Vegetation and the terrestrial carbon cycle:

Modelling the first 400 million years

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Introduction

Overview

This book considers the operation of the terrestrial carbon cycle across a range of spatial and temporal scales, with special emphasis on the photosynthetic carbon metabolism of land plants over the last 400 million years. Chapters 2 and 3 outline some of the fundamental approaches used in attempting to predict the operation of plants in the past from a knowledge of present-day processes, possible means of testing these approaches, and detailed consideration of the nature of the relationship between vegetation, soils and climate in a contemporary climatic setting. The later chapters consider a number of 'globally-averaged' responses of plant processes to changes in global mean temperature and atmospheric composition throughout much of the Phanerozoic. In taking this approach, our view has been to open up investigation and discussion of how predictions of geochemical models impinge on the processes governing the regulation of carbon gain and water loss in leaves of plants, following earlier work of this sort (Beerling, 1994).

Consideration of the global view is initiated in Chapter 4 with a detailed discussion of global climate simulations using computers and examining how these simulations can be modified to predict ancient climates. The discussion is then extended to deal with the development of a model representing the various above- and below-ground processes of the terrestrial carbon cycle. After extensive satisfactory testing of several key model outputs against a variety of ground truth data, including observations from satellites, the stage is set to bring these two global-scale approaches together and investigate changes in the operation of the terrestrial biosphere through geological time.

The following series of chapters (Chapters 5 to 9) consider, at the global scale, the effects of several computer climate simulations, representing particular averaged 'slices' of geological time, on terrestrial ecosystem properties and function. The selection of a particular interval for detailed global investigation was constrained by the availability of palaeoclimate simulations from the climate modelling community. In taking this approach it has been assumed, we hope not unreasonably, that what constitutes an interesting interval for climate modellers to test and apply their models represents a correspondingly interesting time to investigate the impact of the modelled climates on plants, vegetation and terrestrial ecosystem carbon cycling.

The geological timescale

Studies of a geological nature necessarily, by definition, deal with intervals of time typically ranging from thousands to millions of years. These timescales are difficult for the human mind to appreciate yet are those required for considering the gradual processes operating to shape the Earth's climate and the course and pattern of evolution. Indeed, it is interesting to note that amongst other political reasons, the very difficulty humans have of comprehending and accepting a time span of thousands to millions of years bedevilled our ability to formulate the concept of so-called 'deep time' in the first place. The first realisation that the Earth was in fact millions of years old was made by James Hutton in his *Theory of the Earth* (1780s) and was subsequently refined and developed further by Charles Lyell in his *Principles of Geology* (1830–1833). With this advancement in hand, Charles Darwin was able to proceed with the development of his theory of evolution by the accumulation of small gradual changes, via natural selection, over millions of years.

A basic appreciation of the geological time span and the names of the key geological eras, periods and epochs is required for this book. For simplicity, we have refrained from adopting detailed geological names and stratigraphic nomenclature and used only those more widely agreed upon (Table 1.1). Table 1.1 provides diagrammatic representation of the geological column, note that it is not scaled equidistantly through time. The Phanerozoic era extends from 544 Ma (million years ago). Its first three periods, the Cambrian, Ordovician and Silurian encompass the time before the evolution of vascular land plants, the focus of this text, and have been omitted from Table 1.1. Several global simulations deal with the Mesozoic era ('middle life' or the Age of Dinosaurs), which encompasses the Triassic, Jurassic and Cretaceous periods. The name Cretaceous derives from the latin 'creta' meaning chalk (widely deposited in shallow seas during the later stages of the Mesozoic). Following the Mesozoic

Table 1.1. *The geological timetable and key names used in this text*

Time in millions of years ago (Ma)	Eon	Era	Period		Significant biotic events
⇑0	Phanerozoic	Cenozoic	Quaternary		Ice ages.
1.8			Tertiary	Neogene	Establishment of regional differences in floras, including temperate floras and grasslands.
24				Palaeogene	First grasses, first horses, rapid diversification of mammals.
65		Mesozoic	Cretaceous		Origin and diversification of angiosperms. Extinction of dinosaurs at the Cretaceous–Tertiary boundary.
144			Jurassic		Rise of modern ferns, diversification of conifers.
205			Triassic		Cycads and Ginkgos dominant. Massive biotic extinction at the Permian–Triassic boundary.
248		Palaeozoic	Permian		Spread of upland floras into lowlands, demise of lowland swamps.
295			Carboniferous		Major interval of coal formations, forest dominance by arborescent lycopods. First land winged insects, first land vertebrates.
354 ⇓ to 416			Devonian		First seed plants, first sharks. Diversification of plants.

Source: After Haq *et al.* (1998).

is the Cenozoic era ('recent life' or the Age of Mammals) which includes the Tertiary, a term remnant from when Earth history was divided into four intervals: primary, secondary, tertiary and quaternary. The first two are now out of use whilst the name Tertiary is used to define the time between the end of the Cretaceous and the beginning of the most recent succession of ice ages, the Quaternary. The boundary between the Cretaceous and the Tertiary is termed the K/T boundary, K from the German word for chalk ('Kriede') and T to indicate the Tertiary.

Chapters 8 and 9 deal with changes in biospheric operation during intervals represented by subdivisions of the Tertiary and Quaternary periods, respectively, and since these require some familiarity with the timing and names of the different periods and epochs within, these are given in Table 1.2.

The global-scale studies in Chapters 5 to 10 recognise the Earth operating in, broadly, either an ice age or a greenhouse mode.

Ice age Earth

The Earth has experienced four major phases of glaciation over the last billion years (Crowley & North, 1991): the late Precambrian (800–600 Ma), Late Ordovician (440 Ma), Permo-Carboniferous (330–275 Ma) and the late Cenozoic (40–0 Ma). We consider the impacts of two of these ice age episodes on the terrestrial carbon cycle at times of widely differing continental configurations: the late Carboniferous (300 Ma) (Chapter 5), and during the last glacial maximum (LGM) at 18 000 years (18 ka) (Chapter 9). During the Carboniferous several of the continents sutured to form three major land masses (Gondwana, Eurasia and Kazakhstan). These were configured in very different locations from the present day, with the land masses cutting across many parts of zonal circulation, a large portion of land exposed in the low mid-latitudes, and the presence of a warm seaway (Tethys). All of these features combined to exert major effects on the operation of the global climate system with a resultant marked difference between Palaeozoic and contemporary climates (Parrish, 1993).

A further and important difference between the late Quaternary ice ages and those of the Permo-Carboniferous lies in the atmospheric composition. Late Quaternary ice core records indicate that the LGM was characterised by low concentrations of atmospheric CO_2 (180–200 ppm); and geochemical modelling of the long-term carbon cycle, as well as stomatal-based palaeo-CO_2 estimates, suggest a low value for the Carboniferous (300 ppm) (reviewed in Berner, 1998). So both glaciations are likely to have resulted in part from

Table 1.2. *Summarised geological timetable of the Cenozoic era*

Time in millions of years ago (Ma)	Era	Period	Epoch	Climatic comments
⇑0.0	Cenozoic	Quaternary	Holocene	The last 10 000 years before present (ka BP), including a climatic optimum around 6 ka BP.
0.01			Pliestoccene	Interval of repeated glacial–interglacial cycles
1.8		Tertiary	Pliocene	Closure of Panamanian seaway, with profound changes in deep Atlantic circulation at *c.* 4.6 Ma.
4.9			Miocene	Interval of global warmth without evidence of high atmospheric CO_2 content. Global expansion of grasslands with the C_4 photosynthetic pathway in the late Miocene.
24.0			Oligocene	Episodes of large fluctuations in global sea level and polar ice sheet growth and retreat.
34.0			Eocene	Onset of the formation of Antarctic bottom water. India collides with Asia.
54.0			Palaeocene	Abrupt climatic warming at the Palaeocene–Eocene boundary.
⇓65.0				

Source: After Haq *et al.* (1998).

the same mechanism, a lowered greenhouse effect. What differs between them, however, are the processes involved in sequestering carbon from the atmospheric reservoir and the subsequent effects on the atmospheric O_2 content. In the Carboniferous, the massive organic carbon burial, as witnessed by the vast coal swamps of the Carboniferous and early Permian (330–260 Ma), removed CO_2 from the atmosphere, and was calculated to have been accompanied by a rise in atmospheric O_2 content (Berner & Canfield, 1989). During the Quaternary ice ages, CO_2 removal from the atmosphere was mainly driven through changes in Milankovitch orbital insolation lowering global temperatures (Hays *et al.*, 1976) thereby increasing CO_2 solubility into the oceans, but with little effect on their O_2 content since oxygen is relatively insoluble in water. Milankovitch insolation variations probably also operated in the Carboniferous, as revealed by high frequency cyclical sea level variations in sediments of that age (Wanless & Shepard, 1936), but the effects of organic carbon burial dominated atmospheric CO_2 changes at that time. Indeed, it is possible to reasonably predict ice sheet location and growth in the Carboniferous using the same model as that capable of predicting ice sheet occurrence during Quaternary glacial stages (Hyde *et al.*, 1999). The low ice-age atmospheric CO_2 concentrations place severe constraints on the efficiency of the photosynthetic metabolism of plants, constraints further exacerbated by a high Carboniferous O_2 content. The underlying reasons for these constraints in the different periods are discussed in detail in Chapters 5 and 9.

Greenhouse Earth

Three chapters investigate the impact of the Earth's climate in periods of what might broadly be described as a greenhouse mode: the Jurassic (Chapter 6), Cretaceous (Chapter 7) and Eocene (Chapter 8). Chapter 10 deals with vegetation-climate interactions in a future greenhouse Earth, driven by CO_2 accumulation in the atmosphere following the anthropogenic activities of fossil fuel burning and deforestation.

There has been a long-standing interest in assessing the major determinants regulating global climate in the distant past, especially at times when sedimentary rocks and fossilised biota indicate much warmer climates than now. General circulation models of the Earth's climate provide a means of exploring this sensitivity and separating out the relative importance of continental configuration, oceanic circulation and greenhouse gases (e.g. Barron *et al.*, 1995). There has also been the motivation that simulations of these ancient greenhouse climates together with similar models used to make predictions of future global change, offer a means of testing the underlying physics and other mathematical representations of the Earth's climate system. However, it is doubtful (Chapter 8) that any past greenhouse climate provides a realistic representation for a future greenhouse world.

By analogy, these warm greenhouse climates offer us a means of examining the productivity of the terrestrial biosphere under such conditions, and

Chapter 8 gives an explicit comparison between the impacts of the most recent of the 'ancient' greenhouse climate episodes, of the Eocene (50 Ma), and those modelled for the future. Limitations in our knowledge of how the processes represented within the terrestrial carbon cycle model described in Chapter 4 acclimate, or become modified by long-term exposure to a warm climate and/or a high CO_2 environment, have to be conceded in making these model predictions. However, meta-analyses of the responses of photosynthesis to elevated CO_2 generally indicate that a large and continuing stimulation of photosynthesis is well described by the Farquhar *et al.* (1980) photosynthesis sub-model (Medlyn *et al.*, 1999; Peterson *et al.*, 1999) and so this core process might be regarded as somewhat robust. Further discussion of the issue of acclimation by the photosynthetic apparatus can be found in Chapter 6, in which the first global simulation with a higher-than-present CO_2 atmosphere is presented.

Catastrophic climatic change: the end-Cretaceous mass extinction

Abundant and globally-widespread geochemical, morphological, marine and terrestrial evidence has increasingly accumulated, supporting the idea, first proposed by Alvarez *et al.* (1980), that a large extraterrestrial bolide hit the Earth at the end of the Cretaceous. This represents a major perturbation of the global climate system with a correspondingly large expected effect on the functioning of the biosphere. Terrestrial carbon cycle sensitivity studies, with modified global late Cretaceous climate datasets, provide one means of assessing such effects. Therefore, Chapter 7 presents global simulations of vegetation properties and carbon cycling near the end of the Cretaceous (66 Ma) to establish 'baseline' conditions from which to explore the effects of different climatic change scenarios resulting from the impact of a large bolide. The post-impact scenarios contrast the effects of the possible resulting short-term (global darkness, climatic cooling, high atmospheric CO_2 concentrations) and long-term (high CO_2, global warming) climatic change that may have arisen owing to the impact.

Conclusions

The various global simulations described in this book provide representations of contrasting past and future climates and allow us to ask how the physical and chemical nature of the Earth has influenced the functioning of biological systems, with specific emphasis on terrestrial plant photosynthesis and the cycling of carbon through ecosystems. Some aspects of this work point to the importance of climatic feedback on vegetation, its role in determining other geochemical processes, and the possible responses of the terrestrial biosphere to abrupt environmental perturbations at the global scale.

We readily acknowledge that specific gaps exist in geological time which remain to be investigated with a modelling approach and that some of these gaps represent interesting intervals during the course of Earth history and plant evolution. Among these, two in particular stand out: the late Silurian and early Devonian, when the land became colonised by terrestrial plants; and the end of the Permian (*c.* 249 Ma), recognised as the greatest mass extinction in the history of life. The role played by large Devonian vascular land plants in the cycling of carbon was probably substantial, with deep root penetration into soils, and colonisation of drier upland and primary successional areas significantly enhancing rates of chemical weathering and atmospheric CO_2 draw-down (Algeo & Scheckler, 1998; Elick *et al.*, 1998).

In contrast to the early Devonian situation, the end-Permian mass extinctions would have severely altered the global carbon cycle through very different processes. Extinction of many groups of marine organisms would have limited oceanic primary production whilst a major and sudden mass extinction of terrestrial floras, clearly evident in the high southern palaeolatitudes (Retallack, 1995) and elsewhere, would have severely curtailed the terrestrial carbon cycle. This 'bottleneck' in carbon cycling was probably further increased by an extensive insect extinction at this time. As a result, decomposition was probably largely rate-limited by fungal activity, a feature evident in the fossil record by the extraordinarily widespread occurrence of fungal spores at the Permian–Triassic boundary (Visscher *et al.*, 1996).

The development of more flexible and easier-to-use global climate models should in the future allow model-based assessments of some of these intriguing issues. Preliminary palaeoclimate modelling studies for the late Permian (Kutzbach & Ziegler, 1993), and general circulation climate modelling studies with different Palaeozoic continental configurations (e.g. Crowley *et al.*, 1993), offer promise for investigating how significant changes in biological systems influenced biogeochemical cycles, particularly terrestrial carbon cycle dynamics.