research goal of the Global Land Project (GLP) is to measure, model, and understand the coupled human-environmental system (Fig. 25.1) as part of broader efforts to address changes in Earth processes and subsequent human consequences (GLP 2005).

Early ecologists had already pointed out that the ecosystem concept originally included human actions and needs explicitly. Nevertheless, until recently humans were largely treated as exogenous to ecosystems in many studies of the effects of global change on the terrestrial biosphere. For example, ecosystem responses to changes in atmospheric CO_2, plant invasions, or fire were evaluated with a given scenario of disturbances that did not take into

Fig. 25.1.
GLP analytical structure (GLP 2005)



account the socio-cultural factors leading to disturbance, or feedback between ecosystem function and decision-making by individuals and institutions. However, decision-making, ecosystem processes, disturbance, and ecosystem services are inextricably intertwined, and a consideration of ecosystems as coupled human-environment systems is a critical next step in understanding the changing Earth System.

Global environmental changes affect the coupled human-environment system differently in different regions of the world. Biophysical alterations, such as increased atmospheric carbon dioxide concentrations or enhanced erosion of soils, and social forces, such as globalization of markets, generate different responses in Northern vs. Southern hemispheres, urban vs. rural environments, and developed vs. developing countries. These changes, in turn, affect local land-use decisions and the delivery and maintenance of ecosystem services. Links between decision-making, ecosystem services, and global environmental change define important pathways of coupled human-environment activities at the local and regional scale to and from global scales (Fig. 25.2).

The focus of the Global Land Project is largely land-centric which includes the people, biota, and natural resources (air, water, plants, animals, and soil). In addition, critical feedbacks and interactions between the land and the atmosphere, and between the land and oceans will be researched (GLP 2005). This research strategy is designed to bring together elements resulting from over 10 years of research of the individual IGBP and IHDP core projects, Global Change and Terrestrial Ecosystems (GCTE) and Land-Use and Land-Cover Change (LUCC), and assessment efforts such as the Millennium Ecosystem Assessment (Mooney 2003). From a programmatic sense, the GLP is the evolution of the GCTE and LUCC core projects into a new phase of more integrated research and coupled developments between natural and social sciences. This legacy of research and recent efforts in integrated environmental research have opened the opportunity to undertake a more integrated human-environment system set of studies in ways not possible in the past.

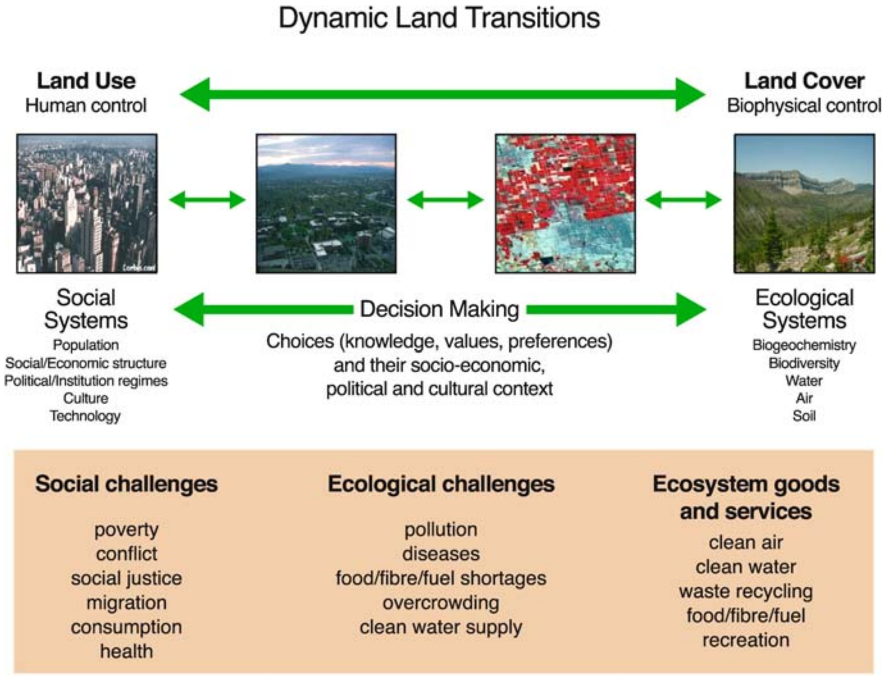
Given this focus on the human-environment system, the research activities need to be formulated to account for place-based differences and to consider the time and spatial scale of changes in human-environmental properties. The human-environment system approach provides a context to better understand the cultural landscape in which changes in the land environment are taking place and the manner in which regional differences in social structures at multiple scales affect biogeochemical cycles, biodiversity, and biophysical processes. The development of the research activities will require the joint efforts of scientists from various communities, including the social, economic, and environmental sciences.

25.2 Research Objectives

The Global Land Project has three objectives that provide the framework for the research:

- to identify the agents, structures and nature of change in coupled socio-environmental systems on land and quantify their effects on the coupled system;

Fig. 25.2.
The continuum of states resulting from the interactions between societal and natural (GLP 2005)



- to assess how the provision of ecosystem services is affected by the changes in the coupled socio-environmental system;
- to identify the character and dynamics of vulnerable and sustainable coupled socio-environmental LAND-SYSTEMS to interacting perturbations, including climate change.

Three thematic research areas define the Global Land Project research framework: (1) Dynamics of Land-Systems; (2) Consequences of Land-System Change; and (3) Integrating Analysis and Modeling for Land Sustainability. These research themes are depicted in Fig. 25.1, and additional research areas are indicated related to *(a)* factors affecting decision making, *(b)* the implementation of land-use management, *(c)* the effects on ecosystem and environmental dynamics, *(d)* the provisioning of ecosystem services, and *(e)* the evaluation of the coupled human-environmental land system's vulnerability to global environmental changes.

25.3 Emergent Concepts

The scope of the Global Land Project includes research on the effects of atmospheric, climatic, and land-use change on ecosystems, but in addition, several emergent concepts provide new directions for land research. These emergent concepts are associated with a greater focus on the social and environmental aspects of land system decision making, the valuation and provisioning of ecosystem services, and factors affecting vulnerability and sustainability of the coupled human-environment system. The following section provides a brief overview of these emergent concepts.

25.3.1 Land-Use Decision Making and Adaptive Management

Our increased understanding of the decision-making process related to land management provides a basic foundation for evaluating the interactions between human activities and their impacts on ecosystem structure and function. In this context, the decision making processes affecting land management are of particular interest in understanding how the range of settlement patterns, extraction of natural resources and production practices, land conversion methods, and conservation practices affect ecosystem dynamics.

The turn of the century has been marked by political and economic processes labeled globalization. The term refers to the worldwide reach and dominance of market institutions, engendered by the virtual instantaneous delivery of information, whose spread carries with it political and cultural implications (Stiglits 2002). These changes, associated with demographic and labor-flow trends, are occurring concurrently with climate change, CO_2 effects, and N deposition across different regions around the world. One outcome of globalization is the increasing separation of places of consumption from places of production, such that land systems often cannot be adequately understood without considering linkages to decisions made elsewhere (Blaikie and Brookfield 1987; Kasperson et al. 2001). For example, commodity crops throughout Africa are directly contracted from Europe (Bassett 2001) and large-scale deforestation in Borneo is driven by Japanese timber and pulp wood industries, although the translation of the demand to land systems is typically mediated by local policies and institutions (Angelsen and Kaimowitz 1999). In either case, the dynamics in question are embedded within and often directly tied to decisions made halfway around the world or processes operating globally.

Research is needed on the ways in which the socio-economic forces of globalization are tied to specific land-use practices and the role of institutions in mediating their outcome, including their impacts on ecosystem services. Analysis of economics, institutions, and the role of multiple stakeholders in land-use decision-making in regions undergoing socio-economic and environmental change is critical for various kinds of land change models. This research will provide insight into what types of coping strategies might be utilized at the local and regional scale. An area of emphasis will be socio-economic and political changes resulting in the relocation of significant numbers of people, both between regions, and within them. Understanding these interactions and how they affect ecosystem services (which are in many cases altered by changing land-use practices) will facilitate the development of coping and mitigation strategies to offset further perturbations.

Demographic factors, including growth, density, fertility, mortality, age, and sex composition of households, are known to be important factors influencing land-use and cover change. Research in the past decade has shown that while population growth is strongly related to land-cover dynamics, such as deforestation (Allen and Barnes 1985), this relationship is mediated by many other factors, such as land settlement policies and market forces (Geist and Lambin 2002). A key aspect of demographic dynamics is human migration, including shifts to and from rural and urban areas, and migratory flows linked to globalization processes. While urban areas continue to draw labor from rural agricultural areas, global labor markets induce the movement of large numbers of people across countries and continents (Massey 1998). Meanwhile, large-scale planned re-settlement continues in Amazonia and Indonesia, where land-use patterns have been found to depend on household composition, income, soil fertility, distance to markets, and the duration of tenancy (Pichon 1997; Perez and Walker 2002). Land tenure itself can affect fertility decision-making at the household level, with more secure tenure, *ceteris paribus*, resulting in lower fertility rates (Moran 1993). Establishing the generality of such findings is an important research challenge.

25.3.2 Ecosystem Services

Interactions between ecosystem structure and function, and with society, have consequences for the provisioning of ecosystem goods and services. There is much progress to be made in explicitly linking ecosystem processes as they have been traditionally evaluated and the services that ecosystems provide to society. Because of this focus on ecosystem services, it is essential that natural and social scientists develop reasonable sets of metrics of these services. Recent research has heightened awareness among scientists, policy makers and the public of the vital role of ecosystem services not only in the provisioning of key economic goods but also in the services that sustain, regulate and support life on Earth (Constanza et al. 1997; Daily 1997; Daily et al. 2000; Mooney 2003). Human well-being depends on a wide array of goods and services that terrestrial ecosystems provide. Whereas consumptive goods provided by land systems, such as grains, animal protein, and fiber and wood products, are typically valued through well developed markets, the contributions to human well-being and ecosystem functioning of the 'underpinning' services provided by ecosystems often remain 'invisible' and unvalued (or undervalued).

The array of such services is broad, from those services that regulate critical human-environment processes (e.g., climate, disease, flooding, detoxification) to services that support economic activity (e.g., soil formation, primary productivity, nutrient cycling, pest control, pollination). Indeed, our reliance on ecosystem services extends well beyond economic welfare, encompassing income, assets and capabilities, to health, security, food and nutrition, as well as, cultural identity, aesthetics and spirituality. Changes in land systems (in land-use practices and land cover) can disrupt the provisioning of services, degrade the quality of ecosystem services, and reduce the ability of ecosystems to maintain delivery of essential services upon which human well-being depends. One major feature of coupled human-environment systems is the notion that ecosystem services are not independent from each other, and that any change results in positive and negative outcomes depending on services considered, i.e., on the trade-offs.

Changes in the delivery and the maintenance of ecosystem services are also being affected by modifications of ecological systems through alterations of community composition or structure brought about by human activities. Inadvertent or sometimes purposeful actions by humans have led to creation of new ecosystems with unique combinations of organisms under modified environmental conditions. Examples of these emergent ecosystems can be found along a range of conditions ranging from urban environments to more natural settings. Examples include invasive species introduced in South Florida which have altered fire and hydrological regimes (Ewel et al. 1986) landscape alteration of hedge row communities in agricultural landscapes of Europe affecting predator-prey and pollinator communities, and salinization of Australian woodlands due to hydrological shifts resulting in changing forest dynamics (Hobbs et al. 2006). These "emergent ecosystems" may lead to modification of ecosystem structure and function in novel ways. However, management regimes can change abruptly as a result of environmental and/or human perturbations. For example, expansion of agricultural lands due to market or local demands for food production, sudden changes in prices of agricultural inputs (e.g., oil prices), policy shifts which alter environmental valuation of certain ecosystem properties, or political crises can result in rapid transitions in land management regimes. This set of examples point out the need to develop an analysis of the ways in which ecosystem processes are affected in terms of changes in biogeochemical cycles, biodiversity characteristics, and biophysical properties along urban-wildland continuums.

25.3.3 Vulnerability and Sustainability Science

The interaction of the coupled human-environment system with global change effects determines the vulnerability or the ability to take advantage of opportunities emerging from global change and access to markets and technologies. Vulnerability is the degree to which a system is likely to experience harm due to exposure to a hazard (Kasperson et al. 1995, 2001; Turner et al. 2003a). Resilience refers to the ability of a system to recover to a reference state following a disturbance and/or its capacity to maintain certain structures and functions despite disturbance (Carpenter et al. 2001; Gunderson 2000; Gunderson and Holling 2002; Harrison 1979). Emerging from risk-hazard studies and ecology, respectively, vulnerability and resilience have been incorporated in frameworks applicable to land systems (Downing et al. 2001; Kasperson and Kasperson 2001; McCarthy et al. 2001; Turner et al. 2003a,b; Watson et al. 1997). These frameworks evaluate how hazards-disturbances and exposure to them affect the sensitivity and resilience of the land system, including the consequences of adjustments and adaptations resulting from the hazards. Their applications have shown, for example, how the changing political economic structures in Mexico due to economic liberalization interact with drought to change the vulnerability of land systems on *ejidos* (communal lands) in different parts of the country (Turner et al. 2003b).

Vulnerability-resilience assessment is central to the Global Land Project for at least two reasons: (1) land systems are exposed and respond to hazards and disturbances, with the resulting mechanisms sustaining the systems or placing them at risk of change; and (2) the identification of those components of the land system most at risk and the mechanisms that enhance risk mitigation are central societal concerns. Information associated with these two reasons will be useful to decision makers. Most vulnerability-resilience work to date, however, has not addressed the land system per se. Risk-hazards approaches have focused on human vulnerability hazards (e.g., hurricanes) or on natural resources (i.e., the provisioning component of ecosystem services). Resilience research, in turn, has focused on ecosystem functioning. Recent work indicates that a more integrated approach is needed and the coupled human-environmental system perspective provides a framework to evaluate these linkages between ecosystem services and society (Adger et al. 2000; Luers et al. 2003).

Multiple perturbations and stresses operating at different spatio-temporal scales affect goods and services, challenging the science community to develop methods and metrics to achieve effective vulnerability analysis. Vulnerability involves more than the exposure of the system to a hazards, such as drought. It also includes the coupled human-environment system's sensitivity to the exposure and its resilience to the consequences. Resilience involves the copying capacity, adjustments, and adaptation of the system. Vulnerability analysis, therefore, must be holistic and integrative in design, and owing to the complexity and variation of coupled human-environment systems and their impacts on environmental goods and services, should be placed-based but explicitly linked to other places, drivers, and consequences to which it is connected.

25.4 Research Framework

The research approach of the Global Land Project is designed around the challenges of integrating the social and biophysical sciences. Three major themes have been developed to enable the research community to better engage in different facets of the research framework. The following section provides an introduction to this research which is being implemented through a network of research activities.

25.4.1 Theme 1: Dynamics of Land System

Research Questions

- How does globalization and population change affect regional and local land-use decisions and practices?
- How do changes in land management decisions and practices affect biogeochemistry, biodiversity, biophysical properties, and disturbance regimes of terrestrial and aquatic ecosystems?
- How do the atmospheric, biogeochemical and biophysical dimensions of global change affect ecosystem structure and function?

Understanding of global change is dependent on better understanding of the role of human activities in altering the structure and functioning of terrestrial and aquatic ecosystems, and the effect of changes in the Earth System on coupled human-environment systems operating at smaller scales. Increased understanding of the decision-making processes related to land-use management provides a foundation for evaluating the interactions between factors influencing human activities and feedbacks within the coupled human-environment system. Particularly dramatic are the impacts of land-use decision-making on the human use of land and the consequent changes in land cover and ecosystem dynamics.

This theme contributes to understanding the mechanisms by which human activities and global environmental changes affect terrestrial and aquatic ecosystems. The research undertaken for this theme will develop and synthesize knowledge on the proximate and underlying causes of land-use change, and hence ecosystems, with particular attention to the role of broader social, demographic and economic forces in shaping land-use decisions. The effects of land-use practices (e.g., agricultural, silvicultural, and pastoral systems) and global change effects on ecosystem services and the resulting feedbacks to the Earth System have not been well studied or quantified. Particular attention is given to the effects of human domination of landscapes, as these effects relate to urbanized areas, habitat management, increasing impact of invasive species, and other environmental characteristics. Likewise, this theme seeks a deeper understanding of the functioning of ecosystems within the context of global environmental change, assessing the effects of changes in atmospheric composition and physics on hydrological and biogeochemical cycles, biodiversity, and ecological disturbance regimes (Box 25.1). The greatest challenge, then, is the integration of this knowledge to forge an understanding of the combined and interactive effects of land-use and broader global environmental change on ecosystem structure and function.

Box 25.1. Fire and Pests

Fire and pest outbreaks have been part of the natural cycle of many forested ecosystems world wide. Fire has often a necessary component of a forested ecosystem to reset the successional cycle of these ecosystems. However, recently studies have indicated the frequency of pest outbreaks have increased due to increased growing season temperatures resulting in large areas of dead or damaged trees (Logan et al. 2003). These expanded areas of insect damaged forests have the potential to enhance the fire extent and intensity under these climate altered conditions.

Fig. 25.3.
a Pine forest in Eastern Oregon, two years after the catastrophic fires of 2002. Note the lack of regeneration in detrimentally burned soils. Provided by Kathy Hibbard. **b** Pine beetle damage (provided by Kathy Hibbard); with inset showing mountain pine beetle (provided by USDA Forest Service)

25.4.2 Theme 2: Consequences of Land-System Change

Research Questions

- What are the critical feedbacks from changes in ecosystems to the coupled Earth System?
- How do changes in ecosystem structure and functioning affect the delivery of ecosystem services?
- How can ecosystem services be linked to human well-being?
- How do people respond to changes in ecosystem service provision, considering the various scales and contexts of decision making?

Land ecosystems, both terrestrial and aquatic, provide a multiplicity of ecosystem services that are vital to human well-being. Agricultural systems, for example, both rely on and contribute to services, such as, soil formation and fertility renewal, freshwater, genetic crop resources, and pollination that result from agro-ecosystem processes. Changes in the availability of ecological services affect the viability, productivity and stability of the coupled human-environmental systems upon which humans rely for sustenance and economic livelihood.

Decisions about land management often result in trade-offs in the delivery of different ecosystem services. A number of factors may change through time which can affect the decision-making process and the evaluation of particular ecosystem services. A first objective of the research for this theme will be to identify these trade-offs, their causes, and the consequences they impose on land management in the context of global change. An effort will be undertaken to quantify how reductions in ecosystem services caused by changes in disturbance or management regimes may provoke shifts in land productivity by modifying physical inputs and economic returns.

Theme 2 addresses the consequences of changes in ecosystems brought about by land-use and global environmental changes studied under Theme 1. These consequences include feedbacks to the people within an ecosystem, and to the broader Earth System. Feedbacks to people are understood as changes in the delivery of a broad range of ecosystem services, such as agricultural productivity, clean air, potable water, and many others. Feedbacks to the broader Earth System occur through biogeochemical cycles, biodiversity, and natural disturbance regimes (Box 25.2). Finally, Theme 2 examines the combined effects of such ecosystem feedbacks, along with the effects of broader social, demographic and economic forces, in shaping local land-use decisions.

25.4.3 Theme 3: Integrating Analysis and Modeling for Land Sustainability

Research Questions:

- What are the critical pathways of change in LAND-SYSTEMS?
- How do the vulnerability and resilience of LAND-SYSTEMS to hazards and disturbances vary due to changes in human and environment interactions?
- Which institutions and policies enhance land sustainability?

Box 25.2. Urban Carbon Dioxide

Just as most ecosystems on Earth are now influenced by human activities, human dominated land systems such as cities remain influenced by ecological processes, including plant and soil biogeochemistry. The Biosphere-Atmosphere Stable Isotope Network (BASIN) organized within IGBP uses isotopic tracers to detect the influence of ecosystem processes on the atmosphere and how these processes are modified by global change. In this figure from Pataki et al. (2003), measurements of CO_2 isotopes in Salt Lake City, Utah, USA were used to separate nighttime CO_2 concentrations into a biogenic component originating from respiration of the urban forest and anthropogenic components originating from fossil fuel combustion. The results show that despite the large influence of fossil fuel emissions on the urban atmosphere, biological processes are easily detectable. These processes contribute to the urban carbon cycle and provide a variety of services for urban residents, including carbon sequestration, removal of atmospheric pollutants, and the cooling effects of transpiration and altered albedo.

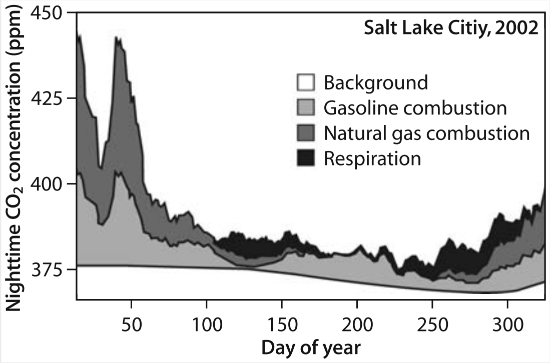


Fig. 25.4. Partitioning of 2002 night time carbon dioxide concentrations for Salt Lake City, Utah (Pataki et al. 2003)

Theme 3 seeks to integrate the dynamic interactions of human and environment subsystem characteristics (i.e., integrated land-change science) for assessment of vulnerability, resilience, and adaptation towards sustainable land systems and to provide this understanding in ways that are meaningful to decision making and policy (Box 25.3). To accomplish this goal, Theme 3 integrates findings from Themes 1 and 2 of the Global Land Project.

The sciences addressing complex systems have revealed the roles of emergent and path-dependent properties of coupled human-environment systems, and the thresholds in these systems that change their structure and function (e.g., Berkes and Folke 1998; Holling 1978; Levin 1998; Schellnhuber and Wenzel 1998). The sciences addressing vulnerability, resilience, and ecosystem services have demonstrated the nature of threats to land systems, especially in regard to the provisioning of food, fiber, and water (Daily et al. 2000; Dow and Downing 1995; Folke et al. 2002; Kasperson et al. 1995; Raskin et al. 1996; Rosenzweig 2003; Turner et al. 2003a,b). Studies of social learning and decision making have improved understanding of how coupled human-environmental systems, including land systems, are sustained or cope with forces of change (Cash et al. 2003; Kates et al. 2001; Lubchenco 1998; Mooney 2003; NRC 1999; Raven 2002). Recent advances in agent-based and other integrated modeling permit these complex factors to be treated systematically and holistically, providing land-based outcomes and near-term projections (e.g., Parker et al. 2001, 2003). The complexity of land systems, the variability in the forcing functions acting on them (e.g., Berkes and Folke 1998; Lambin et al. 2003; Lambin et al. 2001; Levin 1998) and the synergy of the human and environmental subsystems (Schellnhuber et al. 1997) enhance the need for place-based analysis (e.g., production unit, ecosystem, landscape) to address vulnerability, resilience, and sustainability (Cutter et al. 2000; Cutter 2001; NRC 1999; Wilbanks and Kates 1999). Yet, profound scalar dynamics (Parker et al. 2003; Schellnhuber and Wenzel 1998; Steffen et al. 2004) in land systems and the multiple needs of science and society regarding these systems also require that integrative analysis and assessment address multiple spatio-temporal resolutions to the problem.

25.5 Implementation Strategy

The GLP will engage in a variety of approaches to achieve its research goals. Working groups and networks of researchers will serve a fundamental role in the implementation of the science plan. The guiding principle associated with the GLP is that studies will *(a)* be place-based research studies, *(b)* require the establishment of interdisciplinary teams, *(c)* be cognizant of the need to be able to scale up and down and across disciplines, and *(d)* define the relationship of the research to the broader coupled human-environmental framework.

The research activities will include:

- case studies, manipulative studies and comparative studies
- networks of experimental and case studies across gradients of land systems
- long-term observations/experiments (remote sensing, sites, cross-site analysis)
- process models (e.g., vegetation/ecosystem, agroecosystem, agent-based models)
- land-use meta-analyses
- integrated analytical tools, not only models but also advances in field techniques
- decision-making models
- integrated regional studies
- interdisciplinary database development and archival systems

Box 25.3. Vulnerability

Determining and examining linkages between vulnerability and resilience with reference to LAND SYSTEMS and among the varying perspectives of the participating sciences remains an exciting challenge.

The vulnerability theme emerged from the social and application sciences dealing with risk-hazards. It invariably addresses the characteristics of individuals or groups in terms of their capacity to anticipate, cope with, resist, and recover from the impacts of a hazard (Blaikie et al. 1994), natural hazards for LAND SYSTEMS. Resilience, implying the opposite of vulnerability, is used in the wider ecological community (e.g., Folke et al. 2002) to understand how components of an ecosystem are configured to enable it to rebound after a perturbation of stress (for vulnerability, both are hazards). To date, natural systems are transparent in most vulnerability assessments, while ecosystem resilience focuses primarily on the biophysical processes in question.

The vulnerability and resilience of LAND SYSTEMS is determined by complex interactions among ecosystem and a suite of political, economic and social conditions and processes. Not only do shocks or perturbations (e.g., war, conflict, and climate change) and 'every day' stressors (e.g., economy, land use, and nutrient cycling) affect the environmental and human components of the LAND SYSTEM, but the consequences on either component interact in ways that change vulnerability-resilience. LAND SYSTEMS are coupled human-environment systems that require their vulnerability-resilience to be treated in an integrated manner. The vulnerability and resilience of land systems must be studied in an integrated manner: a research challenge for GLP.

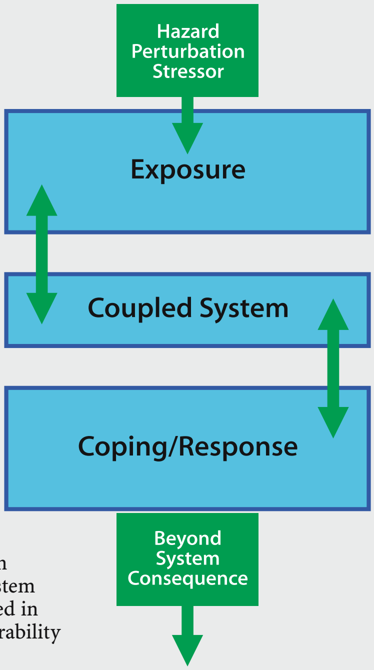


Fig. 25.5. The linkages between perturbation and system response encapsulated in the concept of vulnerability (GLP 2005)

Initial implementation Steps

Taking advantage of existing case study examples and initiatives, e.g.:

- On urban-rural gradient, linking GLP efforts to studies of the effects of conversion of rural to urban land on ecosystem functioning, and the subsequent effects and feedbacks related to ecosystem services.
- On arid lands to address dryland problems in a comprehensive an integrative way.
- On mountain ecosystems providing opportunities for comparative regional studies and for analyses of regional differentiation of environmental change processes in fragile ecosystems threatened by both systemic and cumulative human impacts.
- On managing the carbon cycle by contribution to the assessment of carbon sequestration potential; this is of the potential gain in carbon stocks in biomass and in soils within a given land area resulting from a change in land use, land cover or land management.
- On agricultural land, responsible for growing food, fiber and energy as primary provisional services for humankind, and the impact of global environmental change on agricultural production.
- On aquatic ecosystems, which closely interact with terrestrial ecosystems in providing habitat for diverse flora and fauna species, transport of nutrients and sediments and numerous other elements, and support diverse biogeochemical activity.

25.6 Summary and Conclusions

The Global Land Project (GLP) represents the joint, land-based research agenda of two major global change science programmes: *(i)* the International Geosphere-Biosphere Programme (IGBP), which originally focused mainly on biophysical processes in the Earth System through its Global Change and Terrestrial Ecosystems (GCTE) core project, and *(ii)* the International Human Dimensions Programme through its core project on Land-Use and Land-Cover Change (LUCC). The focus of the new project includes people, biota, and other natural resources (air, water, and soil). The strategy presented here critically emphasizes changes in the coupled human and environmental system, which is an extension of the ecosystem concept to explicitly include human actions and decision-making. The research planning builds upon the extensive heritage of global change research including the research discussed in the other chapters in this volume. The Global Land Project is designed to promote greater integration of social and biophysical sciences to meet the current challenges to coping and adapting to global change impacts the world is facing today and the near future. The sustainability of the coupled human-environment system and of ecosystem services is highly vulnerable to global change impacts as we move toward Earth System dynamics not yet faced by our societies.

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