

FORUM

Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats

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Introduction to the forum

The habitability of our planet depends on interlocking climate and biogeochemical systems. Living organisms have played key roles in the evolution of these systems. Now man is perturbing the climate/biogeochemical systems at an unprecedented pace. In particular, the global carbon cycle is being forced directly by changes in carbon fluxes (e.g. fossil fuel burning and deforestation/reforestation), and indirectly through changes in atmospheric chemistry (e.g. stratospheric ozone depletion and increases of green house gases). Nutrient cycles are also being perturbed, with implications for the carbon cycle. It is imperative that we learn how these changing conditions will influence terrestrial and oceanic photosynthesis and biogeochemistry.

Understanding the controls on primary productivity of the biosphere is one of the fundamental aims of global change research. This forum addresses several key questions regarding the role of the biota in the carbon cycle. It begins with Ian Woodward's overview of the global carbon cycle and concludes with John Raven's historical perspective of the negative feedbacks that influenced the evolution of embryophytes in the Devonian. In between, the forum focuses on the process of net primary production (NPP).

Despite differences in the structures of planktonic and terrestrial ecosystems, notably of response of biomass to environmental change, there are common problems affecting both terrestrial and oceanic studies of NPP. This has resulted in the parallel evolution of approaches to NPP research in very different milieux involving advances in the technology required to study interacting processes that cut across a range of space and time scales (Table 1). The problems include estimating NPP of whole plants and phytoplankton populations from gas exchange measurements on leaves or subpopulations,

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Table 1 A chronology of technological innovations in NPP research

Terrestrial	Marine
1940s Lindeman establishes approaches based on energetic considerations.	NPP estimated from O₂ light-dark bottle technique. Riley develops dynamic food-chain models of phytoplankton production.
1950s A range of methods based on various biomass measures and energy efficiency estimates introduced.	NPP estimated from <i>in situ</i> diel O₂ changes. Spectrophotometric method for measuring chlorophyll developed. Steemann-Nielsen introduces ¹⁴C technique to estimate NPP. Models of water-column NPP developed.
1960s International Biological Programme (IBP) develops standardized techniques for NPP estimation of major terrestrial biomes.	Introduction of use of ¹⁵N labelled compounds to estimate new and regenerated production. Development of fluorometric method for measuring chlorophyll.
1970s Micrometeorological method applied to crop and grassland systems. Errors resulting from biomass turnover in estimates of NPP demonstrated. Problems of estimating below-ground component NPP with any precision highlighted. Concepts of light interception and conversion efficiencies introduced.	<i>In situ</i> fluorometry applied to systematic mapping of the subsurface chlorophyll <i>a</i> maximum and frontal features. Independent estimates of NPP and export production lead to questioning of the accuracy of the ¹⁴C technique.
1980s Eddy covariance technique developed. Underestimation of NPP from IBP methods demonstrated. Satellite remote sensing of leaf area and interception efficiency developed (NDVI). Rhizotrons and computerized image analysis for estimating below-ground NPP. Effective models for scaling from the photosynthetic process to canopies developed. Mass isotope analysis allows separation of C₄ and C₃ components.	High precision TCO₂ and O₂ determinations allowed extension of <i>in situ</i> diel techniques to oligotrophic regions. Satellite remote sensing of pigments introduced and bio-optical algorithms for obtaining productivity developed. Questions about ¹⁴C technique largely resolved. Emergence of coupled physical-biological modelling. Trace element clean techniques allow iron-limitation to be demonstrated in bottles. HPLC technique for measuring phytoplankton pigments perfected.
1990s Long-term eddy flux networks developed. Links to routine satellite monitoring of regional NDVI. Chlorophyll fluorescence and absorption spectroscopic methods for remote sensing of photosynthetic conversion efficiency attempted.	Fast Repetition Rate fluorescence technique introduced for <i>in situ</i> estimation of photosynthetic efficiency. Iron limitation demonstrated unambiguously during Lagrangian studies involving water mass labelling with SF₆. Widespread application of analytical flow cytometry to phytoplankton populations.
2000+ <i>Major breakthroughs needed:</i> Plant respiration models of the detail available for photosynthesis together with resolution of the direct effects of rising CO₂.	<i>Major breakthroughs needed:</i> Remote sensing of photosynthetic efficiency to complement remote sensing of pigments and light attenuation.

Table 1 (continued)

Terrestrial	Marine
Below ground NPP remains poorly known and a major weakness in ground-truthing.	Extend remote sensing of pigments and productivity to near shore waters with high sediment and dissolved organic matter.
Effective method of remote sensing of conversion efficiency to complement satellite remote sensing of NDVI.	Establish the contribution of nitrogen fixation to new production
	Increase biological and spatial resolution of global or basin scale physical-biological-geochemical models to link biological production to the flows of carbon between the atmosphere and deep ocean.

Table 2 Scales of variability and experimental approaches in NPP research

Terrestrial Systems		Planktonic Systems	
Scale	Approach	Scale	Approach
Cell/tissue/leaf	Leaf gas exchange	Single cell	<i>In vitro</i> incubations
Whole plant	Physiological models whole plant gas exchange		
Canopy	Free air measurements	Water column	<i>In situ</i> measurements
Landscape	Free air measurements	Water mass	Water parcel marking with SF ₆ (25 km ²) and <i>in situ</i> measurements
Biome	Satellite remote sensing of vegetation and extrapolation to NPP	Biogeochemical province	Satellite remote sensing of chlorophyll and extrapolation to NPP
Biosphere	Biogeochemical models		Biogeochemical models

accounting for heterotrophic metabolism in gas exchange measurements, extrapolating from small scales to global NPP (Table 2), developing mechanistic models of NPP and biomass accumulation, and relating NPP to the cycling of other elements. Although small-scale measurements will continue to be a staple tool in investigations of NPP, use of open system measurements systems have necessarily come to the fore. These include free-air CO₂ exchange in terrestrial systems and water mass tracking in aquatic systems. Deliberate experimental manipulations will increasingly supplement correlative studies to derive insights into environmental regulation of NPP and the feedback between plant productivity and biogeochemical cycles.

The net primary production of planet earth has recently been estimated to equal about 10¹⁷ g C year⁻¹ (Field *et al.* 1998; Table 3). The recent estimate for terrestrial production of 56 Pg C year⁻¹ is remarkably similar to Whittaker & Likens (1975) value of 59 Pg C year⁻¹. The estimates for oceanic production have converged on values of around 40–50 Pg C year⁻¹

(Longhurst *et al.* 1995; Field *et al.* 1998). Despite the consistency of these estimates, their accuracy is still an open question. John Grace notes, based on free-air techniques, that we may find that the terrestrial biosphere is 20–50% more productive than hitherto supposed. There also remains difficulty in reconciling biogeochemical evidence of high productivity on the annual and longer time scales with measurements of marine NPP made on physiological time scales (Jenkins & Goldman 1985).

Our current understanding of global NPP is based on the extrapolation of local studies to the global scale (Field *et al.* 1998). Satellite sensors provide measurements of vegetation cover on land and chlorophyll *a* concentrations in the sea from which the rates of light absorption are calculated. These are converted to estimates of NPP using algorithms that describe the dependence of photosynthesis on the rate of light absorption. These algorithms, and hence estimates of global NPP, depend critically on a data base of gas exchange measurements. As emphasized by Tom Vogelmann, an understanding of

Table 3 Annual and seasonal net primary production (NPP) of the major units of the biosphere. All values are in petagrams of carbon (1 Pg = 10^{15} g) based on data and citations contained in Longhurst *et al.* (1995) and Field *et al.* (1998)

Marine	NPP	Terrestrial	NPP
Trade Winds Domain (tropical and subtropical)	13.0	Tropical rainforests	17.8
Westerly Winds Domain (temperate)	16.3	Broadleaf deciduous forests	1.5
Polar Domain	6.4	Mixed Broadleaf and needleleaf forests	3.1
Coastal Domain	10.7	Needleleaf evergreen forests	3.1
Salt marshes, estuaries and macrophytes	1.2	Needleleaf deciduous forest	1.4
Coral Reefs	0.7	Savannas	16.8
		Perennial grasslands	2.4
		Broadleaf shrubs with bare soil	1.0
		Tundra	0.8
		Desert	0.5
		Cultivation	8.0
Total	48.3		56.4

the fundamental determinants of photosynthesis within leaves will facilitate the scaling of photosynthesis from the leaf to the whole plant. Similarly, an understanding of the fundamentals of light absorption and photosynthetic responses of phytoplankton cells will facilitate scaling to water column NPP. Shubha Sathyendranath, Trevor Platt and Venetia Stuart describe the dual role of phytoplankton absorption that influences both the rate of light-limited photosynthesis and the quantity and spectral quality of underwater light. Todd Kana describes the common mechanisms of acclimation of the photosynthetic apparatus to multiple environmental factors that should facilitate extrapolation at the global scale.

There is still considerable uncertainty in the physical and chemical factors and ecological interactions that limit NPP in both terrestrial and aquatic systems. Colin Prentice points out that major uncertainties and discrepancies among models when projected into different climates arise because basic theoretical issues have not been resolved. It has become increasingly evident in recent years that integration of investigations from basic biochemistry and biophysics of photosynthesis to whole plant responses to regional and global studies are essential for developing a predictive understanding of NPP. Steve Long notes the potential for intensive studies of individual stands subjected to field-scale manipulation of climate and atmosphere to provide a way forward in the development of more mechanistic models of terrestrial NPP. Similarly, Lagrangian studies, in which parcels of water are marked with the tracer SF₆ and subjected to deliberate manipulation, such as addition of iron, are providing a new and powerful tool for investigating plankton systems (Coale *et al.* 1996).

The wedding of ecology with biogeochemistry presents a challenge to oceanographers and terrestrial systems scientists. It is widely recognized that NPP cannot be isolated from other biogeochemical considerations. Less widely recognized are the ecological interactions that determine community structure and, in turn, influence NPP.

Bottom-up controls provide a link between NPP and biogeochemistry. There is a need to move from single factor models, to multifactor models that recognize a multiplicity of controls. Julie La Roche describes the need to establish a hierarchy of controls by N, P, Si and Fe for understanding oceanic primary productivity and selection of functional groups of phytoplankton. However, Victor Smetacek warns that plankton evolution is driven by efficacy of defence systems rather than competitiveness of resource-acquisition mechanisms, and that bottom-up processes will be insufficient to describe plankton population dynamics.

Steve Long notes the need for mechanistic models capable of predicting biological feedback to the carbon cycle under atmospheric change. In contrast, Philip Grime argues that models based on plant functional types are more likely to lead to insights into the ecological responses of NPP to climate change than are the more traditional plant growth models that have been derived from agronomy. Evan DeLucia and colleagues conclude that NPP of young forests will increase as the level of CO₂ in the atmosphere continues to rise, but that the magnitude and duration of these increases are highly uncertain. More needs to be learned about the modulation of NPP and maximum biomass by the availability of other resources.

On seasonal, annual and decadal time scales, the dynamics of O₂ and CO₂ reservoirs provide a rich data

set for validation of global carbon cycle models. However, these integrative measurements can only be interpreted within the context of models of the geographical distribution of sources and sinks. Colin Prentice indicates the need to keep an open mind about the structure of terrestrial carbon budget models and that the atmospheric observations and experimental evidence should be critically evaluated in the light of alternative theories. Paul Falkowski has a similar message regarding marine systems. He warns that ocean primary productivity is unlikely to be in steady state on any time scale and that the feedbacks between marine productivity and the climate/biogeochemical cycle system are not easily predicted.

Predictive models of the responses of the interlinked climate and biogeochemical systems to anthropogenic forcing are essential for providing rational decisions on the use of fossil fuel and the potential for deliberate manipulation of the carbon system to mitigate against rising atmospheric CO₂. However, at this stage in our understanding of planet earth, we lack predictive power and it is important that we recognize the limits of our knowledge. Whether the climate/biogeochemical systems will ever be wholly predictable is uncertain. What is certain, however, is that avenues for fruitful research continue to open up as technological opportunities and our knowledge-base expands.

The global carbon cycle (F. IAN WOODWARD)

The pool of carbon in the atmosphere and its monthly, annual and decadal dynamics is the best-quantified component of the global carbon cycle (Keeling & Whorf, 2000). The terrestrial and oceanic carbon pools exchange primarily with the atmosphere, but none of the individual pools or fluxes are known with great precision, due to their marked spatial variability and large sizes. However, the net effect of large terrestrial and oceanic source and sink fluxes on the atmospheric pool of carbon can be determined from the trends in atmospheric CO₂ recorded since continuous monitoring was instituted in 1958 (Keeling & Whorf, 2000). Between 1991 and 1997 only about 45% of industrial CO₂ emissions accumulated in the atmosphere (Battle *et al.* 2000), indicating that the terrestrial and oceanic sinks must influence the atmospheric accumulation. There is also now an improving capacity to differentiate between terrestrial and oceanic fluxes (e.g. Battle *et al.* 2000). These measurements show that the carbon cycle is out of equilibrium as a result of human activities. Releases of carbon through fossil fuel burning are quite well quantified but the impacts of deforestation on carbon release are less well characterized (Nepstad *et al.* 1999) and are not readily distinguishable, by atmospheric measurements, from

fluxes to and from vegetation. The current situation is that a poorly quantified pre-industrial global carbon cycle is being subjected to human forcing, directly through changes in carbon fluxes and pools and indirectly through changes in climate. In terms of anthropogenic concern there are two major questions regarding the global carbon cycle. How will the cycle respond in this non-equilibrium mode, in particular how will increasing concentrations of atmospheric CO₂ influence terrestrial and oceanic photosynthesis and chemistry? In an era when mitigation strategies are on the international agenda, how effective and for how long will natural carbon sinks absorb significant fractions of anthropogenic carbon releases?

The oceanic sink

Most of the early ocean work was concerned with defining environmental impacts on the solubility of CO₂ in water – the so-called solubility pump. The effectiveness of the solubility pump at sequestering anthropogenic releases of CO₂ depends on ocean temperature, vertical mixing and global circulation patterns (Falkowski *et al.* 2000). More recent work has also considered biological uptake of CO₂ in the oceans – the biological pump. The biological pump describes the processes by which phytoplankton absorb CO₂ from the surface waters by photosynthesis. Following respiratory losses, dead organic matter and commonly associated calcium carbonate descend from the photic ocean surface to the ocean interior, effectively locking carbon away from the atmosphere for extended periods. This pump has not generally been considered important in absorbing further increases in anthropogenic CO₂ because CO₂ uptake by phytoplankton is primarily limited by the supply of nutrients such as nitrogen, phosphorus and iron, and increasing CO₂ supply should have little impact (Heimann 1997). Future changes in ocean circulation patterns and stratification, in response to global warming, will exert significant impacts on the availability of nutrients and the effectiveness of the biological pump. Sarmiento *et al.* (1998) suggest that changes in the biology of the pump may be the most critical component of the oceanic responses to future changes in climate and CO₂. Unfortunately, for future projections, Sarmiento *et al.* (1998) conclude that the response of the biological oceanic community to the climate change is difficult to predict on present understanding. Perhaps the future approach may need to be closer to that taken for terrestrial ecosystems, with a greater emphasis on carbon flux physiology, nutrient exchange capacity and community dynamics.

The terrestrial sink

The turnover of marine phytoplankton is very rapid, on the order of a week, and so any increases in productivity, through CO₂ and nutrient enrichment, will have rather little impact on standing stocks. This contrasts with the decadal-scale turnover for trees, the dominant terrestrial sinks and for which even small increases in productivity could lead to substantial increases in carbon storage. The longevity and dynamics of trees, particularly through natural and anthropogenic disturbances, are critical for defining the terrestrial part of the global carbon cycle. There is abundant evidence that plants can increase their photosynthetic capacity with CO₂ enrichment. However this response slows with increasing CO₂ and, like the phytoplankton, is also influenced by the supply of other nutrients, in particular nitrogen and phosphorus. Modelling (Cao & Woodward 1998) and experiment (DeLucia *et al.* 1999) now indicate clearly that ecosystems can increase their carbon sequestering capacity with CO₂ enrichment, but that the oft-vaunted impacts of pollutant N deposition are rather small (Nadelhoffer *et al.* 1999).

Absorbing anthropogenic releases of CO₂ with climatic change

Increased oceanic sequestration of atmospheric CO₂ as organic matter causes a transfer to the ocean interior. Unfortunately, this also locks away the nutrients that limit carbon sequestration. Projections of the future climate indicate warming and an increase in precipitation, both of which will tend to increase stratification and reduce upwelling of nutrients. In addition, the supply of wind-blown iron, a limiting marine nutrient, from the dry continents may be reduced with a wetter climate. In combination, these features should decrease the capacity of the biological pump (Falkowski *et al.* 1998) to sequester anthropogenic carbon. However, changes in oceanic circulation patterns and, in areas with increased precipitation, increased estuarine runoff with high concentrations of nutrients, may partially compensate for this reduced oceanic activity.

Experimental observations on plants suggest that CO₂ enrichment can stimulate the carbon sequestering capacity but warming, with no change in water supply will tend to reduce this capacity. Models at the global scale (e.g. Cao & Woodward 1998) indicate that global climate model simulations of future climatic warming alone would cause a global decrease in the terrestrial sink capacity for sequestering carbon, with vegetation and soils adding to the atmospheric pool of carbon. The inclusion of the direct effects of increasing atmospheric CO₂ with this warming reverses this trend, with vegetation and soils increasing their carbon sequestration

capacity. However, there is evidence for a decline in this capacity as the CO₂ stimulation of productivity reaches saturation.

Uncertainty

Estimates of oceanic and terrestrial sink capacities for carbon are currently quite uncertain but the best that can be achieved to date comes from three major and largely independent methods of estimation. The three methods are, broadly, the inversion of time series of atmospheric composition (e.g. CO₂, O₂ and $\delta^{13}\text{C}$), *in situ* observations and model simulations. No single technique is currently adequate for a full and accurate global picture of the spatial and temporal activities of the global carbon sinks. The measurements of atmospheric composition are sparse, particularly over the terrestrial biosphere, and sinks can only be estimated from measurements after the use of atmospheric transport models. In some cases maps of vegetation distribution are also required. This is particularly so for the interpretation of $\delta^{13}\text{C}$ data, where the distribution of species with the C₄ pathway of photosynthesis is required. *In situ* observations of CO₂ fluxes, or temporal changes in the sizes of carbon pools, are also sparse, particularly over the oceans and between the tropics. In addition, observations on land need to track impacts on CO₂ fluxes of processes such as disturbance, harvesting and changes in land use. Finally, models have the problems of insufficient understanding of processes, of oversimplification and of severe limitations to adequate testing. Reducing these uncertainties will require improved interactions between these three approaches. This will involve the assimilation of observations, such as from remote sensing, into models and the wider use of statistical techniques for investigating model and data uncertainties. There is still some way to go before the uncertainties of the carbon cycle can be minimized so that, for example, continental-scale sinks can be identified and quantified with precision and small-scale observations can converge with global-scale model simulations.

Light absorption as a determinant of primary productivity in algae (SHUBHA SATHYENDRANATH, TREVOR PLATT AND VENETIA STUART)

Variations in the optical characteristics of phytoplankton can influence primary production in two ways. First, they affect the rate of light transmission underwater, and hence the magnitude of photosynthetically active photon flux density (*I*) at depth. Second, they determine the rate of light absorption by phytoplankton and hence the rate of light-limited photosynthesis.

Absorption and scattering by pure water, the coloured component of dissolved organic matter, and particulate material (which includes phytoplankton) determine the rate of light attenuation with depth. When computing the phytoplankton contribution to light attenuation, it is not important to distinguish between photosynthetic pigments, degradation products, or photoprotective pigments. What is required in this context is that the phytoplankton component account for all pigments, regardless of their role in photosynthesis.

The requirements are, however, quite different and far more stringent if one is interested in calculating the amount of light that reaches the photosystems of phytoplankton at a particular depth. In this context, it becomes important to distinguish between absorption and scattering; between absorption by phytoplankton and absorption by other components of the system; and between absorption by photosynthetic pigments and non-photosynthetic pigments (in which group one might combine degradation products and photoprotective pigments). This is important, since the realized maximum quantum yield of photosynthesis, ϕ_m , will depend on whether or not the absorption is by photosynthetic or non-photosynthetic pigments.

In addition to modifying the amount of light available at depth, phytoplankton influence the spectral quality of light at depth. The spectral dependence of photosynthesis ensures that primary production is a function of both the magnitude of the underwater radiant flux (I) and the spectral quality of the light field. There is ample evidence in the literature that these spectral effects, if ignored, can lead to significant errors in computed production (Kyewalyanga *et al.* 1992).

In all models of photosynthesis (P^B) as a function of I , the initial slope, α^B , and the available light, I , are coupled together as a product. Note that the superscript B indicates normalization to the concentration of the main phytoplankton pigment chlorophyll a (including divinyl chlorophyll a), treating chlorophyll as an index of phytoplankton biomass (B). The proper way to incorporate fully the spectral dependence of photosynthesis is to replace the product $\alpha^B I$ in non-spectral models by the spectrally weighted integral $\int \alpha^B(\lambda) I(\lambda) d\lambda$, where λ is the wavelength, and the wavelength integral is taken over the whole of the photosynthetically active range from 400 to 700 nm. To introduce the biomass-normalized absorption coefficient ($a_B^*(\lambda)$), explicitly into the spectral model, we can write $\alpha^B(\lambda) = \phi_m(\lambda) a_B^*(\lambda)$ by which we recognize that α^B , ϕ_m and a_B^* are all wavelength dependent.

An interesting consequence of the spectral dependence in light absorption by phytoplankton is that the presence of phytoplankton in the surface layers of the ocean contributes to the rapid depletion of flux at those wavelengths favourable for phytoplankton absorption.

Thus, the light regime at depth may be spectrally unfavourable for absorption by pigments, and hence for photosynthesis (that is to say, the wavelength integral of the product of $\alpha^B(\lambda)$ and $I(\lambda)$ may be small, even if $I(\lambda)$ is high at some wavelengths). This effect may be mitigated if the phytoplankton are able to adapt chromatically to the light field at depth by modifying their pigment composition. The high amounts of divinyl chlorophyll b relative to divinyl chlorophyll a that are often found at depth in some marine prochlorophytes (Moore *et al.* 1998) may reflect, in part, an adaptation to the spectral quality of the light field.

All these considerations demonstrate that primary production in the water column is strongly influenced by the absorption characteristics of phytoplankton. This has led to a considerable interest in understanding natural variability in the optical properties of phytoplankton.

Absorption characteristics of phytoplankton in the aquatic environment

The biomass normalized absorption spectra, referred to as specific absorption spectra, can be treated as an intrinsic property of phytoplankton at the time of measurement, independent of their concentration. All measurements confirm certain common traits in the specific absorption spectra: they all have a broad absorption maximum in the blue part of the spectrum and a secondary absorption maximum in the red. However, measurements made in the last decade confirm that these spectra also exhibit a great deal of variability around the common trends. Specifically, the magnitude of the specific absorption maximum in the blue can vary over a factor of five from one sample to another, whereas the magnitude of the red peak can vary by a factor of two or more. The shapes of the peaks are also variable.

Two factors are responsible for most of the observed variations in phytoplankton absorption: changes in pigment packaging and in pigment composition. Based on theoretical considerations, it has long been demonstrated that the absorption efficiency of pigments within cells depends on how the pigments are packaged into discrete particles (Duysens 1956). When packaged into cells, the pigments tend to shade themselves, such that the total absorption by the pigments would be less than the absorption by the same pigments if they were distributed uniformly in solution. Using simple mathematical models, Duysens (1956) showed that the 'package effect' would increase (or the efficiency of absorption decrease) as a function of the spherical equivalent diameter of the cells and the intracellular absorption coefficient of the pigments. The decrease in efficiency of absorption due to packaging is most pronounced at the absorption maxima

and least pronounced at the absorption minima, such that the absorption spectra of pigments packaged into particulate matter would appear flatter than those of the same pigments in solution.

The second well-known cause of variation in phytoplankton specific absorption spectra is the varying influence of absorption by pigments other than chlorophyll *a* (Sathyendranath *et al.* 1987). Phytoplankton are known to have pigment complements that are characteristic of their taxa. Nutritional status and photoacclimation can superimpose additional variations. Normalizing the absorption spectra to chlorophyll *a* eliminates variations in the magnitude of the spectra due to variations in the absolute quantity of chlorophyll *a*, but it does not account for changes in the composition and relative concentrations of other pigments in the sample.

Typically, phytoplankton cells in oligotrophic oceanic waters are small and contain relatively high amounts of non-photosynthetic carotenoids, favouring high absorption efficiencies (Bricaud *et al.* 1995). The specific absorption spectra tend to get flatter and lower in magnitude towards eutrophic waters with large cells, and towards greater depths where the concentration of photoprotective pigments is low. Adaptation of cells to low light tends to increase pigment concentration per cell, which will also tend to decrease the specific absorption with an increase in depth.

The last decade has seen considerable progress in our understanding of the factors that cause variations in phytoplankton absorption characteristics. However, we do not have enough information for quantitative parameterization of phytoplankton absorption *in vivo*, given the pigment composition and particle size distribution. A major impediment is our imperfect knowledge of the *in vivo* absorption characteristics of individual phytoplankton pigments. Whereas the absorption and fluorescence characteristics of major phytoplankton pigments are well known, we still know very little about how these characteristics may vary once the pigments are bound to proteins and arranged in complex structures within cells. In spite of encouraging beginnings (Hoepffner & Sathyendranath 1991), we are still a long way from establishing a definitive catalogue of the intracellular absorption characteristics of individual pigments. An open question at the moment is whether the characteristics of individual pigments vary significantly between different types of phytoplankton cells, due to differences in internal cell structure and organization.

Concluding Remarks

Phytoplankton absorption has a strong effect on the quantity and spectral quality of the underwater light available for aquatic photosynthesis. Furthermore,

absorption influences primary production through its effect on the light-limited photosynthesis rate. Clearly, any study of aquatic primary production would be grossly inadequate if it did not account correctly for this dual role of phytoplankton absorption. Efforts to do this properly are, however, confounded by the fact that there is a considerable variability in the absorption characteristics of phytoplankton in the natural environment, about which we still have much to learn.

Photosynthetic mechanisms and biological constraints on primary productivity of algae (TODD M. KANA)

An important issue in understanding the effects of global change on NPP is partly one of understanding how the photosynthetic process is regulated by multiple environmental factors. Physiological regulation is under genetic control at the level of gene transcription and translation for key photosynthetic components and under biochemical control at the level of enzyme activation and excitation energy quenching (Falkowski & Raven 1997). Algae can provide important insights into physiological regulation of photosynthesis, because they are evolutionarily diverse and exhibit broad variations in metabolism, cell size, pigmentation, photosynthetic biochemistry and biophysics, and habitat preference. Evolution of light harvesting components, in particular, has been extensive, and the importance of spectral light absorption in the ecology of algae, both within and between species, has been documented (Kirk 1994). Moreover, there are significant differences among taxa in the regulation of energy flow through the photosynthetic apparatus. Despite this diversity, there exists a general pattern of regulation of light harvesting in response to light, temperature and nutrient availability.

Algae are able to alter key photosynthetic attributes that affect utilization of light energy. These include cellular light absorption, quantum efficiency and maximum photosynthetic capacity. A change in cellular pigment concentration is an important mechanism that modifies these attributes. Pigment concentrations respond to the immediate environment and are influenced by a variety of factors, including irradiance, nutrient availability and temperature. Pigment concentrations are also affected by the 'physiological state' of the cell, which depends on the cell's environmental history (Geider *et al.* 1998). Given the number of factors involved, it is not surprising that quantitative relationships among pigment concentration, photosynthesis and environmental variables are complex. Despite the complexity, broad patterns are consistent among taxa and across environmental factors and it is possible to define

unifying principals of photosynthetic regulation in response to environmental cues.

Integration of light and material fluxes in algae

All algae are exposed to environments with fluctuations of irradiance, temperature and nutrient availability at multiple frequencies. Despite this environmental complexity, algal cells maintain a relatively constant elemental (e.g. C, N and P) composition. This is accomplished partly through mechanisms that modulate photosynthesis. These mechanisms operate at several dominant frequencies including seconds (energy quenching), minutes (xanthophyll cycle quenching) and hours to days (acclimation).

Light, temperature and nutrient availability are important environmental factors that affect the concentration of photosynthetic pigments in algal cells. Changes of cell pigment concentrations directly affect the efficiency of light utilization and instantaneous photosynthesis rate, and are thus important in algal ecology. Recent models integrate these factors and predict acclimated pigment concentrations for an arbitrary environment (Kana *et al.* 1997; Geider *et al.* 1998). The various models incorporate an energy balance 'signal' that affects the rate of synthesis or degradation of pigmentation. The energy balance is formulated as the ratio of excitons entering the photosystems relative to electrons removed from the photosystems (Kana *et al.* 1997). This signal may be sensed by the redox state of the plastoquinone pool or some other redox sensitive component of the light reactions that influences synthesis or degradation of light harvesting compounds (Escoubas *et al.* 1995). In the steady-state, the cellular pigment concentration is poised at a level such that light energy input is in balance with the flow of assimilate for growth. This condition illustrates the basic principal that regulation on long and short time scales tends towards a balanced energy flow with respect to light absorbed and the capacity to utilize photosynthetic energy (Weis & Berry 1987).

This balance can be parameterized as the ratio of cellular light absorption to maximum assimilation rate, or $I \times A_{\text{cell}}/P_{\text{max}}$, where I is irradiance impinging on the cell, A_{cell} is the fraction of incident irradiance absorbed, and P_{max} is the maximum photosynthesis rate. A_{cell} is determined by the acclimation response of the cell and is roughly proportional to pigment concentration. P_{max} is determined largely by the physiological state of the cell, which is affected by environmental factors such as temperature and nutrient availability. Quantitative differences in these parameters among algae subjected to different environments arise from differences in cell size and pigment complement which affect A_{cell} and the

ability of a cell to utilize photosynthetic reductant by carbon assimilation and other reduction pathways that affect P_{max} .

Many of the quantitative differences among taxa can be accounted for by relating photosynthetic parameters to relative growth rate (Kana & Gilbert 1987), or a related irradiance index such as the light-saturation parameter, I_K , for growth. This works because there is a high degree of conservation of material and energy utilization by algae and cellular growth is related to the rate of photosynthetic carbon assimilation. In particular, under conditions of balanced growth A_{cell} declines as I increases and the rate of cellular growth is given by $G = I \times A_{\text{cell}}$. This is accomplished through regulation of pigment synthesis/degradation by the energy balance ratio (e.g. $I \times A_{\text{cell}}/P_{\text{max}}$) at subgenerational time-scales which translates to an energy (or material) balance at generational time-scales. This is consistent with negative feed-back regulation of cellular light harvesting. Significantly, A_{cell} influences G , but it is also constrained by the maximum value of G . The value of G is subject to a genetic constraint on the maximum cell division rate, but can be modified by nutrient-limitation or temperature. This makes the photosynthetic apparatus as much a slave to the cell's ability to utilize energy as it is a provider of that energy.

Photosynthetic pigment regulation

Two schemes have been proposed for the regulation of the cellular pigment concentration according to the short-term energy balance of the photosynthetic apparatus. These are regulation of pigment synthesis rates by changes in the expression of genes controlling synthesis of pigment-proteins (Escoubas *et al.* 1995) and regulation of pigment losses associated with photoinhibitory mechanisms (Kana *et al.* 1997). Considerable work needs to be done to determine how these mechanisms interact in a cell to modulate pigment concentrations under both steady-state and transient-state conditions and to determine how other cellular processes modulate the energy balance. The nature of these energy and material balance constraints on regulation of photosynthesis has made it possible to broadly predict chlorophyll *a* : carbon ratios in natural environments (Taylor *et al.* 1997). This suggests that physiological regulation according to energy balance is more important than differences in a species' optical properties or metabolism at large – ranging up to global – scales. In some respects this is surprising, given the diversity among taxa in cell size, temperature optima and the efficiency of nutrient uptake. As in the terrestrial realm it has increased the value of remote sensing of light absorption (Table 1). The uncoupling of these species-specific factors at the largest scales is likely

due to the large range in resource ratios found in nature. The influence of resource availability on growth rate and physiological acclimation may be overriding on a global scale.

Implications for global primary productivity

In the context of global change and NPP, broad-scale patterns in steady-state physiological response are likely to be predictable given a knowledge of changes in resource availability. On the other hand, local transient phenomena associated with higher frequency fluctuations in resources, such as blooms, will be more difficult to predict. In environments that vary on the scale of physiological to multi-generational (hours to days), species-specific responses are likely to be more important. Cell mobility, nutrient storage, mixotrophy and optical characteristics are amongst the factors that can determine short-term competitive success of specific species in transient environments and affect the relationship between primary productivity and environmental variables. The importance of biological diversity (the opposite of biological constraints) is most important at this intermediate scale. Prediction at these scales is considerably more difficult than at narrower or broader scales. This is a major contrast to the terrestrial environment, where species' changes affecting NPP require years to centuries. In the aquatic realm significant shifts occur in days.

Assessing oceanic productivity (PETER WILLIAMS)

The *in vitro* ^{14}C technique, introduced by Steemann-Nielsen in 1952, provides the basis for our knowledge of oceanic primary productivity. The success of this approach can be measured by the development of global maps of oceanic productivity within a comparatively short period of the introduction of the technique. These maps, especially that of Koblents-Mishke *et al.* 1970), are remarkably accurate with respect to contemporary measurements in describing distribution pattern of plankton productivity, although they are less accurate in describing the absolute rates. These successes, largely unchallenged, and the comparative simplicity and sensitivity of the approach meant that there was minimal pressure to develop new approaches. However, three developments in the post mid-1970s required that other approaches be examined.

The first development was a concern over the accuracy of the *in vitro* ^{14}C technique itself. Potential errors of the ^{14}C technique were assessed by cross calibrations against high accuracy oxygen measurements. Potential errors associated with containment of the sample, i.e. contamination and lack of turbulence, called for *in vitro* vs. *in*

situ comparisons. The broad problem of the accuracy of the ^{14}C measurement, which was perceived to be most acute in the vast oligotrophic parts of the ocean, was addressed by the US PRPOOS programme. Two papers from that programme largely laid to rest the concerns over *in vitro* methodology. Marra & Heinemann (1984) showed that potential contaminants from the incubation vessels did not introduce a serious error when there was adequate attention to clean procedures. Williams & Purdie (1991) showed that *in vitro* techniques returned similar rates of photosynthetic oxygen evolution as *in situ* techniques. Thus the earlier spectres were laid to rest and the ^{14}C data base was again recognized as a key resource for calibrating all other approaches for estimating oceanic productivity.

The next development came with the application of *in situ* fluorometry to measure the spatial distribution of phytoplankton. Over the mid 1970s and 1980s, fluorometers were incorporated into systems that allowed continuous sampling with high spatial resolution in the vertical (approximately 1–10 m) and horizontal (approximately 10–100 m). This facilitated near real time, two-dimensional mapping (e.g. Watson *et al.* 1991) and achieved three things. First, it showed the mesoscale (1–100 km) variability of phytoplankton distribution and thus the limitations of *in vitro* methodology. Second, it made very clear the short-term influence of physical processes on plankton distribution. Third, it broadened horizons of the scale over which plankton processes need to be measured. With the introduction of the fast repetition rate fluorometer (Falkowski & Kolber 1993), the ability to measure biomass has been supplemented with the ability to measure photosynthetic efficiency. This instrumentation is now being used in basin wide studies. Mapping chlorophyll and productivity on these scales in a relatively inaccessible area such as the ocean may be seen as a considerable technical and scientific advance in itself, but more important is that the scale of the measurement matches those of satellite ocean observations, so providing the essential 'ground truth'.

The launching of the Nimbus 7 satellite in 1978 and the operation of the Coastal Zone Colour Scanner (CZCS) radiometer it carried until 1986 opened up the potential to measure surface chlorophyll *a* concentrations on an ocean-wide scale and at a level of detail previously unattainable (Feldman *et al.* 1989). It was quickly realized that satellites could provide the necessary biomass data to model planktonic photosynthesis on an ocean-basin scale. At its simplest, from knowledge of the *in situ* chlorophyll *a* concentration, the relationship between irradiance and photosynthesis, and the beam attenuation coefficient of the water column, the wherewithal exists to model plankton primary production. There are a number of technical problems that had to be surmounted. The

CZCS radiometers had low precision, at best 35%; this in part arises as only 10% of the satellite signal comes from ocean colour – the remaining 90% is associated with processes occurring in the atmosphere and has to be independently assessed and subtracted from the 'chlorophyll *a* signal'. Perhaps more fundamental, satellite observations only return information on the upper 10–20 m of the ocean which represents only the upper 20% of the photic zone. This exacerbates the problem of estimating primary production as chlorophyll *a* distributions are neither constant nor monotonic, especially in open ocean waters. There is often an intermediate deep chlorophyll *a* maximum, characteristically between the 10% and 1% light levels that occur at depths of 25–100 m.

Platt *et al.* (1995) discussed the strategies for determining photosynthetic rates from satellite observations and the problems associated with the distribution of chlorophyll *a* within the water column. Their solution was to use the rationalization of Longhurst *et al.* (1995) that separated the oceans into four primary ecological domains (Table 3) and some 56 secondary ones. Within these ecological provinces it was possible to use generalized parameters to describe the photosynthesis vs. irradiance (PI) curve and the distribution of chlorophyll *a* with depth. Given this, it was possible to produce global maps of annual planktonic production (Longhurst *et al.* 1995). Field *et al.* (1998) used a simpler approach to modelling marine production by using the data base of ^{14}C observations to determine the light utilization efficiency of photosynthesis. It is significant to note that although the Field *et al.* (1998) approach differed in detail from that of Longhurst *et al.* (1995), the two approaches produce estimates for total annual oceanic productivity within 5% of one another. This, in all probability, is greater than our ability to interpret the ^{14}C field observations (Williams 1993). As such, these two papers must be seen to represent the completion of a major chapter – if not the major chapter – on the estimation of oceanic productivity.

The above approaches assume that planktonic photosynthesis is some function of four properties: these are the local irradiance, chlorophyll *a* concentration, quantum yield and local inorganic nutrient concentration. Generally, the fourth factor may be contained within the quantum yield or observed photosynthesis–irradiance relationship.

There remain major questions surrounding the control of production by the inorganic environment of the open oceans. Regardless of whether nitrogen or phosphorus controls production, where inorganic nutrients are clearly limiting there are difficulties in reconciling calculations of nutrient input due to physical processes with the estimated or measured rates of new production. The problem is particularly acute for the subtropical

Atlantic. Jenkins (1988) in part resolved this by showing that diapycnical transfer (e.g. across constant density contours), using historical estimates of diffusion coefficients, would fail by an order of magnitude to account for the rate of nitrate input needed to sustain net ecosystem production. He also showed that the rates of mixing could account for the required rate of nitrate input using the distribution of ^3H in the upper oceans. However, the physical mechanism driving the process is unresolved. Jenkins (1988) suggested that it was due to isopycnal mixing (e.g. along constant density surfaces), but as things stand neither this nor any other physical mechanism has general acceptance.

In conclusion, ocean productivity studies have made a remarkable and almost seamless transition from *in vitro* measurement of carbon fixation in bottles to whole ocean productivity calculations based on satellite observations. Thus, a sound and singularly consistent pattern of oceanic productivity has been attained. However, the physical and chemical controls on the process remain unclear.

Aquatic primary productivity: the ultimate limiting nutrient, biogeochemical cycles and phytoplankton species dominance (JULIE LA ROCHE)

In the last decade, oceanographers have gained significant insight into the conditions and geographical locations that are associated with P, N, Si or Fe limitation of primary productivity. However, we have not reached a consensus regarding the nutrient that is most important in limiting aquatic primary productivity. There has been a long-standing debate regarding which nutrient, N or P, ultimately limits marine primary productivity. Despite accumulated biological evidence that nitrogen limits phytoplankton productivity over the largest area of the world's ocean surface waters (Falkowski *et al.* 1998), geochemists continue to argue, on theoretical grounds, that phosphorus must be the ultimate limiting nutrient, globally and on geological time scales (Tyrrell 1999).

The cycling of N is much more complex than that of P, with significant biologically mediated exchanges between the atmosphere and the oceans, in the form of dinitrogen fixation and denitrification. Nitrogen has a very large atmospheric reservoir, in the form of N_2 gas, which in theory can be fixed into reactive nitrogen by diazotrophs. Proponents of P limitation argue that any imbalance between reactive N and P, due to low fixed nitrogen input to the ocean or increased denitrification, will be rapidly counterbalanced by increased N_2 fixation. Experimental evidence and field data suggest that this may be the case for terrestrial habitats (Chadwick *et al.* 1999). In fact, there is overwhelming evidence supporting

P-limitation of primary production in most freshwater ecosystems. In contrast, there is little support for P-limitation in marine ecosystems. With a few exceptions, nutrient addition bioassays and the distribution of N : P ratios over the major oceanic basins, coastal areas and estuaries demonstrate that N, and not P, stimulates primary productivity (Falkowski *et al.* 1998). Until recently, there have been relatively few new arguments to reconcile these opposite views.

The oceanographic community has recently come to terms with the crucial role that Fe availability plays in some marine ecosystems (Coale *et al.* 1996). The basic findings of the *in situ* Fe-enrichment studies are so convincing that most scientists agree that the case for Fe-limitation in certain high nutrient, low chlorophyll regions has been established beyond reasonable doubt. More controversially, Behrenfeld & Kolber (1999) provide evidence that iron limits primary productivity in large areas of the low-nutrient oligotrophic Pacific Ocean. This has revitalized the debate of N- vs. P-limitation. It has been suggested that low Fe availability in seawater, prevalent since the rise of oxygen in the atmosphere approximately 2 billion years ago, has greatly restricted oceanic nitrogen fixation throughout geological times via the prevention of a major radiation in the diazotrophic branch of marine cyanobacteria and in the present via limitation of nitrogenase synthesis, an enzyme extremely rich in Fe (Falkowski 1997).

Tyrrell (1999) has recently countered, using a parsimonious model of N and P biogeochemical cycles, that phosphate is the ultimate limiting nutrient. In this model, phosphate controls the standing stock of nitrogen and the observed oceanic N : P ratio, without the need to invoke a significant role for Fe. This is achieved in his model by the assumption that dinitrogen fixation is inversely related to the availability of fixed nitrogen. This assumption is well supported by molecular biological studies demonstrating the repression of nitrogenase gene expression by fixed nitrogen species in a multitude of diazotrophs (Zhang *et al.* 1997). Other factors that can affect nitrogen fixation are lumped in an overall reduction of the maximum growth rate of diazotrophs rather than incorporated as dynamic components of the model. This gives non-diazotrophs a competitive advantage when fixed nitrogen is abundant. However, the assumption that the sole dynamic control of nitrogenase lies in the relative abundance of nitrogen and phosphorus may not be justified. Specifically, given the large Fe requirement of nitrogenase, it seems logical that the control by Fe of the synthesis of functional nitrogenase will tend to override the control exerted by fixed nitrogen. Very little is known about the effect of Fe availability on the growth of diazotrophs in general, and on the nitrogen fixation pathway in particular, but there are reports that iron

stimulates nitrogen fixation (Paerl *et al.* 1994). While the effect of Fe-limitation on diazotrophy may simply be manifested by an overall decrease in growth rate, it is almost certainly a dynamic response as a function of Fe concentration.

Recent work has demonstrated that we know very little about iron cycling, bioavailability and the physiological effects of Fe-limitation on phytoplankton. The predominance of Fe as a cofactor in the nitrate assimilation enzymes makes an obvious case for an interaction between nitrogen assimilation and Fe limitation in phytoplankton. Despite this theoretical prediction, there are relatively few studies that convincingly demonstrate a preference for NH_4^+ relative to NO_3^- in Fe-limited phytoplankton. In contrast, a link has been recently uncovered between N, Fe and Si. The decrease in nitrogen uptake in Fe-limited diatoms leads to an increase in the Si : N uptake ratio of the cells (Hutchins & Bruland 1999). The ultimate consequence is that Fe-limited diatoms are heavily silicified and therefore sink faster than their iron-replete counterparts. This unexpected finding has far reaching implications for the oceanic carbon cycle and for estimates of palaeoproductivity that use biogenic opal as a proxy. In a new liaison with the nitrogen cycle, Hutchins *et al.* (1999) found that Fe bound to dissolved porphyrins and linear tetrapyrroles, cytochromes and haem proteins can be utilized preferentially by eukaryotic phytoplankton. Tetrapyrroles, the building blocks of photosynthetic pigments, have been recently identified as a low abundance but significant component of the oceanic dissolved organic nitrogen (DON) pool (McCarthy *et al.* 1997). Tetrapyrrole-like molecules are among the most stable organic nitrogen forms and some of the most highly preserved organic molecules in the marine environments. As strong Fe-ligands, these molecules could significantly affect the residence time of bioavailable Fe in the ocean (Hutchins *et al.* 1999). These new findings suggest that we are not yet in a position to quantitatively model the impact of Fe on primary production relative to that of P and N.

The search for the ultimate limiting nutrient may be misleading because the relative importance of the well-known biolimiting nutrients N, P, Fe and Si may be on the selection of different functional groups of phytoplankton. It is well known that primary production by various functional groups of phytoplankton and at specific locations can have very different impacts on the oceanic carbon cycle and on the interaction between ocean and atmosphere. For example, Si is an essential nutrient only for diatoms. However, Si may still work as a key determinant in the global C-cycle because of the important role played by diatoms in C-fluxes to deep water. Like Fe, low Si concentrations have recently been

implicated in the limitation of primary productivity in some high nutrient, low chlorophyll regions of the oceans (Dugdale & Wilkerson 1998). In some regions, such as the Southern Ocean, the selection of diatoms vs. prymnesiophytes depends on the relative availability of N, P and Si. The bloom forming prymnesiophytes *Emiliana huxleyii* and *Phaeocystis pouchetii* are involved in DMS production, a gas that affects cloud formation, and therefore the heat radiation budget of the oceans (Falkowski *et al.* 1998).

Concluding remarks

The advent of flow cytometry and molecular biology has revolutionized our view of phytoplankton diversity. Although we cannot yet, and may never be able to, accurately predict species succession in a given ecosystem, we are making significant progress in understanding the environmental heterogeneity that leads to the coexistence of functional groups of phytoplankton. For example, the utilization of Fe complexed to different organic ligands may allow eukaryotic and prokaryotic phytoplankton to coexist while being limited by the same nutrient (Hutchins *et al.* 1999). How many such intricate links remain to be uncovered for Fe and for the other known limiting nutrients, P, N and Si? One area that requires more study is the composition of the dissolved organic pools of N and P (McCarthy *et al.* 1997), and the possibility that some phytoplankton species can utilize components of these pools (La Roche *et al.* 1997). Although other biotic and abiotic factors will also contribute to niche differentiation, the diversity in the biogeochemical cycling of biolimiting nutrients goes a long way to resolve the paradox of plankton.

Are marine ecosystems in steady-state with respect to the global carbon cycle? (PAUL G. FALKOWSKI)

On all major geological time scales, from thousands to hundreds of millions (and even billions) of years, marine primary productivity has clearly deviated from a steady state. The same is true on short time scales of days, weeks, months and years. Why then are the biologically mediated fluxes of carbon in the ocean assumed to be in steady state on time scales of decades to centuries in geochemical models? Is this merely wishful thinking on the parts of modellers who wish to constrain, i.e. hold constant, one portion of the C-cycle. While such a steady-state assumption may be mathematically convenient, it flies in the face of knowledge that variance spectra for natural processes are continuous functions. Moreover, climate change, forced by atmospheric processes, will almost certainly have feedbacks on the hydrological

cycle, eolian iron fluxes, stratification intensity, and riverine supplies of key elements (especially silicate). That such closely linked phenomena will affect primary production via one or more of the aforementioned processes is easily envisioned. Unfortunately, the consequences and feedbacks on the climate/biogeochemical cycle system cannot be foretold easily.

Developing a quantitative understanding of the fluxes of carbon between the major active reservoirs, namely the atmosphere, oceans, and terrestrial ecosystems has been the focus of numerous large international scientific research programs. These efforts, spurred on by the realization that increases in atmospheric CO₂ since the industrial revolution sharply deviate from the natural carbon cycle, are the first step in understanding the potential responses and feedbacks of the Earth carbon cycle to anthropogenic energy-driven activities. As the changes in fluxes between the active reservoirs are small relative to both the sizes of the reservoirs and the steady-state fluxes, with the exception of the atmosphere, all other fluxes are ultimately derived from models. While modelled fluxes are based on measurements, interpretation of the measurements inevitably requires assumptions and constraints that potentially can lead to misunderstandings. As models serve as predictive tools, such misunderstandings can, in turn, lead to inaccurate prognostications about the nature and magnitude and feedback between carbon fluxes and climate interactions in decades and centuries to come. One such potential misunderstanding is the assumption that marine ecosystems are in steady state with respect to the global C-cycle.

By virtue of the ease of sampling, the relatively rapid rate of mixing, and the accuracy and precision of measurement, the atmosphere is the best characterized of the major active carbon reservoirs. The early continuous time series data from Mona Loa revealed the seasonal northern hemisphere gas exchange, which corresponds with changes in primary production in terrestrial ecosystems. A subsequent observational network established an inter-hemispheric gradient in the amplitude of the seasonal CO₂ cycle. Based on the phase shift and the gradient in the amplitude, Tans *et al.* (1990) proposed a northern hemisphere terrestrial CO₂ 'sink' on the order of 2.0–3.4 Pg C year⁻¹. Such a sink implies a change in global northern hemisphere NPP of approximately 5% per year; certainly large enough to be confirmed by observations of the terrestrial ecosystems within a decade or two.

Several approaches have been made to confirm and/or constrain the northern hemisphere terrestrial sink hypothesis. Interdecadal interpretation of satellite measurements of terrestrial vegetation have been suggested to confirm an increase in terrestrial biomass. Although the

'visible' biomass (i.e. shoots and leaves) do not appear to quantitatively account for the presumed sink strength (Myneni *et al.* 1997), eddy-covariance accumulated fluxes between the atmosphere and forests are consistent with a terrestrial sink. This has led to the assumption that roots and other 'hidden' biomass reservoirs are critically important. A second approach is based on transcontinental gradients in CO₂ (Fan *et al.* 1998). This approach requires an accurate atmospheric transport model and synoptic, high quality, and internally consistent atmospheric CO₂ measurements. A third approach utilizes high precision atmospheric O₂ measurements (Keeling & Shertz 1992), and is based on the assumption that prompt seasonal changes in O₂ are attributable to terrestrial primary producers, while delayed seasonal changes in O₂ are a consequence of atmosphere-ocean thermal exchanges. All three approaches assume that oceanic biota and their effect on the global C-cycle is in steady-state and therefore irrelevant. Why is such an assumption made and how valid is it?

While it is obvious that biologically mediated changes in the *net* flux of CO₂ into the ocean require a deviation from steady-state fluxes, the conditions that actually influence changes in the air-sea exchange of CO₂ are relatively constrained. Contrary to what had been thought by biological oceanographers in the early 1980s, simply changing the export flux of carbon, i.e. the fraction of primary production that is exported to the ocean interior, will not markedly influence atmospheric CO₂. One can envisage that if we were to take an egg beater and mix the ocean, the export of carbon to depth would increase because nutrients would become more plentiful in the photic zone. This process would lead to an enhancement of the biological pump; however, simultaneously, CO₂ in the ocean interior would be brought to the surface with the other nutrients, where it would equilibrate with the atmosphere. The resulting change in atmospheric CO₂ would essentially be nil (Sarmiento & Siegenthaler 1992). Rather, to change atmospheric CO₂, changes in productivity must be brought about by one or more of the following: (i) a change in the elemental ratio of the sinking flux of organic matter, (ii) a change in the utilization of nutrients in the upper ocean, (iii) a change in concentration of the nutrient most limiting primary production, and/or (iv) a change in the ratio of calcium carbonate/organic carbon exported to the ocean interior. Let us briefly examine these possibilities within the context of known processes.

The elemental composition of plankton has been suggested to be remarkably constant, averaging 106 C : 16 N : 1 P by atoms (Redfield 1958). There is no fundamental understanding why this elemental ratio is apparently so constrained in marine organisms (although a similar elemental ratio holds for the average soft tissues

of humans). Presumably the ratio reflects some intrinsic relationship between proteins (represented by N) and nucleic acids (represented by P). Experimental data suggest, however, that the ratio can be forced to vary, due primarily to variations in CO₂ relative to nitrate and phosphate (Burkhardt *et al.* 1999). While changes in the elemental composition of plankton cannot be ruled out *a priori*, wholesale changes, such as those hypothesized by Broecker & Henderson (1998), are highly unlikely (Falkowski *et al.* 1998).

Changes in the utilization of nutrients in the upper ocean can be readily accommodated within the present understanding of ocean biogeochemistry. In the three major high-nutrient, low-chlorophyll regions of the world oceans, namely the subarctic and eastern equatorial Pacific, and the Southern Ocean, excess surface nitrate and phosphate can be removed by phytoplankton following the addition of iron. In the Southern Ocean in particular, continuous inputs of aeolian iron, would appear to stimulate the utilization of these macronutrients with a simultaneous draw-down of atmospheric CO₂. Almost certainly such a situation occurs during glacial-interglacial transitions (Martin 1990).

Until relatively recently, it was unclear how changes in the nutrient concentrations in the ocean could occur on time scales of decades or centuries. Part of this problem was the unfortunate misinterpretation by Redfield of ocean nutrient cycles. Redfield (1958) concluded that phosphate concentration rather than nitrogen fixation was limiting. This misinterpretation spread through the geochemical community, with the resulting search for processes that would affect phosphate concentrations. Primary productivity in the contemporary ocean is undoubtedly limited by fixed nitrogen, not phosphate. The delivery of fixed nitrogen requires biological nitrogen fixation. It has been proposed that nitrogen fixation is itself limited by the availability of iron (Falkowski 1997). Hence the same element that can enhance the draw-down of CO₂ in high-nutrient, low-chlorophyll regions of the oceans can also help 'top up' the ocean with fixed nitrogen. The combined effect can result in a removal of more than 100 ppm of CO₂ from the atmosphere (Falkowski 1997).

Finally, the ratio of carbonate to organic carbon in sinking particles can strongly influence pCO₂ in the upper ocean and hence the equilibrium concentration of atmospheric CO₂. What controls the ratio of inorganic to organic carbon flux is not well understood; however, that it changes on glacial/interglacial time scales is almost certain (Falkowski *et al.* 1998). During glacial periods silicate fluxes dominate while during interglacial periods carbonate fluxes dominate. Much more organic carbon can be sequestered with the former (Dugdale & Wilkerson 1998).

The role of competition and predation in the productivity of pelagic communities (VICTOR SMETACEK)

Pelagic communities based on the primary production of suspended microalgae – the phytoplankton – differ fundamentally in structure and functioning from terrestrial communities in which the plants are attached. A major difference lies in the production to biomass ratio. Land plants attain and maintain large biomass and their evolution is shaped by competition for resource space (whether light or water). This is reflected in their inherent tendency to outgrow and outlast competitors, whereby local resource availability, and ultimately physics, constrain size. However, land plants have also evolved defence systems to withstand storms and fires, pathogens, parasites and predators, the latter ranging from pathogenic fungi to megafauna. In short, general morphology is driven by competition, but fitness, and hence species selection at the local level, is determined by the ability of a species to outgrow competitors but also to defend itself.

The driving forces shaping plankton evolution are less clear because fluidity of the medium precludes occupation of resource space to the detriment of competitors. Individual phytoplankton species can only sequester resources from other species for periods of weeks, and mortality is more or less equal to growth on an annual basis. Hence it could be argued that evolution of predator defences in phytoplankton is futile. In the following, it is argued to the contrary and concluded that efficacy of defence systems rather than competitiveness of resource-acquisition mechanisms drives evolution in the plankton. The presence of such defence systems will therefore have considerable impacts on productivity and biogeochemical cycles.

As pelagic systems generally operate at the end of some resource tether (light or nutrients), it is taken for granted that individual cells are competing with each other for the limiting resource. Although phytoplankton spend most of their time in the twilight zone, their light-harvesting systems are only marginally different from those of much better illuminated land plants. The chlorophyll-based, carotenoid-supported photosynthesis machinery of all water-splitting autotrophs has remained essentially the same since it arose in ancient cyanobacteria.

Phytoplankton are recruited from very different phyla but there is little indication that any of the various evolutionary trends have improved their light or nutrient uptake ability significantly and hence raised competition levels as in the case of land plants. Based purely on physical considerations, small, solitary picocyanobacteria such as *Synechococcus* (1–2 µm in diameter) should have

the highest growth rates and their populations should corner the bulk of the resources, yet they only dominate biomass in the ocean under oligotrophic conditions. Instead eukaryotic groups – diatoms, haptophytes and dinoflagellates – are responsible for the bulk of bloom biomass in the sea. Limnic species of *Synechococcus* indeed have extraordinarily high growth rates, several times those of their marine counterparts, which corroborates the theoretical considerations, but also indicates that the marine cyanobacteria have suppressed growth rates. This is discussed next.

Although small cells are more effective than large in acquiring diffusely distributed resources such as dissolved nutrients and light, they are more vulnerable to pathogens and predators because contact frequency with viruses, bacteria and small ingesting protists increases with decreasing size and increasing abundance. Thus the mortality risk and the relative cost of building defences such as tough cell walls, an 'immune' system or chemical deterrents declines with increasing cell size. As marine *Synechococcus* are reported to survive gut passage of salps (Pfannkuche & Lochte 1993), they must indeed have tough cell walls that should be expensive to make and could be the reason for their depressed growth rates. The fast-growing limnic species come from eutrophic waters where the potential to build-up dense biomass can swamp predators. Such 'duck ponds' represent the opposite situation to the ocean's subtropical gyres, where algal biomass is restrained by grazing pressure and population growth rate is based on nutrients recently released by heterotrophs. Hence the production rate of these oligotrophic communities can be regarded as driven by the supply rate of the limiting nutrient, i.e. by metabolism of the heterotrophs (Banse 1994).

In contrast to the evolutionary 'stagnation' of the photoautotrophic machinery, heterotrophy is characterized by an enormous diversity of techniques and mechanisms. These mechanisms range from passive uptake of dissolved organic matter by the bacteria to sophisticated search and ingest apparatuses of various degrees of specificity developed by protists and metazoa. Contrast this situation with that on land, where plants are predictable and at the mercy of their predators. Since pelagic predators represent the attack-side of the arms race one must assume that they have evolved in response to camouflage or defence mechanisms of the prey. The greatest proliferation of feeding types is present within the protists, and the bulk of the unicellular algae are consumed by protozoa that are as phylogenetically diverse as their algal food. It follows that evolution amongst the protistan phyla of the pelagic realm has run a very different course when compared with the metazoa and higher fungi on land which, like the metaphytes, are all monophyletic.

The simplest and most ubiquitous phagotrophs are the bacteria-feeding, heterotrophic nanoflagellates (HNF) whose grazing ability is reflected in the fact that they, rather than food availability, control bacterial numbers. Bacterial productivity is probably affected to a lesser extent but selection against unpalatable bacteria by HNF has been reported (Jürgens & Güde 1994). Such 'grazing-resistant bacteria' will grow more slowly but also be eaten less rapidly than their unprotected counterparts. The HNF that feed on such bacteria will have developed specific enzymes to cope with them, the production of which will in turn reduce growth rate of the HNF. Thus, sophistication of the arms race will slow down the turnover rate (economy) of the community. A cheap but effective defence system will do much to loosen this looming gridlock.

Small flagellates which superficially look like HNF but are the motile stages (zoospores) of lower fungi or other protists are widespread in pelagic systems and attack larger prey items such as diatoms (Kühn 1995). Smetacek (1995) has argued that the silica cell wall of diatoms is an effective defence against these small flagellates, as well as viruses and larger protozoa because it is both cheap to make and difficult to circumvent. He speculates that the high growth rates and ubiquity of diatoms is due to the efficacy of their silica cell wall as a defensive barrier. Viruses, now shown to be abundant in the ocean, tend to be highly host-specific (Fuhrman 1999) but can be kept off the living surface by means of an outer finely pored layer, e.g. the double-walled diatom frustule or the *Phaeocystis* colony skin (Hamm *et al.* 1999). *Phaeocystis* colonies are reported to be impervious to viral infection compared to solitary cells that expose living surface directly to the medium.

The larger the size of the predator relative to its prey, the easier for it to overcome defence mechanisms. Thus, large crustacea such as the shrimp-like euphausiids will crush any diatom shell but smaller copepods will struggle with the tougher cell walls. The same applies to the many other armoured groups that characterize the marine phytoplankton. Indeed the groups that form blooms in the sea are all more or less armoured: diatoms, dinoflagellates (cellulose armour) and haptophytes (calcite plates or tough colony skin). Interestingly, the latter groups are also capable of ingesting particles (phagotrophy). The fact that in some genera heterotrophic and autotrophic species are outwardly identical indicates that morphology does not reflect nutrition, in contrast to terrestrial plants. Smetacek (1995) discusses the extent to which defence mechanisms are prevalent in marine plankton and the role of hard mineral shells, plates or cell walls in biogeochemical cycling.

The seasonal waxing and waning of different species, termed 'succession' by plankton ecologists, determines

the build-up and fate of organic matter in the system, but the various forces driving the shift in species composition are unknown. The fact that similar patterns occur in similar habitats in different parts of the world suggests that they are not always governed by proximate causes present in the growth arena. Further, the fact that all species must survive the needle's eye of the off-season, when mortality losses cannot be compensated by growth, also supports the idea that phytoplankton have developed effective defence mechanisms against predators. These include the strategy of hiding from small, specialized predators by being highly dispersed and therefore at dilute concentration. Cycling between proliferation and near-obliteration seem inherent to planktonic life. I have argued that the role of competition in this evolutionarily-derived scheme of things will be secondary but will increase with resource availability. As the ability to sequester resources in the sea is restricted, evolution in the plankton has led to improved defence systems, with diatoms the most recent and successful group.

Regulation of light absorption by whole plants and tissues as determinants of terrestrial productivity (TOM C. VOGELMANN)

As leaves develop, their anatomy is influenced by environmental factors including light quality and quantity, the intensity of ultraviolet radiation and carbon dioxide concentration. Common anatomical modifications in response to the environment include alteration of stomatal density, changes in epidermal and palisade cell size and shape, and numbers of mesophyll cell layers. This developmental plasticity allows leaves to adapt to their environment and, presumably, helps optimize photosynthetic performance under a specific set of environmental conditions.

At the level of the whole leaf, photosynthetic performance is determined by several factors including the amount of available light and carbon dioxide, the photosynthetic capacity of the leaf and regulatory metabolic controls. The photosynthetic performance of a whole leaf is a summation of the performance of the individual cell layers. It may, therefore, be advantageous if leaf anatomy facilitated a relatively uniform internal distribution of light and carbon dioxide so that photosynthetic work could be distributed more equally between the mesophyll layers (Vogelmann *et al.* 1996). Leaves are relatively permeable to carbon dioxide and internal concentration gradients across the mesophyll are usually relatively small (Evans & von Caemmerer 1996). On the other hand, internal light gradients appear to be much steeper. Thus, it may be that internal light distribution imposes a more formidable constraint over uniform

partitioning of photosynthetic activity between the mesophyll layers than does the distribution of carbon dioxide.

Within a leaf, the theoretical maximum amount of photosynthetic work that a cell layer can conduct is determined by how much light is absorbed by that layer. It follows that the distribution of photosynthetic performance within the leaf may be determined by the internal profile of absorbed light across the mesophyll tissues. At first glance, it might seem relatively easy to estimate the amount of light absorbed for photosynthesis by each cell layer. Unfortunately, this is not the case because detailed information is needed about the amount of light, the spectral quality of the light, and the amount of chlorophyll, accessory pigments and their distribution within the cell layer; measurements that are tedious and difficult to make.

Light gradients are determined by absorption and light scattering (Vogelmann 1993)—dynamic processes that make it difficult to calculate the amount of light present in different cell layers within the leaf. It seems obvious that absorption of light by one cell layer decreases the amount of light available in the underlying layers. On the other hand, light scattering increases the internal fluence rate and the probability for absorption; the dynamics of light scattering and how it influences the distribution of light within the leaf are not intuitively obvious. Leaves could control the internal allocation of light energy to the photosynthetic system by (i) changing pigment content and distribution, (ii) controlling the amount of light scattering by altering mesophyll cell size, shape and packing, or (iii) changing both pigment content and cellular light scattering characteristics. It follows that environmentally induced changes in leaf anatomy, which usually encompass changes in both pigmentation and anatomy, could have profound influences on the distribution of light within the leaf and the allocation of light energy to photosynthesis within the mesophyll layers. The situation is even more dynamic because chloroplasts commonly move within leaf cells (Gorton *et al.* 1999).

The potential consequences of a changing environment upon the photosynthetic performance of leaves are considerable. In understanding these, it would be useful to have more detailed information on the relationships among leaf anatomy and internal concentrations of light and carbon dioxide, and on how these physical parameters influence the profiles of photosynthetic performance within the leaf. Obviously, this is a large task. Information is available for some of these parameters but it is disperse, and there is no unifying theory that relates leaf anatomy to internal profiles of photosynthetic performance within leaves or how such profiles could be influenced by the environment. On a more positive note, recent advances in experimental techniques set the

stage for future detailed studies in which it is possible to relate leaf structure with some of the physical factors important for photosynthesis within the leaf.

What do we know about leaf tissue optics, light distribution and photosynthetic performance within leaves? The leaf epidermis clearly plays an important protective role in screening out potentially harmful ultraviolet-B radiation and protecting against desiccation and pathogen attack. Perhaps less appreciated is the fact that these cells frequently focus light and that this phenomenon occurs in most higher plants (Vogelmann *et al.* 1996). Such focusing usually increases the light two- to threefold within the underlying tissues, but in extreme cases can elevate light twenty- thirtyfold, such as within the leaves of tropical understorey plants, where epidermal focusing is more prevalent among species. It is problematic to discern whether or not such focusing serves an adaptive purpose.

Moving into the interior of the leaf, the hypothesis that tubular palisade cells facilitate the penetration of light into the leaf interior has been confirmed experimentally (Vogelmann & Martin 1993). At the same time, mesophyll tissues can create an intensely light scattering medium. The amount of light scattering, and hence path length, is determined in part by mesophyll cell size and shape and it may be that plants control the amount of light absorption through the light scattering characteristics of mesophyll cells. Measurement of photon transit times within *Hibiscus* leaves allowed a direct measure of photon path length (Luk & Vogelmann 1998). These leaves have a relatively small proportion of intercellular air space (21%) and path length enhancement caused by scattering was only 1.2. This figure probably represents a lower extreme and, for more typical leaves with more intercellular air space, scattering probably enhances path length three- to fourfold. More research is needed to ascertain whether plants control path length through development of mesophyll anatomy.

The shape of light gradients within leaves depends upon the amount of absorption. Light gradients are exponential at wavelengths where light absorption is high (Cui *et al.* 1991), whereas at more weakly absorbed wavelengths, the amount of light increases immediately beneath the irradiated surface and then decreases linearly. By contrast, profiles of absorbed light, measured through chlorophyll fluorescence, are complex in shape (Takahashi *et al.* 1994). In spinach and *Camellia*, the proportion of absorbed quanta rises rapidly in the mesophyll and then, following a maximum, declines more gradually across the remainder of the leaf. The shape of the absorption profile is determined by the wavelength of the light and by mesophyll anatomy. These measurements suggest that profiles for photosynthetic performance within leaves may also have a complex

shape. Indeed, in *Vicia* and in sun and shade leaves of spinach this appears to be the case (Vogelmann *et al.* 1996). In both species, profiles of carbon fixation appear Gaussian in shape with maximum fixation positioned midway through the palisade tissue, a location that is substantially distant from the irradiated surface.

Is there a physical basis for such complexly shaped photosynthetic profiles and is it reasonable to assume that we may find similarly shaped profiles in other species of plants? The answer to both questions is a qualified 'yes'. The dynamics of light scattering can create maximum photon fluxes at a location that is well beneath the irradiated surface of a leaf. It may be that the location of maximum carbon fixation midway through the mesophyll simply coincides with the location of maximum photon flux. Alternatively, it may be that the absorption and carbon fixation profiles are determined primarily by the concentration of chlorophyll, which has a Gaussian distribution across the mesophyll in spinach. More research is required to resolve these questions.

What happens to the internal profiles for photosynthesis when leaves are subjected to environmental stress such as excess light and UV-B radiation? As mostly mesophyll tissues, located nearest to the leaf surface, suffer from light stress, it is easy to imagine a significant decline in photosynthesis in those tissues with little effect throughout the remainder of the leaf. In other words, perhaps the shapes of the photosynthesis profiles become altered in response to the type and magnitude of environmental stress. Somewhat surprisingly, current evidence does not support this contention. In spinach and *Brassica* leaves subjected to radiative stress, photosynthesis activity throughout the mesophyll tissues shifted downwards but the overall shape of the photosynthesis profiles did not change. Thus, it appears that that there is marked integration and co-ordination of photosynthetic activity between leaf mesophyll layers.

Aside from contributing to knowledge at the leaf level, where do such leaf structure-function studies fit in the larger scientific picture? Hopefully, understanding the fundamental determinates of photosynthesis within leaves will facilitate scaling and integration of photosynthesis from the leaf to the whole-plant and canopy levels. This may help define the complex interactions associated with how plants adapt to their environment and how they react physiologically in response to climate change.

Mechanisms of response of photosynthesis and primary production in terrestrial ecosystems to atmospheric change (STEPHEN P. LONG)

Understanding the mechanisms by which net primary productivity (NPP) responds to global change is critical

to the development of models capable of predicting biological feedback to the carbon cycle under atmospheric change. NPP (P_n) on a carbon basis for a unit area of land over a given interval of time is:

$$P_n = A_c - R_a = \Delta C + L \quad (1)$$

where A_c is canopy photosynthetic carbon uptake (net of photorespiration), R_a is autotrophic (dark) respiration loss, ΔC is the change in mass of plant carbon, and L is the loss of plant carbon by death either directly to consumers or as litter and input to the detritivore food chain.

Predicting change requires an understanding of the responses of photosynthesis and respiration; while also requiring reliable NPP estimates for validation (Long & Hutchin 1991). However, there are gaping holes in this information, a fact that is perhaps too often overlooked in the rush to provide answers. This contribution outlines the strengths and weaknesses of current information and understanding with respect to the development of mechanistic models of NPP, and notes some potential ways forward.

Short-term responses

The mechanisms underlying the response of photosynthesis to climatic and atmospheric variables are perhaps better understood than those for any other physiological process. Mechanistic biophysical and biochemical models of steady-state leaf photosynthesis, combined with biophysical models of light, energy and gas transfer within plant canopies, provide a strong basis for predicting instantaneous photosynthetic carbon uptake (Drake *et al.* 1997). A good understanding of the bases of variation between vegetation types enhances this. There are no equivalent mechanistic models for plant respiration (Drake *et al.* 1999). Here prediction depends on phenomenological models based on uncertain concepts, in particular growth and maintenance components (Drake *et al.* 1999). For both photosynthesis and respiration there is a long history of study of the effect of climatic variation. In contrast to marine systems, change in atmospheric composition has profound direct effects on terrestrial vegetation.

The atmospheric CO_2 partial pressure ($p\text{CO}_2$) is currently well below that needed both to saturate C_3 photosynthesis and to inhibit the competing process of photorespiration (Long 1991). As a result, photosynthesis is more efficient in its use of absorbed light at elevated $p\text{CO}_2$, regardless of whether light is limiting or saturating. The mechanisms underlying the initial increase in photosynthesis on transfer to elevated $p\text{CO}_2$ as well as the interactions of elevated $p\text{CO}_2$ with light and temperature are well understood, conserved and described

mathematically (e.g. Long 1991). The mechanisms causing decreases in transpiration and in respiration with increased $p\text{CO}_2$ are uncertain.

Phenomenological models effectively capture the decrease in stomatal conductance with elevated $p\text{CO}_2$ and their increase with humidity and photosynthesis (Drake *et al.* 1997). This predicts decreases in regional evapotranspiration and increased foliage temperature – both factors that feedback onto photosynthesis and canopy development. Again there is a good understanding of how major vegetation types vary in this response (Long 1999). Far more contentious is the suggestion that rising $p\text{CO}_2$ inhibits plant respiration. Many studies have reported a decrease, with major implications for NPP, whilst a few have found no decrease or even an increase with no clear pattern to this variation (Drake *et al.* 1999). Whilst there are many potential sites in respiratory metabolism that are affected by CO_2 , at present none is known to have the properties that could explain the observed effects at the whole leaf and plant level (Drake *et al.* 1999).

Long-term responses

The significance of long-term acclimation of photosynthesis to elevated $p\text{CO}_2$ and the mechanisms underlying this are also less certain. However, some patterns are emerging, especially in relation to the interaction between source-sink balance and nitrogen in the plant, that may be explained at the level of gene expression allowing some generalizations about the pattern of response (Rogers *et al.* 1998; Stitt & Krapp 1999). Elevated $p\text{CO}_2$ also feeds back on photoinhibition, decreasing the susceptibility of the canopy to light damage during periods of rapid growth but increasing susceptibility when growth is inhibited, for example in evergreen canopies during the winter (Hymus *et al.* 1999). Significant areas of the northern hemisphere and tropics are experiencing faster rates of increase in tropospheric ozone than in $p\text{CO}_2$. Photosynthesis is strongly and rapidly inhibited by ozone, an effect modified by rising $p\text{CO}_2$ (e.g. McKee *et al.* 1995; Martin *et al.* 2000).

Respiration also shows long-term acclimation to altered temperature and $p\text{CO}_2$. Although a simple Arrhenius plot may explain the response of respiration to temperature in the short term, it is a poor predictor in the long term. Remarkably few studies have actually measured whole plant respiration (as opposed to soil plus plant) and photosynthesis simultaneously. Gifford (1995), in one of these few studies, showed that for a wide range of conditions, plant respiration in the long term appeared a very constant proportion of photosynthesis. This raises the tantalizing possibility that predic-

tion of respiration could be simple, if such a phenomenological link to photosynthesis proves robust.

Unlike the unicellular algae of the ocean, the dependence of NPP upon leaf photosynthesis is complex in terrestrial systems. An increase in photosynthesis might be totally offset by decreased allocation to photosynthetic tissue and vice-versa. Lack of a mechanistic or an adequate phenomenological description of allocation within the higher plant seems the weakest point in developing process-based predictions of change in NPP. However, long-term field experiments, especially Free-Air Carbon dioxide Enrichment (FACE) experiments, show a remarkable correlation between the short-term and mechanistically predictable response of leaf photosynthesis and the observed change in stand production (Long 1999). This is in sharp contrast to the predictions that were made prior to these studies that other limitations to NPP, notably nitrogen, would preclude any long-term stimulation of C-uptake (Melillo *et al.* 1990). These new findings suggest that a functional approach to allocation in which control of NPP is viewed as a property shared between processes rather than residing with a single limiting process or resource (Farrar 1996), may be a useful substitute for our lack of a mechanistic understanding of post-photosynthetic processes.

Validation against measured NPP

A fundamental barrier to prediction of future NPP is the extraordinary lack of reliable measurements of current NPP. Whilst a simple concept, NPP is remarkably difficult to measure in terrestrial systems. Measurements of biomass accumulation and turnover have been the basis of most estimates of NPP (Long *et al.* 1989). However, major errors are introduced by the difficulties of assessing below-ground biomass and of determining the turnover of fine roots and short-lived, above-ground organs. To develop extensive data bases, such as that provided by the International Biological Programme (IBP), short-cut methods were developed to avoid the resource intensive measurements of fine roots and organ turnover (Table 1). Unfortunately, subsequent intensive studies, and analyses of the methods used, have shown these assumptions to be seriously flawed. These can result in threefold underestimates of NPP in the case of the moist tropical grassland biome (Long *et al.* 1989). Simple corrections of this underestimation are also prevented by the lack of information on how organ turnover and fine root production is affected by soil, climate and atmosphere. Measurement of atmosphere-system carbon exchange is greatly improving knowledge of net ecosystem production (NEP). However, estimation of NPP from these NEP estimates is limited by the

difficulty of separating root respiration from other soil sources of CO₂.

Use of the extensive data bases, especially those developed from the flawed methods of IBP and its successors for testing and development of models of NPP must be viewed with great scepticism. Intensive studies of individual sites where detailed measurements of photosynthesis, respiration, biomass partitioning, organ turnover and system to atmosphere exchanges are conducted on the same stands subjected to field-scale manipulations of climate and atmosphere are now underway. These will provide a way forward in the development of more mechanistic models of the response of terrestrial NPP to atmospheric change and provide a sounder basis for validation of remote sensing methods.

Carbon dioxide and forest productivity (EVAN H. DELUCIA, RICHARD B. THOMAS, ADRIEN C. FINZI AND WILLIAM H. SCHLESINGER)

The large stature and enormous spatial coverage of forests contribute to their influence on the exchange of carbon between land surfaces and the atmosphere. The global uptake of carbon by photosynthetic organisms, expressed as net primary production (NPP), is approximately 105 Pg year⁻¹ (Pg = 10¹⁵ g). Forests contribute 33% of this total and 62% of all NPP on land (Field *et al.* 1998; Table 3). Large quantities of carbon are contained in the tissues of trees and even more is sequestered in forest soils (Schlesinger 1997). Changes in the physiology of trees and the global distribution of forests therefore have a direct and immediate impact on the concentration of carbon dioxide in the atmosphere.

Potential effects of elevated CO₂ on forest NPP

The combustion of fossil fuels and other human activities are increasing the concentration of CO₂ in the atmosphere by approximately 0.4% year⁻¹. Trees use C₃ metabolism and their photosynthetic rates are limited by the current atmospheric CO₂ concentration of 370 ppm. It is therefore reasonable to predict that a stimulation of photosynthesis by CO₂ will increase forest NPP and reduce the accumulation of this important greenhouse gas in the atmosphere. Here, we examine recent observations of the response of trees and forests to elevated atmospheric CO₂, and propose the hypothesis that CO₂ enrichment will increase the initial growth rate and cycling of carbon through forest ecosystems, more than it will enhance the maximum accumulation of biomass.

Net primary production is the difference between photosynthesis and autotrophic respiration and repre-

sents the annual input of new carbon into forests. Most of this carbon is returned to the atmosphere in months to decades by decomposition and by infrequent large-scale disturbances such as fire. Humans also convert forest carbon to CO₂ during harvests and land clearing (IGBP 1998). The remaining carbon is stored in wood or sequestered in forest soils.

It appears that elevated CO₂ will increase the photosynthetic rate of trees. Experiments with seedlings and saplings under controlled conditions reveal that a doubling of current CO₂ levels causes a *c.* 54% increase in net photosynthesis (Curtis & Wang 1998). As trees acclimate to CO₂, this enhancement abates, but rates of photosynthesis remain higher than in plants grown under ambient levels of CO₂. In short-term experiments, with ample supplies of soil nutrients and water, this stimulation of photosynthesis contributes to a *c.* 31% increase in biomass production, although suboptimal nutrient levels limit this response substantively (Curtis & Wang 1998). Until recently, it was unknown whether elevated CO₂ would enhance photosynthesis and stimulate NPP in a large, intact forest, with the myriad of biological and physical interactions and resource limitations that characterize natural ecosystems.

To address this question we used a free-air fumigation system to expose an intact forest plantation to an experimental increase in atmospheric CO₂. The concentration of CO₂ in the atmosphere of experimental plots was increased by 200 ppm to approximately 560 ppm, the concentration expected in the year 2050 (Houghton *et al.* 1996). Similar to the response of potted seedlings, increased CO₂ stimulated photosynthesis (Myers *et al.* 1999) and growth of these large trees. After two years of enrichment, NPP increased by 25% (DeLucia *et al.* 1999). While a world-wide stimulation of forest NPP of this magnitude could consume a significant fraction of fossil-fuel derived CO₂ by 2050, nutrient limitations, disturbance and the successional stages of forests will undoubtedly cause carbon storage in woody biomass to be much lower.

The limits of forests to store carbon

The capacity of a forest to store atmospheric carbon ultimately depends on how large trees become and how much of the carbon they deliver to the soil resists decomposition. Using ¹⁴C 'bomb carbon' as a tracer, Richter *et al.* (1999) found that only a small portion of NPP (< 1%) in a re-establishing pine forest accumulated in the mineral soil where it may become sequestered in humus. Most soil carbon was rapidly returned to the atmosphere by decomposition. Schlesinger & Lichter (2001) report a modest increase in the biomass of the forest floor in the CO₂-enriched plots, but no changes in

the carbon content in the mineral soil, despite isotopic evidence for a substantial turnover of soil organic carbon. Globally, carbon stored in soils is roughly three times that in terrestrial vegetation and twice that in the atmosphere (Schlesinger 1997). However, the relatively small proportion of NPP that accumulates in soil each year suggests that this pool is not likely to play a major role in mitigating the rise in atmospheric CO₂ over the next 100 years.

The largest 'sink' for atmospheric carbon in forests over decades to a few centuries is in the standing biomass of stems, branches and large roots of living trees. Net primary production represents the biomass increment at a given time. In our rapidly growing pine plantation, elevated CO₂ stimulated NPP during the first three years of exposure. However, in the fourth year of exposure, basal area increment of the dominant trees was not significantly increased by elevated CO₂. This may be the result of large fluxes of N from vegetation to soils in litterfall and the absence of an increase in soil N availability or N uptake by canopy trees (Finzi *et al.* 2001). Whether this stimulation is sustained through time, resulting in larger total woody biomass per unit of land surface, or whether the trees simply reach the same maximum size faster, has very different implications for the role of forests in the global carbon cycle.

Stimulation of tree growth by elevated CO₂ decreases precipitously with the duration of exposure (Idso 1998). For sour orange and loblolly pine trees, rooted in soil in open-top chambers, the enhancement of standing biomass by 2x CO₂ exceeded 150% in the first two years of exposure, but it dropped below 90% by year five. Oak trees growing near natural sources of geological CO₂ show a similar decline. A reconstruction of growth rates from tree rings indicates that the biomass enhancement of oaks by elevated CO₂ decreased to <30% by 30 years, and it will likely be <5% after 100 years. This decline in the response of growth rate to elevated CO₂ suggests that the enhancement in final biomass will be substantially less than the initial enhancements predicted from short-term experiments. This supports our hypothesis that elevated CO₂ will stimulate the cycling of carbon through forest ecosystems more than the maximum carbon storage.

Individual trees can become massive—the carbon content in a single redwood, for example, can easily exceed 10⁸ g. To predict how elevated CO₂ and other aspects of climate change will influence carbon storage in forests, an improved understanding of the processes determining maximum tree size is necessary. The growth rate of trees declines with increasing size (Enquist *et al.* 1999) and it has been widely assumed that an increasingly unfavourable carbon balance causes this decrease. As a tree grows the volume of wood increases relative to

leaf area. The metabolic parenchyma cells in wood require carbon for maintenance respiration. As a result of this carbon demand, it was accepted that the accumulation of woody tissues, including roots, relative to photosynthetic surface area, was the primary factor slowing the growth of large trees and driving the decrease in NPP as forests age. In this scenario, elevated CO₂ could increase the maximum size of trees through the stimulation of photosynthesis. Recent observations suggest, however, that this explanation for the age-dependent decrease in NPP may be inadequate.

At least in montane coniferous forests, respiration from woody tissues is insufficient to explain the decrease in NPP in large old-growth forests. An alternative mechanism for the decline in NPP is that a size-dependent reduction in the water conducting capacity is associated with decreased photosynthetic rates in large, old trees (Ryan & Yoder 1997). When combined with the observation that elevated CO₂ seems not to influence the conducting capacity of trees and only exerts a minor influence on transpiration rates, this scenario leads to the conclusion that the maximum size of trees, set by hydraulic properties, will be relatively insensitive to elevated CO₂. In this case, the observed increase in growth and NPP under elevated CO₂ will cause forests to grow at a high rate to an inherent maximum size set by their hydraulic properties. Consequently, the rate of stand development and the turnover of trees will increase, but the maximum pool of carbon in wood in a given mature forest will not change.

The weight of evidence suggests that photosynthesis, growth rates and NPP of very young forests will increase as the level of CO₂ in the atmosphere continues to rise. The magnitude and duration of these increases are, however, highly uncertain. In addition to being modulated by the availability of other resources, the growth response to CO₂ will abate sharply as trees age, suggesting that carbon storage in biomass of living trees will be smaller than expected from the initial responses of NPP. Admittedly, this is a speculative statement with important implications for our understanding of the role of forests in the global carbon cycle. A more rigorous understanding of the effect of elevated CO₂ on tree growth and forest productivity will require improved knowledge of the processes defining the maximum size of trees.

Has the primary productivity of the planet been under-estimated? (JOHN GRACE)

The measurement of net primary productivity (NPP) in terrestrial ecosystems is notoriously difficult. There are many models of NPP (see *Global Change Biology* 5, suppl. 1), but without reliable field data these models cannot be

tested. Nor can they be tested at the large scale against atmospheric measurements of CO₂, as the atmospheric signal embraces heterotrophic respiration and biomass burning, which are two other poorly known terms in the global carbon budget. Most authors, in writing about global productivity, turn first to the table of data published by Whittaker & Likens (1975). Here, the productivity of each biome is tabulated along with its area, and the global terrestrial NPP may be computed by summing the products to be about 59 Gt C year⁻¹ (Whittaker & Likens 1975. This is very close to the figure used in all recent versions of the global carbon cycle (e.g. Schimel 1995; Field *et al.* 1998). Where did this NPP data come from? We know they were obtained by harvesting techniques but few details are given, except that the table was 'prepared by the author and G.E. Likens from various sources ... and estimates'.

The traditional approach to measuring NPP by sequential harvesting of sample plots was developed in the late 1960s during the International Biological Programme, and has been much-criticised (see Long *et al.* 1989). Sequential harvesting provides an estimate of above ground increment, to which must be added an estimate of below-ground increment, and then all the other components of plant production which include: litter, fine root turnover, exudates, organic volatiles, carbon flowing from plants to herbivores and from roots to fungal symbionts. These terms are likely to be collectively large, and some of them are exceedingly difficult to measure.

In the last decade we have seen the development of new methods based on CO₂ flux measurement by techniques such as eddy covariance (Moncrieff *et al.* 1997) and mass-balance determinations in the convective boundary layer from balloon and aircraft (Raupach *et al.* 1992). They sample over a much larger area than is ever possible with traditional methods, typically 1 km² for eddy covariance to 1000 km² for the case of boundary layer measurements. They measure the flows of carbon between vegetation and the atmosphere directly and continuously; however, they measure not NPP but the related quantity net ecosystem productivity (NEP), which includes heterotrophic respiration R_h (mainly microbial but also animal) as well as autotrophic respiration R_a :

$$P_n = P_g - R_a \quad (2)$$

$$P_e = P_g - R_a - R_h \quad (3)$$

where P_g is gross primary productivity (essentially the photosynthetic rate of the ecosystem); P_n , the NPP, is what is left after plant (autotrophic) respiration; and P_e is what remains of P_n after heterotrophic respiration is

accounted for (P_e is the total CO₂ exchange of the ecosystem).

The obvious way to estimate P_n from P_e is to subtract R_h from P_e (equation 3). Unfortunately, R_h is hard to measure because the CO₂ flux from the soil includes a component of R_a derived from roots. There have been a few attempts to partition the soil efflux into R_h and R_a (Kelting *et al.* 1998); they suggest that about half the CO₂ flux from the soil is derived from heterotrophic respiration. There are some other relationships that may be helpful in evaluating P_n in equations 2 and 3. For example, Waring *et al.* (1998) present data from several forests that suggest $P_n/P_g = 0.47 \pm 0.04$, although the assumptions on which this estimate is based have been challenged by Medlyn & Dewar (1999). At many eddy covariance sites, there are supplementary measurements of dry mass that may be used with flux data to construct an entire carbon flow diagram (Malhi *et al.* 1999). The pragmatic approach to solving equations 2 and 3 involves three steps.

(1) Assume that ecosystem respiration ($R_a + R_h$) in the day may be estimated from the ecosystem respiration at night. This involves fitting a suitable temperature function to describe the effect of temperature on respiration (Lloyd & Taylor 1994), and using the function to estimate daytime respiration, given daytime temperatures. Then, estimate ecosystem photosynthesis P_g by subtracting daytime $R_a + R_h$ from daytime P_e .

(2) Evaluate R_a/R_h and $R_a + R_h$ for the soil, using appropriate field methods (e.g. Kelting *et al.* 1998); hence find R_a and R_h over the course of the 24-h cycle.

(3) Use estimated R_a , R_h and P_g to obtain P_n .

As the total CO₂ flux includes more of the C-production processes than any harvesting method can possibly do, this approach will almost certainly yield estimates of P_n that exceed those we have already, perhaps by 20–50%. For example, in an analysis of carbon flows at a rain forest in Manaus, Brazil, we found NPP was as much as 15.6 t C ha⁻¹ year⁻¹, whereas neglecting fine root turnover would yield a figure of only 9.8 t C ha⁻¹ year⁻¹. If this discrepancy applies to all biomes, we may expect to find the terrestrial biosphere to be more productive than hitherto supposed.

The productivity of terrestrial plant communities: the role of plant functional types, trophic interactions and biodiversity (J. PHILIP GRIME)

Until quite recently, the research approach of many plant production ecologists was strongly influenced by physics and chemistry, and by methods and philosophies imported from arable crop production. Arable monocultures provide a wholly inadequate model of a mature,

multispecies ecosystem and this has led some theoreticians and population ecologists to develop methods that rely upon more abstract concepts such as competition theory, niche differentiation, biodiversity, trophic dynamics and food webs. Although better adjusted to complex ecosystems, theories of this kind often lack quantitative definition and are weakly rooted in physics and chemistry. The time is ripe for a new synthesis embracing complexity but preserving the necessary focus upon control mechanisms, resource dynamics and limiting factors. The objective here is to visit three areas of current debate in terrestrial plant productivity: plant functional types, trophic interactions and biodiversity, and to assess the prospects for a profitable interaction between 'traditional' and 'ecological' methodologies.

Plant functional types

In Liebig's 'Law of the minimum', the principle was established of identifying the single factor that most limited agricultural productivity at a given location. A similar approach can sometimes allow diagnosis of the factors limiting productivity in natural or semi-natural ecosystems. However, here more complex controls usually operate and it is possible to demonstrate that within communities the limiting factors vary according to species and season, and from year to year (Chapin & Shaver 1985; Dunnet *et al.* 1998). Even if we confine attention to the dominant contributors to the biomass we must contend with many species that have never been the subject of detailed study.

Faced with these difficulties, how, with minimal effort, can we analyse the factors controlling productivity in the large number of relatively unfamiliar multispecies communities occurring through the terrestrial biosphere? One approach is to develop rapid and reliable criteria with which to classify plants in terms of the functional characteristics most likely to influence vegetation productivity and ecosystem responses to perturbation. Whereas classical Linnean taxonomy tells us about the origins of plants, the quite different purpose of an ecological classification is to group plants according to their functional similarities regardless of their evolutionary and taxonomic affiliations.

In our attempts to understand their ecology we can use a variety of criteria to classify plants. These need to be adjusted to serve different research objectives. Sets of plant traits that are useful indicators of climatic tolerance, for example, are likely to be quite different from those that help us to predict the dispersal rates of invading species. Different again are the sets that inform us about ecosystem processes.

Following 10 years of intensive fieldwork and laboratory study of the vegetation of the Sheffield region in

northern England with John Hodgson and Rod Hunt, Grime (1974) hypothesized that much of the information needed for the functional interpretation and classification of plant communities could be summarized by a simple triangular array of primary plant functional types. This system, which has become known as CSR theory, has some resonance with the pioneering work of the Soviet plant ecologist Ramenskii (1938). CSR theory states that within higher plants there are three extremes of adaptive specialization: ruderals (R) are ephemerals, and act as temporary occupants of continuously disturbed habitats; competitors (C) are larger and longer-lived and have the capacity to monopolize productive but relatively undisturbed terrain; and stress-tolerators (S) are very long lived, slow-growing plants capable of surviving conditions of extremely low productivity. The predictive power of this trichotomy depends upon the assertion that C-, S- and R-plants each possess a distinctive set of functional traits that have a consistent relationship to the properties of the ecosystems with which they are associated. For example, the short life spans and rapid reproduction of ruderals confer high resilience following ecosystem perturbation. The monopolistic resource capture exhibited by the competitors imposes low plant biodiversity in productive, relatively undisturbed vegetation. The slow dynamics of the stress-tolerators leads to low recovery rates after physical damage and to long retention times for mineral nutrients.

An objection to CSR theory arises from the proposition that plant evolution has been a stochastic and infinitely diversifying process with the result that the sets of plant traits said to be associated on a world-wide basis with C, S and R simply do not recur with the consistency necessary to provide a predictive basis for ecosystem analysis. There is only one appropriate response, that is to test for the existence of the predicted sets of traits by measuring functional attributes in large numbers of plants drawn from a wide range of contrasted ecosystems.

Some progress can be made, in testing CSR theory, simply by reviewing the existing published literature. There is strong evidence confirming the recurrence of the set of traits predicted for the ruderal (R) functional type. In the floras associated with fertile but frequently and severely disturbed habitats (e.g. arable fields, gardens) the predicted association between ephemeral life-history, rapid growth, early reproduction, and heavy allocation of captured resources to offspring is widely observed. With respect to the C and S functional types, both of which are perennials, much of the information we need for an adequate test is lacking; here it has been necessary to conduct new research.

Plant traits were screened for 43 herbaceous plants of contrasted ecology to provide an objective test for patterns of functional specialization. Standardized meas-

urements were performed on the morphology, anatomy, physiology and biochemistry, yielding quantitative data on 67 traits. Multivariate analyses showed clear consistent patterns of variation involving many plant traits across the species. The most striking feature of the results was the emergence of a primary axis (Axis 1) accounting for 22% of the total variation. A detailed discussion of the significance of this axis has been presented elsewhere (Grime *et al.* 1997). Of particular significance was the recurrence of the sets of traits predicted for the C and S functional types across the species. For the purposes of ecosystem analysis it is particularly exciting to observe that some of the plant traits most strongly varying along Axis 1 (mineral nutrient concentrations of the leaves, leaf longevity, resistance to herbivory and rates of litter decomposition) are directly relevant to ecosystem properties and NPP.

Trophic interactions

The study of Grime *et al.* (1997) clearly differentiated between 'resource acquisitive' (R and C) and 'resource retentive' (S) functional types. Most apparent was a trade-off between rates of resource capture and growth (high in R and C) and defence against generalist herbivores (high in S). This is consistent with the theoretical predictions of Fretwell (1977) linking habitat productivity to the number of trophic levels that can be sustained in an ecosystem. By classifying the dominant plants into functional types it should be possible to predict the length of food chains and to make testable hypotheses concerning losses to herbivory in particular ecosystems. Recently, experimental tests of these relationships have been conducted using herbaceous vegetation and invertebrates occurring naturally along productivity gradients in the field or allowed to assemble on soils of contrasted fertility in outdoor microcosms (Fraser & Grime 1999). The results strongly support the Fretwell (1977) hypothesis and provide evidence of the operation of two quite different kinds of plant defences through low palatability (at low NPP) and through top-down control by predators (at high NPP). This suggests that recognition of plant functional types may provide a basis in future for rapid estimation of losses to herbivory.

The predictive value of plant functional types is not restricted to estimates of NPP and losses to herbivory. Grime *et al.* (1996) show that mechanisms that protect living leaves against generalist herbivores remain operational against decomposer organisms. This opens the possibility for the CSR classification of plant functional types to be used in conjunction with climatic data to predict rates of litter decomposition and carbon accumulation in the soil.

Biodiversity

Where functional traits of plants have been successful in predicting ecosystem properties (e.g. MacGillivray *et al.* 1995), it has been necessary to weight the contribution of each species according to its abundance in the vegetation. This is founded on the assumption that the extent to which the traits of a species affect ecosystem properties is likely to be strongly related to the contributions of the species to processes such as photosynthesis, mineral nutrient capture, transpiration and provision of substrates exploited by herbivores and decomposers. There is a clear implication here that ecosystem processes are determined to a very large extent by the characteristics of the dominant contributors to the plant biomass. As a corollary to this 'mass ratio hypothesis' (Grime 1998) we would not expect minor contributors to the vegetation to exert strong effects on ecosystem properties.

Against a theoretical background in which the traits of dominant plants were widely suspected to be acting as the overriding controllers of ecosystem properties, considerable interest and controversy was generated when, in 1994, two papers appeared purporting to demonstrate immediate benefits to ecosystem properties arising from high species-richness in experimental plant assemblages (Naeem *et al.* 1994; Tilman & Downing 1994). These suggested that benefits arose in the species-rich mixtures from the presence of a wider range of morphologies and physiologies, generating either complementary and more complete exploitation of resources (Naeem *et al.* 1994), or conferring resistance and resilience in the face of an extreme event (Tilman & Downing 1994). Subsequently, doubts have been cast on the validity of the conclusions of the two papers (Huston 1997). It appears that, in both cases, ecosystem properties attributed to high species-richness were in reality due to the presence in the more diverse communities of dominant species with traits attuned, respectively, to high productivity (Naeem *et al.* 1994) and drought (Tilman & Downing 1994). More recent experiments have failed to provide convincing support for the effects of high species-richness on ecosystem functions; the most parsimonious explanation for the data presented in all these papers is that the ecosystem properties examined were controlled by the functional traits of a relatively small number of species accounting for a high proportion of the total plant biomass.

The alacrity with which some commentators and conservation enthusiasts seized upon supposed evidence of direct benefits of species-richness to ecosystems, emphasizes the need for caution in a complex research field and brings the risk that exposure of false conclusions may lead to a sceptical response if and when more substantial evidence of beneficial effects of species-richness are presented. Following CSR theory it has

been proposed that the most potent effects of declining biodiversity are likely to become evident only in the longer term (Grime 1998).

Conclusions

Recent research has provided strong support for the existence of widely recurring plant functional types with characteristic sets of traits that are reliable predictors of ecosystem properties such as NPP, losses to herbivores, resistance and resilience to perturbation and rates of litter decomposition. Plant functional types also provide useful clues to the trophic structure of an ecosystem. It is concluded that the immediate controls of ecosystem properties by vegetation are mediated by the traits of dominant contributors to the plant biomass and are relatively insensitive to plant biodiversity. This, in contrast to one based on biodiversity, provides a tractable approach to predicting current and future NPP across terrestrial biomes.

Controls on the primary productivity of terrestrial ecosystems (I. COLIN PRENTICE)

The controls on terrestrial primary productivity represent a key issue in global change research. We need to understand not only the *impacts* of rising CO₂ and climate change on productivity, but also the attendant *feedbacks* to atmospheric CO₂ and climate. Some key facts (see Prentice *et al.* 2000) illustrate why. First, the gross exchange of carbon between the atmosphere and the terrestrial biosphere is *c.* 120 Pg C year⁻¹. In other words, about one-sixth of all the CO₂ in the atmosphere is fixed in photosynthesis (gross primary production, GPP) every year; about half of this amount is returned to the atmosphere through autotrophic respiration and the other half through heterotrophic respiration and combustion. Second, the fluxes in and out of the terrestrial biosphere are not perfectly balanced. Comparison of trends in atmospheric CO₂ and O₂ concentrations shows that terrestrial ecosystems are taking up enough carbon to more than compensate for deforestation, at least 2 Pg C year⁻¹. Uptake by terrestrial ecosystems thus sequesters on average about a quarter of all anthropogenic CO₂ emissions. Yet this uptake represents a small part, less than 2%, of GPP. The rate of increase of atmospheric CO₂ concentration varies between years by ± 2 Pg C year⁻¹. This variation is clearly linked to climate variability, and can be explained principally by interannual variations in the terrestrial carbon balance.

Thus, the fraction of emitted CO₂ that stays in the atmosphere is partly controlled by a relatively minor (and labile) imbalance between terrestrial ecosystem inputs and outputs of carbon. What then will happen

to terrestrial carbon uptake if and when the Earth warms by as much as climate models predict? Will, for example, Kyoto-inspired schemes to sequester carbon in forests continue to work, or will they prove to have been costly errors? To answer such questions we require a good, quantitative understanding of the underlying processes which can be embedded in predictive models.

Today we have models, but insufficient understanding of some key processes. Models agree that physiological effects of rising atmospheric CO₂ concentration should lead to terrestrial carbon uptake of about the observed magnitude, by creating a transient imbalance between primary productivity and the size of the respiring carbon pools (Kicklighter *et al.* 1999; Cramer *et al.* 2001). They also agree that various processes will progressively limit this response to CO₂. However, current models do not agree even about the sign of the effect of global climate change on primary productivity.

Multiple time scales in a complex system make it inappropriate for modellers to rely on, for example, equilibrium assumptions and space-for-time substitutions in trying to predict the response of primary productivity to environment. For example, it would be most unwise to assume that the response of primary productivity to temperature and precipitation variations on a seasonal basis, or over periods of a few years, could be modelled by the empirical relationships that apply geographically. Instead, we need to understand and model the major underlying processes individually. Some of these are well understood: for example, the instantaneous response of photosynthesis to light, temperature and the internal partial pressure of CO₂. Others are less well understood. Here, I focus on two inter-related, and to a surprising extent unresolved, issues: (i) the role of nitrogen limitation and (ii) the effects of temperature changes in determining NPP over periods of months to years. These issues are considered here from the perspective of optimality theory which forces a re-examination of several tacit assumptions that can be found in the literature.

The idea that photosynthetic capacity (and with it, the concentrations of photosynthetic enzymes, and leaf nitrogen content) is optimized with respect to light availability came originally from classical observations of the photosynthetic characteristics of 'sun' and 'shade' leaves. Leaves with high photosynthetic capacity, able to achieve high rates of photosynthesis in high light, invariably have high dark respiration rates and are therefore ill-adapted to life in shade. More recently, several groups independently (Dewar 1996; Sellers *et al.* 1992; Haxeltine & Prentice 1996) proved that if all leaves have the photosynthetic capacity that maximizes their individual carbon balance, then total canopy photosynthesis (over periods long enough to

allow acclimation, i.e. not hours, but days to weeks) should be *proportional to absorbed light*. This result, which I will call the 'strong optimality hypothesis', is mathematically robust and provides a valuable heuristic tool even if the underlying assumptions are somewhat violated in practice, e.g. because of the uneven spatial and temporal distribution of light in the lower canopy. The result is appealing because it explains the long-standing observation that plant growth over longer periods is proportional to absorbed light. This would not be predicted simply by scaling-up a leaf-level physiology model and assuming invariant photosynthetic characteristics of leaves.

A superficially similar result can be proved using econometric arguments when it is assumed that the size of the canopy and the total amount of nitrogen in it are set independently, i.e. the optimization problem then consists of distributing this nitrogen through the existing canopy so as to maximize total productivity at the canopy level (Field 1988). However, this 'weak optimality hypothesis' leaves entirely open the question of how much carbon (and how much nitrogen) are *allocated* to leaves. According to the strong optimality hypothesis, environmental conditions including light availability determine the nitrogen content of leaves (on a per area basis) and leaf area index is regulated through allocation in such a way that the total plant nitrogen requirement does not exceed the amount of nitrogen available to the plant. In other words, nitrogen deficiency should primarily lead to carbon being allocated away from leaves and into tissues with a lower nitrogen concentration. A great deal of experimental evidence seems to support this proposition, at least in a qualitative sense. Moreover, if the model of Dewar *et al.* (1999) – in which the concentrations of photosynthetic proteins are regulated by the rate of photosynthesis – is correct, then strong optimality may be a general and unavoidable consequence of leaf physiological function. Dewar *et al.* (1999) has also argued for an extension of the strong optimality hypothesis to the whole plant level, which could explain the observed tendency for total plant respiration to represent a fixed fraction of GPP.

Haxeltine & Prentice (1996) explored some of the implications of strong optimality using a simple theoretical model. They found, *inter alia*: a modest and plausible down-regulation of photosynthetic capacity, accompanied by a decrease in leaf respiration, in response to raised ambient CO₂ concentration; realistically reduced nitrogen concentrations in the leaves of C₄ plants; and an increase in nitrogen concentration with latitude for leaves of a given functional type. This last effect was shown to be consistent with observations along a north–south gradient in North

America. It can be explained as the resultant of the opposing effects of declining light flux and declining temperature. At low temperatures, reaction rates are slower and more protein molecules are therefore required to maintain a given photosynthetic capacity. In terms of leaf nitrogen content, this effect proves stronger than the reduction in optimal photosynthetic capacity that accompanies the shift towards lower light flux at higher latitudes.

The strong optimality hypothesis makes two more general predictions that are plausible even though they seem to conflict with conventional wisdom. First, foliage nitrogen content does *not* determine photosynthetic capacity (although this is a commonly stated interpretation of observed empirical correlation between these two variables). Instead, foliage nitrogen content is indirectly regulated by the variables that determine photosynthesis: ambient CO₂ concentration, light, temperature and stomatal responses to these variables and to transpiration rate. Second, the primary productivity of C₃ plants, all else being equal, is determined by the quantum efficiency of photosynthesis and therefore *declines* with increasing temperature at current atmospheric concentrations of CO₂ and O₂. This second proposition may seem counterintuitive, but it is not. Productivity in high latitudes *can* respond positively to warming (i) through a longer growing season (longer green season in deciduous plants, reduced snow cover and longer photosynthetic period in evergreens) and (ii) by allowing higher rates of decomposition and nitrogen mineralization (Melillo *et al.* 1993), leading to greater allocation of carbon and nitrogen to foliage. These mechanisms would not apply to tropical forests with a year-round growing season, low leaf nitrogen requirements (because of faster reaction rates), and high nitrogen mineralization rates. We should be careful to avoid high-latitude bias.

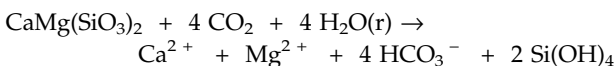
Results obtained with global ecosystem models (BIOMEn and LPJ) that incorporate the strong optimality hypothesis provide a minimal test of its plausibility. These models perform well against standard benchmarks, including seasonal cycles and interannual variability of atmospheric CO₂ (Prentice *et al.* 2000). However, so do other models built from different assumptions. Models can be right for the wrong reasons. In the race to produce functioning global models, theoretical issues like those raised here have been obscured. Such issues deserve more rigorous analysis, while observational and experimental evidence should be critically evaluated in the light of alternative theories. Otherwise, we will continue to be stuck with major uncertainties and discrepancies among models when they are projected into different climates.

Photosynthesis and plant productivity in transition: limitations and constraints during early land plant colonization (JOHN A. RAVEN)

Photosynthesis has probably occurred in the ocean since 3.85 Ga (3.85×10^9 years before the present); with global oxygenation and the evolution of eukaryotes occurring about 2.1 Ga, limited terrestrial primary productivity by cyanobacteria and algae occurring since about 1.2 Ga onwards, and the evolution of embryophytes occurring about 0.51–0.45 Ga ago (see Raven 1998; Raven & Edwards 2001). Oxygenation of the atmosphere had impacts on the land surface as a potential habitat for photolithotrophs by oxidizing Fe^{2+} to Fe^{3+} , and Mn^{2+} to Mn^{4+} and thus not only diminishing Fe and Mn availability but also P availability, just as had occurred with earlier local and then complete oxygenation of the oceans in restricting supply of these nutrients to marine photolithotrophs.

The evidence for algal photolithotrophs on land 1.2 Ga is rather tenuous, and comes from estimates of weathering rate of palaeosols. These exceed those from a solution in equilibrium with the atmospheric CO_2 concentration required for the greenhouse effect inferred from the likely temperature at the Earth's surface (see Raven 1998; Raven & Edwards 2001). A 'pumping' of CO_2 from the atmosphere into rocks makes up for the mismatch of CO_2 concentrations. This results from photosynthetic assimilation of atmospheric CO_2 by photolithotrophs at or in the rock surface, advection of organic carbon (particulate or dissolved) into fissures in the rock, and chemoorganotrophic metabolism which elevates CO_2 to a higher concentration than that found at air-equilibrium due to restricted diffusion of CO_2 back to the atmosphere. This CO_2 released below the rock surface, and any organic acids produced in metabolism, would increase the rate of weathering, and hence the rate of release of plant nutrients such as P and K, and (chelated) Fe^{3+} . Combined N could be provided by lightning from N_2 and O_2 as NO_x and hence HNO_3 , and by biological N_2 fixation (Raven 1998).

As well as releasing plant nutrients which could become available to terrestrial and (by run-off) freshwater and then marine photolithotrophs, weathering consumes CO_2 by reactions such as:



This speeds up the land surface part of the exogenic component of the 'geological' carbon cycle, and gives a lower steady-state CO_2 content in the atmosphere. This effect would have been small before significant higher plant embryophytic vegetation occurred on land. It became more significant in the Cambrian (about 510 Ma

(5.10×10^6 years before present)) and, especially, Ordovician (about 450 Ma) as embryophytic vegetation developed (Raven 1998; Raven & Edwards 2001). It became even more significant as vascular plant roots (or the analogues of modern roots) penetrated to one metre depth in plants with aerial shoots 2–3 m tall (Berner 1998). By the end of the Devonian (c. 360 Ma) there were trees (e.g. *Archaeopteris*; Meyer-Berthaud *et al.* 1999) up to 30 m tall with correspondingly extensive root systems and the potential for very significant CO_2 uptake in weathering. The increasing maximum mean size of embryophytes, and presumably increasing longevity, also meant that terrestrial organic carbon became an increasingly significant carbon compartment. However, the great majority of this organic carbon has a fairly rapid turnover *post mortem*. This contrasts with the millions of years needed for the atmospheric CO_2 that was sequestered as bicarbonate during silicate weathering and subsequently precipitated as carbonate in oceans to become part of the endogenic cycle. This ultimately re-releases CO_2 to the atmosphere in vulcanism. Thus, the main impact of the larger biomass and productivity of embryophytic (and especially vascular) vegetation on the carbon cycle was *via* weathering rather than organic biomass build-up. However, vascular plant biomass may have been less readily and rapidly degraded early in their evolution due to the presence of novel compounds such as lignin; it is not clear how long it took decomposer organisms to come to terms with the decomposition of lignin. Today the major lignin-degraders are basidiomycetes; the timing of the radiation of the higher fungi (ascomycetes and basidiomycetes) has been put on a firmer footing by the discovery of very well preserved remains of an ascomycete fungus in the Rhynie Chert by Taylor *et al.* (1999), placing their appearance on land with the first land tracheophytes. If all else failed, fire could have removed much terrestrial plant biomass, including lignin.

The timing of the atmospheric CO_2 drawdown attendant on the increased weathering rate engendered by embryophytic and, especially tracheophytic land vegetation, is not easy to assess independently of arguments based on the assumed extent of plant-induced weathering of rocks on land (Berner 1998; Raven 1998). Other proxies for atmospheric CO_2 include stomatal density (McElwain & Chaloner 1996) and the natural abundance stable carbon isotopes of soil carbonate. Both depend on plant activities, but not directly on weathering rate (Raven 1998). It appears reasonable to accept that there was a large decline in atmospheric CO_2 during the Devonian (c. 400–360 Ma) in parallel with an increase in biomass and mean height (and probably of rooting depth) in terrestrial plants (Raven & Edwards 2001).

This feedback of greater rooting depth increasing the amount of rock weathered and hence increasing the

removal of CO₂ from the atmosphere has a number of consequences for the evolution of terrestrial vascular plants. Further selective advantages of becoming taller are in limiting the extent to which the organism is shaded by surrounding vegetation and providing a launch platform into turbulent air for its propagules (meiospores). However, the physics of water movement up the plant dictates that the water potential at the top of a tall plant is, all other things being equal, less than that at the top of a shorter plant, unless the cross-sectional area of xylem provided per unit photosynthetic area is increased in taller plants in proportion to the height of the plant (Raven & Handley 1987). This exacerbates the problem of water supply to the photosynthetic transpiring tissue attendant on the decreased carbon gain per unit water lost in an optimally allocating C₃ plant growing in CO₂-limiting rather than in CO₂-saturating conditions, so that maintenance of growth under fluctuating water supply requires deep soil, with deep roots, to, respectively, store and extract water.

A further point is that taller plants tend to have more carbon per unit nitrogen, phosphorus, potassium, etc., than do shorter plants due to the larger fraction of supporting tissue containing only carbon, oxygen and hydrogen (Raven *et al.* 1992). The ultimate extreme of effective nutrient recycling within the plant would be that a given rate of gross primary productivity (mol C m⁻² ground area second⁻¹) could be achieved with little more nutrient (N, P and K, etc.) in the biomass per m² ground area for tall long-lived plants than for smaller plants. The small increment of nutrients for the larger plant would be needed for the small mass of living cells in the structural tissue involved in secondary growth, phloem transport, resource storage and defence. Whether this economy in mineral elements was evident in early plants depends on the extent to which there was an effective phloem transport system. This would be necessary to remove nutrients from differentiating structural tissues and from resource acquiring structures which are about to be lost (e.g. by abscission) and then transfer them to growing points. Such a transport system was presumably needed for photosynthate transport from photosynthetic to non-photosynthetic tissues. However, recognizable phloem was first found in the fossil record in the mid-Devonian in secondary tissue of progymnosperms, and was apparently never very strongly developed in earlier tree-like organisms such as the lepidodendrids (Taylor & Taylor 1993). If there were no nutrient retranslocation from maturing to developing structural tissue there would be more nutrient capital tied up in living plants. Furthermore, failure to retranslocate nutrients from roots and leaves to the plant axis prior to their death would involve external recycling of the nutrients to new growing tissue *via* decomposition

and uptake from the soil. Both eventualities mean more nutrient capital in the plant-soil system than would be the case with better internal recycling, with a consequent need for more mining of rock by weathering to yield the phosphorus, potassium and iron, etc., to support a given biomass of tall plants.

Both the water and the nutrient argument provide rationales for deeper rooting. In the case of water, there would be a need for more water per unit biomass produced as the atmospheric CO₂ level is drawn down by the weathering which is needed to provide the water supply from soil when precipitation is variable. Such negative feedback effects must have been very influential in the evolution of embryophytes in the Devonian.

Synopsis and conclusions (BRUCE A. OSBORNE)

Evolution and biodiversity

The colonization of land by embryotrophic plants during the Ordovician period initiated a significant shift in the partitioning of global net primary productivity (NPP) between marine and terrestrial systems. For the preceding 3000 million years, global productivity was predominantly associated with aquatic habitats with a limited terrestrial component. Today, land plants are the greatest contributors to global NPP (Table 3).

A land-based existence offered several advantages related largely to the physical features of the environment (Table 4). In comparison to aquatic environments, rates of CO₂ diffusion were greater. There was also increased availability of light and increased concentrations of essential nutrients. Multicellularity, apparently a prerequisite for survival out of water, formed the basis for differentiation of specialized tissues and cells involved in regulating plant water balance and reproduction (Niklas 1997). Multicellularity also allowed increased size, greater longevity, increased competitive ability and a more flexible investment into photosynthetic structures in response to the more variable demands of an aerial environment. Thus, the increased contribution of terrestrial plants to global NPP was associated with a change from unicellular to multicellular structures.

Today, one group of plants, the angiosperms, dominates terrestrial habitats. These comprise 86% (~240 000) of the total number (~270 000) of terrestrial plant species, and a greater proportion of biomass (Falkowski & Raven 1997). However, the dominance of angiosperms on land is relatively recent. For much of the time since the invasion of land gymnosperms, ferns and horsetails dominated the terrestrial landscape. In contrast, aquatic systems have fewer species (~17 000 in marine environments; ~25 000 in freshwaters environments) distributed amongst a larger number of divisions. Only the

Table 4 A comparative summary of the typical biological and physical characteristics of terrestrial (aerial), marine and freshwater environments. Biological data from a variety of sources, including Begon *et al.* (1990), Falkowski & Raven (1997) and Field *et al.* (1998). Physical data obtained from Denny (1993)

	Terrestrial	Open marine	Freshwater
Number of species	270 000	17 000	26 000
Typical organization	Multicellular	Unicellular	Unicellular
Typical size range	cm to m	µm to mm	µm to mm
Photosynthetic pathways	C ₃ , C ₄ , CAM, C ₃ -C ₄	C ₃	C ₃ , CAM
Limiting nutrients	N, P, CO ₂	N, Fe, P	P, N
Standing biomass (10 ¹⁵ g)	800	2	< 0.1
Standing biomass per unit area (kg m ⁻²)	< 0.2–200	< 0.001–6	< 0.1–0.1
Turnover time (years)	1–20	0.02–0.06	0.02–0.06
C : N mean (by atoms)	36	6.6	10
C : N range (by atoms)	5–100+	5–15	< 5–20
N : P mean (by atoms)	28	16	30
N : P range (by atoms)	5–65	5–50	5–65
Biota-mediated sequestered carbon	Humics CaCO ₃	DOC, TCO ₂ TCO ₂ , CaCO ₃	Humics, DOC,
Area (10 ⁸ km ⁻²)	1.5	3.6	—
Density at 20 °C (kg m ⁻³)	1.205	1024.76	998.23
Dynamic viscosity at 20 °C (10 ⁻⁵ N s m ⁻¹)	1.818	1010	1090
Oxygen diffusion coefficients at 20 °C (m ² s ⁻¹)	20.3 · 10 ⁻⁴	2.1 · 10 ⁻⁹	2.1 × 10 ⁻⁹
Carbon dioxide diffusion coefficients at 20 °C (m ² s ⁻¹)	16.0 · 10 ⁻⁴	1.77 · 10 ⁻⁹	1.77 × 10 ⁻⁹
Oxygen concentration at 20 °C (mol m ⁻³)	8.71	0.231	0.284
Carbon dioxide concentration at 20 °C (mol m ⁻³)	0.014	0.010	0.012
Typical bicarbonate concentration at 20 °C (mol m ⁻³)	—	1.5	1.3
Specific heat capacity at 20 °C (J kg ⁻¹ K ⁻¹)	1006	4182	4182
Thermal conductivity at 20 °C (W m ⁻¹ K ⁻¹)	0.0261	0.6011	0.6011
Refractive index at 20 °C and λ = 700 nm	1.003	1.335	1.330
Typical annual temperature range (°C)	0–40	–1.9–28	0–40
Speed of movement of medium (m s ⁻¹)	0–100	0–20	0–10

Heterokonta, mainly diatoms (~43%) and the Rhodophyta (~35%) in marine habitats and the Chlorophyta (~58%) in freshwaters, occur on anywhere near the same scale (Falkowski & Raven 1997). However, estimates of the NPP of diatoms (~20 Pg), one of the more important marine primary producers, are higher than tropical rainforests or savannahs (Table 3), two of the most productive terrestrial ecosystems.

Photosynthetic physiology and productivity

Global NPP is clearly based on the C₃ photosynthetic pathway. Whilst C₄ photosynthesis and CAM may confer an advantage in dry environments with a high evaporative demand, neither is a unique feature of plant communities in these habitats. Differences in NPP per unit area are generally thought to be in the order C₄ > C₃ > CAM, broadly consistent with potential differences in maximum photosynthetic rate, although there is considerable overlap. Due to a bias towards single leaf measurements of photosynthesis (Table 1), it may be difficult to extrapolate the results of many studies to

obtain an estimate of the NPP of whole plants or communities. Additional factors, such as alterations in biomass allocation, can have a significant influence on whole plant carbon gain. New techniques, based on measurement of CO₂ fluxes over stands of vegetation, should provide us with a better picture of NPP at landscape and even biome scales, although separation of soil CO₂ efflux due to autotrophs and heterotrophs remains a major obstacle.

For phytoplankton, photosynthetic physiology may exert less control on NPP than does nutrient assimilation or grazing resistance. Although phytoplankton possess a C₃ photosynthetic pathway, photorespiratory metabolism is typically suppressed by biophysical CO₂ concentrating mechanisms. In contrast to terrestrial plants where differences in the allocation of photosynthate confounds the extrapolation from single leaf measurements to whole plant NPP, a good correlation can often be obtained between photosynthetic rate and NPP with aquatic unicellular species.

Estimates of NPP (per unit area) for terrestrial and marine communities indicate a wide range of overlap-

ping values (Table 3). Perhaps the most obvious difference between terrestrial and aquatic productivity is the nature of the producers themselves. The standing biomass per unit area of terrestrial vegetation is some $2\text{--}200 \times 10^3$ fold higher than that in many aquatic systems (Table 4). Clearly, greater size, increased complexity and longevity has not occurred at the expense of reductions in NPP.

Limiting factors

Carbon dioxide is a major factor limiting NPP in terrestrial ecosystems. Arid ecosystems may be very sensitive to CO_2 enrichment, due to increased efficiency of water use (Smith *et al.* 2000), with important implications for global NPP as these ecosystems occupy approximately 20% of the land surface area. However, many species may be constrained in their response to elevated CO_2 , as a consequence of low CO_2 episodes in the past (Sage & Coleman 2001) and there is still uncertainty about the responsiveness of C_4 species. Whilst the impact of increased CO_2 on many aquatic plants is small in the short term, presumably because of the presence of CO_2 concentrating mechanisms, there is little information on the effect of long-term exposure to elevated CO_2 on community composition. In both terrestrial and aquatic systems, the long-term response to elevated CO_2 can be limited by the supply of other nutrients.

It is often asserted that terrestrial NPP is limited by the availability of N. In contrast, NPP of marine systems may be limited by either N (c. 50% of ocean surface area), Fe (c. 30% of surface area) or, in some cases by P, whilst freshwaters are limited primarily by P. Such generalizations should, however, be treated with caution. The similar atomic ratios of N : P for 'plant' tissues from a wide range of freshwater and terrestrial habitats (Elser *et al.* 2000; Table 4) suggests that both elements may often constrain freshwater as well as terrestrial NPP.

Free-living nitrogen-fixing species and symbiotic associations could have important roles in the acquisition and use of nutrients, such as N, P and Fe. Intuitively, a role for N-fixation seems obvious in N-limited environments, although the ecological distribution of symbiotic N-fixing associations in terrestrial environments is enigmatic. Nitrogen-fixing symbioses may comprise a minor component of some severely N-limited ecosystems. Plants occupying these environments are often characterized by low growth rates and make modest demands on potentially limiting resources (Grime 1979). In nutrient deficient open ocean waters, there is a wide range of free-living N-fixers including *Trichodesmium* spp., as well as of yet uncharacterized symbiotic associations. As in

terrestrial habitats, N-fixers comprise a small, slow-growing component of the phytoplankton.

In recent years, Fe has been identified as a potentially limiting factor in about one-third of the open ocean (Coale *et al.* 1996). Iron is highly insoluble in seawater and most is ultimately derived from land as wind blown particulate material, so that large areas of the ocean receive inadequate amounts of Fe. In oceanic regions where a major input of nitrogen may be via N-fixation, Fe availability could limit NPP indirectly (Falkowski 1997). Iron would rarely have the same significance in terrestrial environments. There is, however, an intriguing inverse link between terrestrial NPP and Fe-determined marine NPP, as the input of wind-blown material is likely to be greater from land with a low vegetation cover.

Grazing by herbivores and losses due to disease can be important factors influencing the structure and NPP of terrestrial and aquatic plant communities. The impact of grazing on NPP may also depend on the nutrient composition of the vegetation as the lower C:N and C:P ratio of terrestrial tissues (Elser *et al.* 2000) may deter grazers that have a high nutritional requirement. Research on the roles of viruses, bacteria and fungi is still in its infancy, particularly in oceanic planktonic communities.

Future predictions

A major research effort continues to be directed at the impact of increases in $[\text{CO}_2]$ on NPP. Predictions of the responses of plant communities to rising CO_2 based on experimental studies must be treated with caution because of complex interactions with temperature, as well as a number of other environmental variables. Predictions based on physiological models of individual plant responses to environmental factors are also uncertain because of uncertainties in scaling up to ecosystems. There are also difficulties in interpretations of the impact of climate change on plant community production based on strict adherence to so-called 'functional types' (Dyer *et al.* 2001).

A major challenge remains the accurate assessment of NPP for different ecosystems. We have reasonable broad-scale maps of the major terrestrial vegetation types, but these often have limited quantitative value and lack fine-scale detail. Whilst algorithms are available for predicting chlorophyll *a* concentration in open ocean waters, these are of limited use for the more productive coastal and lake ecosystems due to the presence of a range of optically active substances. As well as improvements in sensor technology, further developments in the remote sensing of global NPP will require algorithms that incorporate a greater understanding of the interactions among light, vegetation and photosynthesis.

References

- Banase K (1994) Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. *Oceanography*, **7**, 13–20.
- Battle M, Bender ML, Tans PP, White JWC, Ellis JT, Conway T, Francey RJ (2000) Global carbon sinks and their variability inferred from atmospheric O_2 and $\delta^{13}C$. *Science*, **287**, 2467–2470.
- Begon M, Harper JL, Townsend CR (1990) *Ecology. Individuals, Populations and Communities*, 2nd edn. Blackwell scientific Publications, Boston.
- Behrenfeld MJ, Kolber PG (1999) Widespread iron limitation of phytoplankton in the South Pacific Ocean. *Science*, **283**, 840–843.
- Berner RA (1998) The carbon cycle and CO_2 over the Phanerozoic time: the role of land plants. *Philosophical Transactions of the Royal Society*, **B 353**, 75–82.
- Bricaud A, Babin M, Morel A, Claustre H (1995) Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parameterization. *Journal of Geophysical Research*, **100**, 13321–13332.
- Broecker WS, Henderson GM (1998) The sequence of events surrounding Termination II and their implications for the cause of glacial-interglacial CO_2 changes. *Paleoceanography*, **13**, 352–364.
- Burkhardt S, Zondervan I, Riebesell U (1999) Effect of CO_2 concentration on C: N: P ratio in marine phytoplankton: a species comparison. *Limnology and Oceanography*, **44**, 683–690.
- Cao M, Woodward FI (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, **393**, 249–252.
- Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. *Nature*, **397**, 491–497.
- Chapin FS III, Shaver GR (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, **66**, 564–576.
- Coale KH, Johnson KS, Fitzwater SE, Gordon RM, Taner S, Chavez FP, Ferioli L, Sakamoto C, Rogers P, Millero F, Steinberg P, Nightengale P, Cooper D, Cochlan WP, Landry MR, Constantinou J, Rollwagen G, Trasvina A, Kudela R (1996) A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the Equatorial Pacific Ocean. *Nature*, **383**, 495–501.
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley J, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Dynamic responses of global terrestrial ecosystems to changes in CO_2 and climate. *Global Change Biology*, **7**, 357–373.
- Cui M, Vogelmann TC, Smith WK (1991) Chlorophyll and light gradients in sun and shade leaves of *Spinacia oleracea*. *Plant, Cell and Environment*, **14**, 493–500.
- Curtis PS, Wang X (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. *Oecologia*, **113**, 299–313.
- DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendrey GR, Schlesinger WH (1999) Net primary production of a forest ecosystem under experimental CO_2 enrichment. *Science*, **284**, 1177–1179.
- Denny MW (1993) *Air and Water: The Biology and Physics of Life's Media*. Princeton University Press, Princeton.
- Dewar RC (1996) The correlation between plant growth and intercepted radiation: an interpretation in terms of optimal plant nitrogen content. *Annals of Botany*, **78**, 125–136.
- Dewar RC, Medlyn BE, McMurtrie RE (1999) Acclimation of the respiration/photosynthesis ratio to temperature: insights from a model. *Global Change Biology*, **5**, 615–622.
- Drake BG, AzconBieto J, Berry J, Bunce J, Dijkstra P, Farrar J, Gifford RM, GonzalezMeler MA, Koch G, Lambers H, Siedow J, Wulfschleger S (1999) Does elevated atmospheric CO_2 concentration inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment*, **22**, 649–657.
- Drake BG, GonzalezMeler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2 ? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.
- Dugdale R, Wilkerson F (1998) Silicate regulation of new production in the equatorial Pacific upwelling. *Nature*, **391**, 270–273.
- Dunnett NP, Willis AJ, Hunt R, Grime JP (1998) A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology*, **86**, 610–623.
- Duysens LNM (1956) The flattening of the absorption spectrum of suspensions, as compared to that of solutions. *Biochimica et Biophysica Acta*, **19**, 1–12.
- Dyer AR, Goldberg DE, Turkington R, Sayre C (2001) Effects of growing conditions and source habitat on plant traits and functional group definition. *Functional Ecology*, **15**, 85–95.
- Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham S, McCauley E, Schulz KL, Siemann EH, Sterner RW (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature*, **408**, 978–980.
- Enquist B, West GB, Charnov EL, Brown JH (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, **401**, 907–911.
- Escoubas JM, Lomas M, La Roche J, Falkowski PG (1995) Light intensity regulation of *cab* gene transcription is signalled by the redox state of the plastoquinone pool. *Proceeding of the National Academy of Sciences USA*, **92**, 10237–10241.
- Evans JR, von Caemmerer S (1996) Carbon dioxide diffusion inside leaves. *Plant Physiology*, **110**, 339–346.
- Falkowski PG (1997) Evolution of the nitrogen cycle and its influence on the biological sequestration of CO_2 in the ocean. *Nature*, **387**, 272–275.
- Falkowski P, Barber R, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. *Science*, **281**, 200–206.
- Falkowski P, Kolber Z (1993) Estimation of phytoplankton photosynthesis by active fluorescence. *ICES Marine Science Symposium*, **197**, 92–103.
- Falkowski PG, Raven JA (1997) *Aquatic Photosynthesis*. Blackwell Science Ltd, Oxford.
- Falkowski P, Scholes RJ, Boyle E, Canadell J, Cranfield D, Elser J, Gruber N, Hibbard K, Höglberg P, Linder S, Mackenzie FT, Moore B, Pedersen T, Rosenthal Y, Seitzinger S, Smetacek V, Steffen W (2000) The global carbon cycle: a test of our knowledge of earth as a system. *Science*, **290**, 291–296.
- Fan S, Gloor M, Mählmann J, Pacala S, Sarmiento J, Takahashi T, Tans P (1998) A large terrestrial carbon sink in North America

- implied by atmospheric and oceanic carbon dioxide data and models. *Science*, **282**, 442–446.
- Farrar JF (1996) Sinks-integral part of a whole plant. *Journal of Experimental Botany*, **47**, 1273–1279.
- Feldman G, Kuring N, Ng C, Esaia W, McClain CR, Elrod J, Maynard N, Endres D, Evans R, Brown J, Walsh S, Carle M, Podesta G (1989) Ocean colour. Availability of the global data set. *EOS Transactions of the American Geophysical Union*, **70**, 634–635.
- Field CB (1988) On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. *Australian Journal of Plant Physiology*, **15**, 343–358.
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski PG (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**, 237–240.
- Finzi AC, Allen AS, Schlesinger WH, DeLucia EH, Ellsworth DS (2001) Forest litter production, chemistry and decomposition following two years of free-air CO₂ enrichment. *Ecology*, **82**, 470–484.
- Fraser LH, Grime JP (1999) Interacting effects of herbivory and fertility on a synthesised plant community. *Journal of Ecology*, **87**, 514–525.
- Fretwell SD (1977) The regulation of plant communities by food chains exploiting them. *Perspectives in Botany and Medicine*, **20**, 169–118.
- Fuhrman JA (1999) Marine viruses and their biogeochemical and ecological effects. *Nature*, **399**, 541–548.
- Geider RJ, MacIntyre HL, Kana TM (1998) A dynamic regulatory model of phytoplanktonic acclimation to light, nutrients, and temperature. *Limnology and Oceanography*, **43**, 679–694.
- Gifford RM (1995) Whole plant respiration and photosynthesis of wheat under increased CO₂ concentration and temperature: Long-term vs short-term distinctions for modelling. *Global Change Biology*, **1**, 385–396.
- Gorton HL, Williams W, Vogelmann TC (1999) Chloroplast movement in *Alocasia macrorrhiza* (L.) G. Don. *Physiologia Plantarum*, **106**, 421–428.
- Grime JP (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 2631.
- Grime JP (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chichester, UK.
- Grime JP (1998) Benefits of plant diversity to ecosystems; immediate, filter and founder effect. *Journal of Ecology*, **86**, 902–910.
- Grime JP, Cornelissen JHC, Thompson K, Hodgson JG (1996) Evidence of a causal connection between anti-herbivore defense and the decomposition rates of leaves. *Oikos*, **77**, 489–494.
- Grime JP, Thompson K, Hunt R *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.
- Hamm CE, Simson DA, Merkel R, Smetacek V (1999) Colonies of *Phaeocystis globosa* are protected by a thin but tough skin. *Marine Ecology Progress Series*, **187**, 101–111.
- Haxeltine A, Prentice IC (1996) A general model for the light-use efficiency of primary production. *Functional Ecology*, **10**, 551–561.
- Heimann M (1997) A review of the contemporary global carbon cycle and as seen a century ago by Arrhenius and Högberg. *Ambio*, **26**, 17–24.
- Hoepffner N, Sathyendranath S (1991) Effect of pigment composition on absorption properties of phytoplankton. *Marine Ecology Progress Series*, **73**, 11–23.
- Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K, eds (1996) *Climate Change 1995. Technical Summary*, pp. 9–49. Cambridge University Press, Cambridge, UK.
- Hungate BA, Holland EA, Jackson RB, Chapin FS, Mooney HA, Field CB (1997) The fate of carbon in grasslands under carbon dioxide enrichment. *Nature*, **388**, 576–579.
- Huston MA (1997) Hidden treatments in the ecological experiments; evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–460.
- Hutchins DA, Bruland KW (1999) Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. *Nature*, **393**, 561–564.
- Hutchins DA, Witter A, Butler A, Luther GW III (1999) Competition among marine phytoplankton for different chelated iron species. *Nature*, **400**, 858–861.
- Hymus GJ, Ellsworth DS, Baker NR, Long SP (1999) Does free-air carbon dioxide enrichment (FACE) affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology*, **120**, 1183–1191.
- Idso SB (1998) The long-term response of trees to atmospheric CO₂ enrichment. *Global Change Biology*, **5**, 493–495.
- IGBP Terrestrial Carbon Working Group (1998) The terrestrial carbon cycle: implications for the Kyoto Protocol. *Science*, **280**, 1393–1394.
- Jenkins WJ (1988) Nitrate flux into the euphotic zone near Bermuda. *Nature*, **331**, 521–523.
- Jenkins WJ, Goldman JC (1985) Seasonal oxygen cycling and primary production in the Sargasso Sea. *Journal of Marine Research*, **43**, 465–491.
- Jürgens K, Güde H (1994) The potential importance of grazing-resistant bacteria in planktonic ecosystems. *Marine Ecology Progress Series*, **112**, 169–188.
- Kana TM, Geider RJ, Critchley C (1997) Regulation of photosynthetic pigments in micro-algae by multiple environmental factors: a dynamic balance hypothesis. *New Phytologist*, **137**, 629–638.
- Kana TM, Gilbert PG (1987) Effect of irradiances up to 2000 $\mu\text{E m}^{-2} \text{s}^{-1}$ on marine *Synechococcus* WH7803. II. Photosynthetic responses and mechanisms. *Deep-Sea Research*, **34**, 497–516.
- Keeling RF, Shertz SR (1992) Seasonal and interannual variations in atmospheric oxygen and implications for the global carbon cycle. *Nature*, **358**, 723–727.
- Keeling CD, Whorf TP (2000) In: *A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, TN, USA.
- Kelting DL, Burger JA, Edwards GS (1998) Estimating root respiration, microbial respiration in the rhizosphere, and root-free soil respiration in forest soils. *Soil Biology and Biochemistry*, **30**, 961–968.
- Kicklighter DW, Bruno M, Dönges S, Esser G, Heimann M, Helfrich J, Ift F, Joos F, Kadku J, Kohlmaier GH, McGuire AD, Melillo JM, Meyer R, Moore B, Nadler A, Prentice IC, Sauf W, Schloss AL, Sitch S, Wittenberg U, Würth G (1999) A first order analysis of the potential of CO₂ fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus*, **51B**, 343–366.

- Kirk JTO (1994) *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK.
- Koblents-Mishke OJ, Volkovinsky VV, Kabanova YG (1970) Plankton primary production of the World Ocean. In: *Scientific Exploration of the South Pacific* (ed. Wooster W), pp. 183–193. National Academy of Sciences, Washington DC.
- Kühn S (1995) Infection of marine diatoms by parasitoid protists. PhD Thesis. University of Bremen, Bremen.
- Kywalyanga M, Platt T, Sathyendranath S (1992) Ocean primary production calculated by spectral and broad-band models. *Marine Ecology Progress Series*, **85**, 171–185.
- La Roche J, Nuzzi R, Waters R, Wyman K, Falkowski PG, Wallace DWR (1997) Brown Tide blooms in Long Island's coastal waters linked to interannual variability in ground-water flow. *Global Change Biology*, **3**, 397–410.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations—Has its importance been underestimated? *Plant, Cell and Environment*, **14**, 729–739.
- Long SP (1999) Understanding the impacts of rising CO₂: the contribution of environmental physiology. In: *Physiological Plant Ecology* (eds Press MC, Scholes JD, Barker MG) Symposia of the British Ecological Society, pp. 263–282. Blackwell Science Ltd, Oxford.
- Long SP, Garcia Moya E, Imbamba SK, Kamnalrut A, Piedade MTF, Scurlock JMO, Shen YK, Hall DO (1989) Primary productivity of natural grass ecosystems of the tropics: a reappraisal. *Plant and Soil*, **115**, 155–166.
- Long SP, Hutchinson PR (1991) Primary production in grasslands and coniferous forests with climate change—an overview. *Ecological Applications*, **1**, 139–156.
- Longhurst A, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research*, **17**, 1245–1271.
- Luk TS, Vogelmann TC (1998) Ultrafast transit time measurement of leaves. *Journal of Photochemistry and Photobiology*, **44**, 53–62.
- MacGillivray CW, Grime JP, Band SR, Booth RE, Campbell B, Hendry GAF, Hillier SH, Hodgson JG, Hunt R, Jalili A, Mackey JML, Mowforth MA, Neal AM, Reader R, Rorison IH, Spencer RE, Thompson K, Thorpe PC (1995) Testing predictions of resistance and resilience of vegetation subjected to extreme events. *Functional Ecology*, **9**, 640–649.
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment*, **22**, 715–740.
- Marra J, Heinemann KR (1984) A comparison between non-contaminating and conventional incubation procedures in primary production measurements. *Limnology Oceanography*, **29**, 389–392.
- Martin JH (1990) Glacial-interglacial CO₂ change: the iron hypothesis. *Paleoceanography*, **5**, 1–13.
- Martin MJ, Farage PK, Humphries SW, Long SP (2000) Can the stomatal changes caused by acute ozone exposure be predicted by changes occurring in the mesophyll? A simplification for models of vegetation response to the global increase in tropospheric elevated ozone episodes. *Australian Journal of Plant Physiology*, **27**, 211–219.
- McCarthy M, Pratum T, Hedges J, Benner R (1997) Chemical composition of dissolved organic nitrogen in the ocean. *Nature*, **390**, 150–154.
- McElwain JG, Chaloner WG (1996) The fossil cuticle as a skeletal record of environmental change. *Palaaios*, **11**, 376–388.
- McKee IF, Farage PK, Long SP (1995) The interactive effects of elevated CO₂ and O₃ concentration on photosynthesis in spring wheat. *Photosynthesis Research*, **45**, 111–119.
- Medlyn BE, Dewar RC (1999) Comment on the article by RH Waring, JJ Landsberg and M Williams relating net primary production to gross primary production. *Tree Physiology*, **19**, 137–138.
- Melillo J, Callaghan TV, Woodward FI, Salati E, Sinha SK (1990) Effects on ecosystems. In: *Climate Change: The IPCC Scientific Assessment* (eds Houghton JT, Jenkins GJ, Ephraums JJ), pp. 283–310. Cambridge University Press, Cambridge, UK.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B, IIVörösmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.
- Meyer-Berthaud B, Scheckler SE, Wendt J (1999) *Archaeopteris* is the earliest known modern tree. *Nature*, **398**, 700–701.
- Moncrieff JB, Massheder JM, deBruin H, Elbers J, Friborg T, Heusinkveld B, Kabat P, Scott S, Soegaard H, Verhoef A (1997) A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, **189**, 589–611.
- Moore LR, Rocap G, Chisholm SW (1998) Physiology and molecular phylogeny of coexisting *Prochlorococcus* ecotypes. *Nature*, **393**, 464–467.
- Myers DA, Thomas RB, DeLucia EH (1999) Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell and Environment*, **22**, 473–481.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Nadelhoffer KJ, Emmett BA, Gundersen P, Kjønaas O, Koopmans CJ, Schleppil P, Tietema A, Wright RF (1999) Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, **398**, 145–148.
- Naem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–737.
- Nepstad DC, Verissimo A, Alencar A, Nobre C, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, Cochrane M, Brooks V (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.
- Niklas KJ (1997) *The Evolutionary Biology of Plants*. University of Chicago Press, Chicago.
- Paerl HW, Prufertbebout LE, Guo CZ (1994) Iron-stimulated N₂ fixation and growth of the planktonic marine cyanobacterium *Trichodesmium* spp. *Applied and Environmental Microbiology*, **60**, 1044–1047.
- Pfannkuche O, Lochte K (1993) Open ocean pelago-benthic coupling: cyanobacteria as tracers of sedimenting salp faeces. *Deep-Sea Research*, **1** (40), 727–737.
- Platt T, Sathyendranath S, Longhurst A (1995) Remote sensing of primary production in the ocean: promise and fulfilment. *Philosophical Transactions of the Royal Society of London*, **B 348**, 121–264.

- Prentice IC, Heimann M, Sitch S (2000) The carbon balance of the terrestrial biosphere: ecosystem models and atmospheric observations. *Ecological Applications*, **10**, 1553–1573.
- Ramenskii LG (1938) *Introduction to the Geobotanical Study of Complex Vegetations*. Selkzgiz, Moscow.
- Raupach MR, Denmead OT, Dunin FX (1992) Challenges in linking atmospheric CO₂ concentration to fluxes at local and regional scales. *Australian Journal of Botany*, **40**, 697–716.
- Raven JA (1998) Extrapolating feedback processes from the present to the past. *Philosophical Transactions of the Royal Society of London*, **B 353**, 19–28.
- Raven JA, Edwards D (2001) Roots: evolutionary origins and biogeochemical significance. *Journal of Experimental Botany*, **52**, 381–401.
- Raven JA, Handley LL (1987) Transport processes and water relations. In: *Frontiers of Comparative Plant Ecology* (eds Rorison IH, Grime JP, Hunt R, Hendry GAF, Lewis DH), pp. 217–233. Academic Press, New York and London.
- Raven JA, Wollenweber B, Handley LL (1992) Ammonia and ammonium fluxes between photolithotrophs and the environment in relation to the global nitrogen cycle. *New Phytologist*, **121**, 5–18.
- Redfield AC (1958) The biological control of chemical factors in the environment. *American Scientist*, **46**, 205–221.
- Richter DD, Markewitz D, Trombore SE, Wells CG (1999) Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature*, **400**, 56–59.
- Rogers A, Fischer BU, Bryant J, Frehner M, Blum H, Raines CA, Long SP (1998) Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology*, **118**, 683–689.
- Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. *Bioscience*, **47**, 235–242.
- Sage RF, Coleman JR (2001) Effects of low atmospheric CO₂ on plants: more than a thing of the past. *Trends in Plant Science*, **6**, 18–24.
- Sarmiento JL, Hughes TMC, Stouffer RJ, Manabe S (1998) Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature*, **393**, 245–249.
- Sarmiento JL, Siegenthaler U (1992) New production and the global carbon cycle. In: *Primary Productivity and Biogeochemical Cycles in the Sea* (ed. Falkowski PG), pp. 316–317. Plenum Press, New York and London.
- Sathyendranath S, Lazzara L, Prieur L (1987) Variations in the spectral values of specific absorption of phytoplankton. *Limnology and Oceanography*, **32**, 403–415.
- Schimel DS (1995) Terrestrial ecosystems and the global carbon cycle. *Global Change Biology*, **1**, 77–91.
- Schlesinger WH (1997) *Biogeochemistry: An Analysis of Global Change*, 2nd edn. Academic Press, NY.
- Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature*, **411**, 466–469.
- Sellers PJ, Berry JA, Collatz GJ, Field CB, Hall FG (1992) Canopy reflectance, photosynthesis, and transpiration 3. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of the Environment*, **42**, 187–216.
- Smetacek V (1995) Diatoms and the ocean carbon cycle. *Protist*, **150**, 25–32.
- Smith SB, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seeman J, Nowak RS (2000) Elevated CO₂ increases productivity and invasive success in an arid ecosystem. *Nature*, **408**, 79–82.
- Stitt M, Krapp A (1999) The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant, Cell and Environment*, **22**, 583–621.
- Takahashi K, Mineuchi K, Nakamura T, Koizumi M, Kano H (1994) A system for imaging transverse distribution of scattered light and chlorophyll fluorescence in intact rice leaves. *Plant, Cell and Environment*, **17**, 105–110.
- Tans PP, Fung IY, Takahashi T (1990) Observational constraints on the global atmospheric CO₂ budget. *Science*, **247**, 1431–1438.
- Taylor AH, Geider RJ, Gilbert FJH (1997) Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll *a* ratios: results of a modelling study. *Marine Ecology Progress Series*, **152**, 51–66.
- Taylor TN, Taylor IE, (1993) *The Biology and Evaluation of Fossil Plants*. Prentice Hall, New York.
- Taylor TN, Hass T, Kerp H (1999) The oldest fossil ascomycetes. *Nature*, **399**, 648–648.
- Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363–365.
- Tyrrell T (1999) The relative importance of nitrogen and phosphorus on oceanic primary production. *Nature*, **400**, 525–531.
- Vogelmann TC (1993) Plant tissue optics. *Annual Review of Plant Physiology and Plant Molecular Biology*, **44**, 231–251.
- Vogelmann TC, Bornman JF, Yates DJ (1996) Focusing of light by leaf epidermal cells. *Physiologia Plantarum*, **98**, 43–56.
- Vogelmann TC, Martin G (1993) The functional significance of palisade tissue: Penetration of directional versus diffuse light. *Plant, Cell and Environment*, **16**, 65–72.
- Vogelmann TC, Nishio JN, Smith WK (1996) Leaves and light capture: light propagation and gradients of carbon fixation within leaves. *Trends in Plant Science*, **1**, 65–70.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.
- Watson AJ, Robinson C, Robertson JE, le Williams PJB, Fasham MJ (1991) Spatial variability in surface carbon dioxide in the North Atlantic. *Nature*, **350**, 50–53.
- Weis E, Berry J (1987) Quantum efficiency of photosystem II in relation to 'energy'—dependent quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta*, **894**, 198–208.
- Whittaker RH, Likens GE (1975) The biosphere and man. In: *Primary Productivity of the Biosphere* (eds Whittaker RH, Likens GE), pp. 305–328. Springer, Berlin.
- Williams PJ le B (1993) Chemical and tracer methods of measuring plankton production: what do they in fact measure? The ¹⁴C technique considered. *ICES Marine Science Symposium*, **197**, 20–36.
- Williams PJ le B, Purdie DA (1991) *In vitro* and *in situ* derived rates of gross production, net community production and respiration of oxygen in the oligotrophic subtropical gyre of the North Pacific Ocean. *Deep-Sea Research*, **38**, 891–910.
- Zhang YP, Burris RH, Ludden PW, Roberts GP (1997) Regulation of nitrogen fixation in *Azospirillum brasilense*. *FEMS Microbiology Letters*, **152**, 195–204.