

OPINION

Changing the way we think about global change research: scaling up in experimental ecosystem science

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Abstract

Scaling is a naturally iterative and bi-directional component of problem solving in ecology and in climate science. Ecosystems and climate systems are unquestionably the sum of all their parts, to the smallest imaginable scale, in genomic processes or in the laws of fluid dynamics. However, in the process of scaling-up, for practical purposes the whole usually has to be construed as a good deal less than this. This essay demonstrates how controlled large-scale experiments can be used to deduce key mechanisms and thereby reduce much of the detail needed for the process of scaling-up. Collection of the relevant experimental evidence depends on controlling the environment and complexity of experiments, and on applications of technologies that report on, and integrate, small-scale processes. As the role of biological feedbacks in the behavior of climate systems is better appreciated, so the need grows for experimentally based understanding of ecosystem processes.

We argue that we cannot continue as we are doing, simply observing the progress of the greenhouse gas-driven experiment in global change, and modeling its future outcomes. We have to change the way we think about climate system and ecosystem science, and in the process move to experimental modes at larger scales than previously thought achievable.

Keywords: biosphere 2 laboratory, chlorophyll fluorescence, coral reefs, experimental ecosystem science, global change, stable isotopes

Received 10 November 2003; revised version received and accepted 19 December 2003

There is only one argument for doing something; the rest are arguments for doing nothing (Cornford, 1908).

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Experimental ecosystem science in the context of global climate change

The climate of Earth today is the product of what geochemists have described as 'the first environmental crisis on Earth' (Lovelock, 1990) in which, over billions of years, photosynthetic organisms used solar energy to convert a CO₂-rich atmosphere into an O₂-rich atmosphere (Raven, 1998; Beerling & Royer, 2002). The thin

green veneer of the biosphere, at sea and on the land, remains one of the principal engines of sustainable human habitation on Earth. Numerous, imperfectly understood feedback processes between ecosystems and climatic systems, between the biosphere and the geosphere, have modulated the evolution of the Earth's atmosphere in the past and still do so today (Schimel *et al.*, 2001). The Vostock ice-core reveals that over the last 400 000 years or so the planet has shown a robust response to changing atmospheric CO₂ concentrations with four excursions in the range of 180–280 ppm. The feedbacks in the Earth system (ES) have produced an environment stable enough for the emergence of *Homo sapiens*, the dominant mammal.

Over the last few hundred years human activities have precipitated another environmental crisis on Earth, commonly described as global climate change. Since discovery of fossil carbon as a convenient form of energy, the residues of some hundred million years worth of past photosynthetic carbon assimilation have been combusted to CO₂ and returned to the Earth's atmosphere 10–100 times faster than at any time in the Vostock record. The atmosphere has become a third more enriched in CO₂ and 100% more enriched in methane: 'We have left the domain that defined the Earth system for the 420 000 years before the Industrial Revolution' (Falkowski *et al.*, 2000). There is abundant evidence that the Earth's climate system can undergo rapid change within a few decades (Taylor, 1999), and the potential vulnerability of a human population approaching 10–11 billion to such an event has been noted (Broecker, 1997).

The possible socioeconomic consequences of global climate gone amuck are daunting, and it needs to be recognized that in the course of this uncontrolled experiment in global atmospheric change, humankind is now exposing itself to selective pressure from the physical environment never before experienced in its short evolutionary history (short compared with the successive planetary experiments portrayed in the Vostock cores). Emission of CO₂ from combustion of fossil fuels is driving the planetary atmosphere back towards that of the Cretaceous about a million times faster than the biosphere of the ES was able to achieve its preindustrial composition. Amplified by other greenhouse gases such as water and methane, global climate change is already having dramatic effects on ecosystems (Walther *et al.*, 2002; Root *et al.*, 2003). Anything short of a major adjustment in energy technologies and policies is likely to have little impact on the progress of the greenhouse gas-driven global change (Hoffert *et al.*, 2002).

We cannot continue as we are doing, simply observing the progress of the global experiment and modeling its future outcomes. We have already seen how 'our lack of detailed understanding of the changing balance of CO₂ on land, in the atmosphere and in the sea, undercuts

predictions about the effects of climate change and could impede the clear implementation of the Kyoto proposals for reduction of emissions' (May, 1999). Some of the challenges in changing the way we think about ES science arise because there has been a polarization of the Newtonian (physical) and Darwinian (biological) approaches in the discipline: 'Physicists seek simplicity in universal laws. Ecologists revel in complex interdependencies' (Harte, 2002). Put another way, scientists from different traditions may view the chemical and physical limits of biological processes differently; while the physicist looks for simple generalizations, the ecologist may view these as evolutionary challenges that may have been met in different ways in different organisms and, therefore, abhor generalizations. Just as Snow (1959) provoked more strident discourse between the 'two cultures' of natural and social sciences, experimental ecosystem science may be stimulated by Harte's assessment of the 'dysfunctional consequences of this biomodal legacy', and his assertion that 'a sustainable future for our planet will probably require a look at life from both sides'. As the first ingredient for synthesis, he identified the need for 'a Fermi approach', with simpler models that capture the essence of the problem, leading to experiments and measurements that render them falsifiable. In this essay, we discuss ways in which the Newtonian–Darwinian divide can be bridged with experiments using large-scale, synthetic model ecosystems in controlled environments.

Although it is now recognized that the quantitative importance of terrestrial carbon cycles match those of ocean–atmosphere interactions in global climate models, the stark reality is that our understanding of biological feedbacks in both terrestrial and marine ecosystems is sketchy at best. For example, exaggerated positive feedback associated with stomatal closure ('stomatal suicide' Randall *et al.*, 1992) may have caused simulations of El-Nino-induced drought in the Amazon (Tian *et al.*, 1998; Cox *et al.*, 2000) to predict a switch from sink to a source by 2050, accelerating the increase in atmospheric CO₂ concentration and global warming. Clearly, we have to move quickly, conceiving and conducting experiments at large enough scales and with sufficient complexity to effectively define ecosystem-level feedbacks. Such experiments need to proceed in concert with observation and modeling, and as the sense of urgency with respect to climate change issues grows (US Climate Change Science Program (CCSP), 2002), an experimental approach is needed to fast-track resolution of key issues and to guide more secure policy decisions.

The challenge of scaling-up

May (1999) also observed that 'many of the most intellectually challenging and practically important

problems of contemporary ecological science are on much longer time-scales and much larger spatial scales' than are currently being investigated. He noted earlier surveys showing only 25% of manipulative field studies exceeded 10 m in size, and 40% lasted less than a year, only 7% exceeded 5 years. Experimental ecosystem science has to expand the size and duration of controlled experiments with complex natural systems, such as coral reefs and forests, to test hypotheses leading to mechanistic understanding of large-scale processes in the biosphere.

This challenge has been confronted before by plant ecophysiologicalists who recognize that 'Scaling is not simply integration or aggregation of values at one level to achieve estimates at a more encompassing level of consideration. Rather, scaling represents the transcending concepts that link processes at different levels of space and time'. The art of scaling 'involves not being distracted by those factors that are less important in transitions among scales' (Caldwell *et al.*, 1993). Simple scaling frameworks abound for the states and processes in photosynthesis research and in the biosphere over some 15–20 powers of 10 in size of functional systems (in microns) and relaxation times of associated processes (in seconds) from molecular biology to global ecology (Kamen, 1964; Osmond, 1989). To some extent, these scaling considerations are already reflected in the range of complementary devices and approaches available for experimental climate change and ecosystem science in the terrestrial biosphere, as summarized in Table 1.

Over the past few decades, plant ecophysiology has changed the way we think about photosynthesis through, for example, understanding of the light reactions of xanthophyll cycle photoprotection (Osmond *et al.*, 1999) and the biology of the dark reactions of C₄ carbon assimilation (Sage & Monson 1999). Molecular biophysical and biochemical insights have transformed our understanding of light reactions of photosynthesis at the leaf and organism level in the natural environment (Falkowski, 1992; Björkman & Demmig Adams 1994; Gamon *et al.*, 1997) and potentially can be scaled up for remote sensing of these processes at the canopy and ecosystem level. Analogously, the stable isotopic signatures of ¹³C and ¹⁸O used to integrate the dark reactions of CO₂ exchange in photosynthesis and respiration, and to link them with H₂O exchange at the leaf level, can be scaled to ES processes (Berry 1992; Osmond *et al.*, 1994; Yakir & Sternberg 2000) (Fig. 1). We firmly believe that these transcending concepts will help identify the mechanistic bases of feedbacks in the biosphere that link ecosystem functions to global climate change (Schulze *et al.*, 1994; Lloyd *et al.*, 1995; Lin *et al.*, 1998). Our

experience gives confidence that experimental ecosystem science can meet the challenges of scaling through multidisciplinary experiments with complex, large systems under controlled conditions.

Yet the direct experimental approach to scaling seems more of a problem in biology and ecology than in physics and astronomy. This may be because the huge investments in large-scale controlled experimental facilities necessary to uncover the laws of particle physics and for observing systems to explore the limits of the Universe have not been available in biology or ecology. Terrestrial ecologists have not had access to the apparatus needed for experimental manipulations of ecosystems, or access to the levels of support needed to run large-scale experiments over long periods of time. The Earth Observing Systems of NASA notwithstanding, we have yet to see significant investment on Earth in the facilities needed to scale up observations from organisms to ecosystems, and to undertake large-scale experiments with complex model systems in controlled environments. Direct study of processes at the scale and time step required for the models is a primary requisite. Given the magnitude of the problems to be addressed, it is only a matter of time before such facilities become available, and we need to be developing now the infrastructure, the mind set, and the problem spaces, for future programs.

The requirements for such facilities include, but are not limited to:

- *Open flow control*: conditions of CO₂, isotopic composition, temperature, precipitation and humidity need to be controlled so all inputs and outflows can be measured and mass balance achieved;
- *Intermittent closure*: rates of change in parameters need to be measured with precision during draw down following brief periods of closure;
- *Replication*: experimental conditions need to be replicated time after time, so response functions can be established with precision;
- *Replacement*: biological components (soil, vegetation, microbial communities, etc.) need to be changed to suit the objectives of different research teams over tens of years;
- *Modeling*: intensive instrumentation is needed to set and monitor boundary conditions to facilitate model parameterization and verification;
- *Access*: the structure of the enclosure must provide ready access to forest canopies and soil zones for observation, manipulation and measurement;
- *Coordination*: extrapolation from experiments with synthetic model systems to natural ecosystems requires coordination with field experiments and

Table 1 Approximate scaling in space (m²) and relaxation time of observations (10³ s) in systems for experimental climate change and ecosystem science with representative citations, showing major control and measurement features of the systems (open systems shown in italics)

Facility and relaxation times ($\times 10^3$ s)	Area (m ²)			
	1–10	10–100	100–1000	1000–10 000
Growth chambers (1–10) (Körner & Arnone, 1992)	Sophisticated control and flux measurement, problematic light and soil regimes			
Ecocells (10–100) (Tingey <i>et al.</i> , 1996)	Precise atmospheric control, limited flux measurement, some control of temperature, nutrition and precipitation, reduced sunlight and disturbed natural soils			
Open top chambers (10–1000) (Norby <i>et al.</i> , 1999)	Precise atmospheric control, limited flux measurement, natural light and soil, some control of temperature, nutrition and precipitation			
FACE rings (100–10 000) (Oren <i>et al.</i> , 2001)	Limited range of atmospheric CO ₂ and trace gas control, limited flux measurement, natural light and soil, some control of temperature, nutrition and precipitation			
Biosphere 2 Laboratory (10–1000) (Lin <i>et al.</i> , 1998)	Sophisticated control and flux measurement, limited light and problematic soil regimes			
Flux towers (100–10 000) (Andreae <i>et al.</i> , 2002)				Natural atmosphere, light and soil, limited control of precipitation and nutrition, limited flux capabilities

FACE, free atmosphere carbon dioxide enrichment.

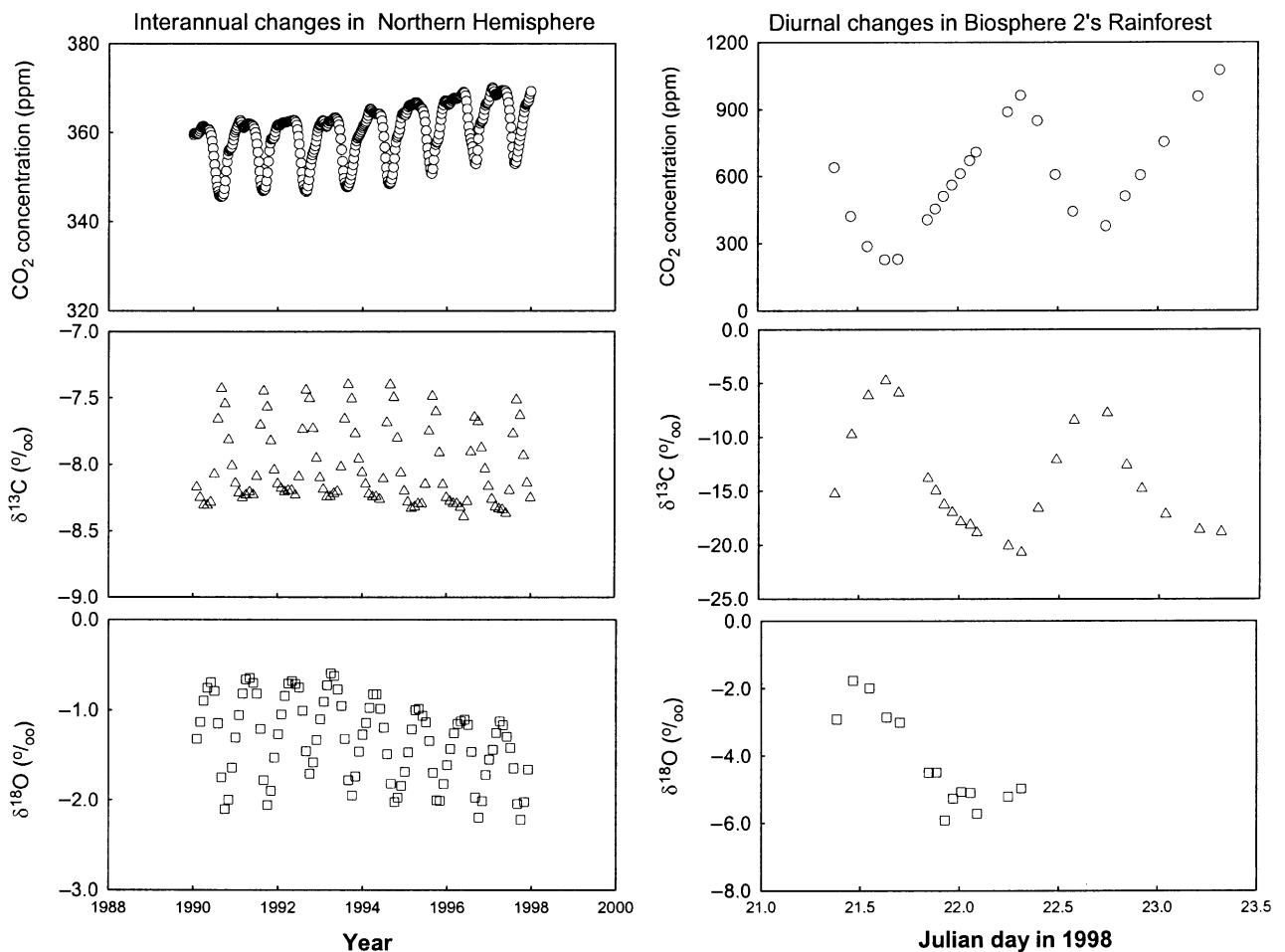


Fig. 1 Comparison of net ecosystem CO₂ and isotope exchanges in the closed systems of Earth (left, interannual variations for a decade), and the Biosphere 2 Laboratory-tropical forest mesocosm (right, daily variations); data provided by G. Lin.

collaboration with free atmosphere carbon dioxide enrichment and flux tower studies.

There have been several attempts to expand the scale of controlled environment facilities in these directions to meet the needs of experimental ecosystem research (e.g. Körner & Arnone, 1992; Tingey *et al.*, 1996) but only a few, such as the ecocells at the Desert Research Institute, Reno, NV, USA, and the mesocosms of the Biosphere 2 Laboratory (B2L), Oracle, AZ, USA approach the scale of complexity and control required (Table 1). Biosphere 2 was originally designed as a large-scale, long-term, holistic observational ESs project in a single closed system (Allen, 1991) and was not designed to support a multidisciplinary experimental program. Unexpected outcomes – in expensive, large-scale endeavors – often provide the impetus for driving a discipline forward. With uncommon prescience, Thomas Kuhn (1960) might have had Biosphere 2 in mind when he wrote: 'On occasions a piece of equipment designed and constructed for the purpose

of normal research fails to perform in the anticipated manner, revealing an anomaly that cannot, despite repeated effort, be aligned with professional expectation. In these and other ways besides, normal science repeatedly goes astray. And when it does – when, that is, the profession can no longer evade anomalies that subvert the existing tradition of scientific practice – then begin the extraordinary investigations that lead the profession at last to a new set of commitments, a new basis for the practice of science. The extraordinary episodes in which that shift of professional commitments occur...are the tradition-shattering complements to the tradition-bound activity of normal science'.

The facility became available to the experimental research community because soil respiration, still a much-debated aspect of ecosystem metabolism (Melillo *et al.*, 2002; Murthy *et al.*, 2003), unexpectedly escaped from the controls that were expected to keep the atmosphere balanced in the closed system. Rich soil C and N reserves supported high rates of soil metabolism and O₂ uptake. Photosynthetic O₂ evolution lost the

competition for CO₂ to an unexpectedly strong sink in the unsealed concrete (Severinghaus *et al.*, 1994). The engineering of the tightly closed apparatus was so effective that the imbalance of metabolism led to an alarming O₂ deficit and the project was doomed, so far as sustainable human occupation was concerned (Walford, 2002). Modifications that enable each of the mesocosms in B2L to be separately controlled have eliminated this problem, and the re-engineering of B2L is a good example of the transition of proven research systems to operational status that may help fill both operational and research requirements in a more cost-effective way (US CCSP, 2002; Grand challenges p. 136). The facility now comes close to fulfilling the need to perform large-scale (over an acre) whole-ecosystem experiments that vary both CO₂ and climate (National Assessment Synthesis Team (NAST), 2001). As the only device available that approaches the scale envisaged by NAST, the B2L has had an important role in helping to define the new discipline of experimental ecosystem science. With an estimated annual running cost as a fully serviced, international multiuser experimental facility of some \$6 million, B2L is less expensive than many research vessels and telescope facilities, and in the small-change category when compared with many national centers and laboratories engaged in climate change and ecosystem science.

Reducing complexity for scaling purposes through controlled experiments

An ecosystem is unquestionably the sum of all its parts, to the smallest imaginable scale, but for practical purposes the whole needs to be construed as a good deal less than this. In the process of scaling-up, it seems prudent to reduce complexity on the basis of experimental evidence, not by preconceptions of graininess and arbitrarily assigned black-box relationships. Contemporary definitions of reductionism send mixed messages but it has long seemed clear that scaling-up depends on reduction of detail to simple 'laws' so that the whole becomes rather less than the sum of its parts. By either definition, reductionism has an essential role in experimental ecosystem science. Scaling down, the quest for more detailed understanding of processes and mechanisms is the only informed basis for scaling-up.

As became abundantly clear during the original missions of Biosphere 2, we do not yet know enough of complex process interactions at the ecosystem scale to set initial conditions for sustainability of complex systems. Progress in mechanistic understanding of ecosystems requires control and manipulation of complex systems at large enough scale to identify rate-limiting processes, and to discover and apply integrative

technologies that can be applied to read the 'barometers' of climate change impacts in natural systems. Experience in most disciplines of natural science suggests it is sensible to examine parameters a few at a time; to examine producer functions in an ecosystem in the absence of consumers for example, and to add trophic complexity step by step. Most approaches to experimental ecosystem science in the field begin with model complex systems and simply accept that 'apparently there are no general laws for complexity. Instead, one must reach for 'lessons' that might, with insight and understanding, be learned in one system and applied in another' (Goldenfield & Kadanoff, 1999).

While some ecologists believe that the mechanistic basis of responses to climate change have been adequately established (Walther *et al.*, 2002), they also concede that complexity of ecological interactions make it difficult to extrapolate from individuals to communities, and to predict from short-term responses to the long-term, especially in the face of stochastic climatic variables. In many cases, extrapolations depend on a few laboratory or field studies from the halcyon days of plant ecophysiology. For example, the uncoupling of the stomatal feedback loop at high leaf temperatures indicated by experiments of Drake *et al.* (1970) might improve parameterization of the drought-precipitated rainforest models of Tian *et al.* (1998) and Cox *et al.* (2000), and who knows the impact of buffering effects on stomata of the within canopy environment?

Researchers differ in the weight given to control and complexity, and in the extent of acceptable compromise. Environmental control requires containment. Although glass-enclosed structures exclude solar UV, sunlight under glass is a whole lot more desirable than artificial illumination (Tingey *et al.*, 1996). Even so, such shortcomings can be turned to advantage, as for example in the measurement of emissions of UV-photolabile trace gasses (Rosenstiel *et al.*, 2003). Few controlled environment systems allow realistic simulation of the soil environment, and artifacts of root binding have often complicated the scaling up of observations based on pot experiments. It may never be possible to satisfy all pedologists, but in the course of a decade, the artificial soil in intensive forestry mesocosm (IFM) of B2L has developed a profile and biological composition characteristic of intensively managed forest soils. This soil represents a huge advance on the potting mix used for most small-scale controlled environment studies that remain the foundation for scaling-up feedbacks in the terrestrial biosphere. For example, the size, containment, and subsoil sampling capabilities in B2L have permitted experiments that significantly qualify the scaling of soil respiration from pot to field (Murthy *et al.*, 2003).

Replication in time (in series) is routine for experimental research in the laboratory and is well appreciated in site-specific measurement systems such as flux towers. Although serial replication runs the risk of memory effects, especially in long-term experiments, these effects can and have been tested in successive years in controlled facilities such as B2L. Replication in space (in parallel), a necessity in most field-based experimental ecosystem research, can be arranged to some extent in open-top chambers (Norby *et al.*, 1999), free atmosphere carbon dioxide enrichment (FACE) treatments and flux towers. Although Buchmann (2002) observed that only 14% of all eddy covariance flux studies in forests published in the decade before 2002 ($n = 196$) include plant ecophysiological measurements or biomass and growth estimates, the benefits of multiple, comparative studies is increasingly obvious (Matamala *et al.*, 2003). However, in these experiments it is often difficult to systematically combine and control treatments such as temperature, precipitation (amounts and timing), and other atmospheric components (e.g. N deposition and O₃) with elevated CO₂ (Isebrands *et al.*, 2001, Oren *et al.*, 2001). The mini-FACE experimental design (Shaw *et al.*, 2002), which sacrifices plot area but incorporates multifactorial climate change parameters (e.g. warming, N-deposition, precipitation) with elevated CO₂ is especially suited to grasslands and small model systems. There is an obvious need, but presently impracticable, for access to suites of B2L-like facilities for simultaneous replication of large-scale experiments, but in the interim, replication in time under reproducibly controlled conditions using the facilities available is a whole lot better than nothing at all. It is much more powerful to test models in the same time domain as the models operate. It is much more difficult to use integration of complex processes through time to validate a differential equation.

Bridging the Newtonian–Darwinian divide through experimental ecosystem science

Successful bridges between observations, models and ecosystems can be built through experimental ecosystem science. For example, a clear consequence of increasing atmospheric CO₂ concentration is a change in the chemistry of the surface ocean, with a lowering of pH, carbonate ion activity and carbonate saturation state. Field observations by physical oceanographers had shown that there is a correlation between the calcification rate of a reef and the saturation state ($[\text{Ca}^{2+}][\text{CO}_3^{2-}]/K_{\text{sp}}$) of the overlying water (Broecker & Takahashi, 1966; Ohde & van Woesik, 1999). These studies established that the longer water resides over any particular reef the more the carbonate ion activity,

and hence carbonate saturation state, is reduced and the lower the calcification rate of the reef. However, coral reef ecologists did not accept this as evidence of a cause and effect relationship because it went against theories of coral calcification, namely, that corals achieved their high rates of calcification by pumping Ca²⁺ and CO₃²⁻ ions from the environment into a highly supersaturated internal space and hence were not sensitive to changes in their external chemical environment. From the Darwinian point of view, organisms could evolve mechanisms to overcome this thermodynamic limitation on their growth and many examples can be put forward to support this hypothesis.

Experimental ecosystem science in this problem space has produced what may be the first evidence for a direct deleterious effect of elevated CO₂ concentration on a key ecosystem process, and may have resolved a key question with respect sedimentation of inorganic carbon at sea. Manipulation of Ca²⁺ and CO₃²⁻ concentrations independently under controlled conditions in the laboratory showed that coral growth was indeed sensitive to changes in the carbonate saturation state of the water (Leclercq *et al.*, 2000). Field-scale experiments in the ocean mesocosms at B2L showed convincingly that at all light intensities examined, coral calcification was depressed by 40–50% – in seawater with a carbonate chemistry equivalent to that in equilibrium with the atmospheric CO₂ concentration expected mid-21st Century (Langdon *et al.*, 2000; Marubini *et al.*, 2001). Moreover, there is a good correspondence between controlled environment experiments and field observations (Fig. 2). Subsequent system-level studies show that although elevated CO₂ accelerates biological carbon assimilation in the model coastal ecosystem, respiratory turnover is also stimulated, and there is no change in organic C-sequestration (Langdon *et al.*, 2003). The dominant effect on the carbon sink in this marine ecosystem was a 7 times reduction of inorganic C-sedimentation.

Although only a small part of the ocean carbon sequestration cycle, coral reef ecosystems bear the brunt of the consequences of global climate change at sea, and will be exposed to a double whammy of bleaching following warm water incursions during El Niño events, and impaired skeletal growth as a consequence of changing seawater carbonate chemistry in equilibrium with rising atmospheric CO₂ concentrations. The well-being of millions of coastal dwelling peoples in the Pacific and Caribbean is at risk within the next generation. Scientists have identified some additional problem spaces for experimental evaluation, including:

- Effects of rising sea surface temperature on symbiosis and bleaching of coral: what is the relationship

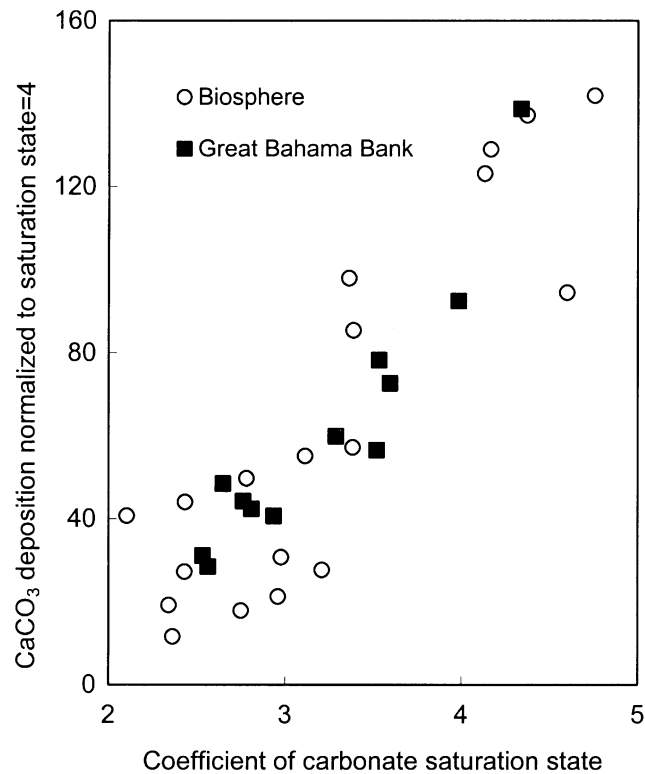


Fig. 2 Normalized rates of carbonate production in the Biosphere 2 Laboratory coral reef mesocosm and in a macroalgal-dominated natural ecosystem, as a function of saturation state (from Broecker *et al.* (2001). Factors controlling the rate of CaCO₃ precipitation on Grand Bahama Bank. *Global Biogeochemical Cycles*, 15, 58–596. Copyright [2001] American Geophysical Union. Reproduced/modified by permission of American Geophysical Union).

of impaired calcification to other interacting stresses such as the incursions of warm water and grazing?

- How do the marine C and N cycles respond to elevated CO₂?
- What determines the ratio of net ecosystem photosynthesis and respiration in coral and other benthic communities in the light and dark?
- What are the effects of increasing water motion from storms on community structure and function through breakage, biogeochemical mass transfer between water and organisms, and input and output of materials?
- What are the effects of rainstorm properties (droplet size and frequency) on transfer of gases into seawater, and how do raindrop impact and wave action interact during mixing at the ocean surface?
- How do these factors interact with wind-generated aerosols and how does biological activity in the ocean influence the chemistry and physics of aerosol formation?

Things are not always worse at sea; estimates of the terrestrial carbon 'sink' differ by almost an order of

magnitude. 'The range of uptake rates projected by process-based models for any one scenario is, however, considerable, due to uncertainties about (especially) terrestrial ecosystem responses to high CO₂ concentrations, which have not been resolved experimentally, and uncertainties about response of global NPP to changes in climate' (Houghton *et al.*, 2001). Some model simulations (Chambers *et al.*, 2001), atmospheric CO₂ analyses (Battelle *et al.*, 2000) and flux tower measurements (Malhi & Grace, 2000) indicate that a significant fraction of the terrestrial sink (approximately 1 Gt yr⁻¹, 1 Gt = 10¹⁵ g) may be located in tropical rainforests, and there is concern that this sink may switch to a source of CO₂ in response to drought events in El Niño years. However, we should not continue to labor under the illusion that terrestrial forest sinks are likely to significantly mitigate anthropogenic CO₂ emissions (Field *et al.*, 1998; Falkowski *et al.*, 2000). If some ceiling for future atmospheric CO₂ concentration can be set through international agreements, at best, the terrestrial carbon sink can offset a corresponding increment in fossil fuel consumption. Understanding of feedbacks between ecosystem carbon fluxes and model parameters is required to constrain ES models. In the absence of this understanding, formulation of

policy on emissions is likely to be hazardous. Experimental ecosystem science puts such knowledge within reach now, and a concerted campaign is needed.

Most ES models are derived from weather-forecasting models. Among other things, these forward models are anchored in huge data sets of simple physical measurements from over a century of observations of climate systems, and in scaling up the principles of fluid dynamics in models of atmospheric and/or ocean circulation for the whole planet. These models integrate a set of processes represented by differential equations through time. The problem is that the equations are not well known, the starting conditions are not defined, and the models 'drift' with time. Ecology cannot yet deliver anything like the observational data sets, or the ecosystem analogs of the laws of fluid dynamics, needed to refine contemporary ES models, and moreover, ecosystems both respond to and interact with the physical climate simulated by these ES models. Predictions of the magni-

tudes of pool sizes, fluxes and residence times of carbon and key nutrient elements as rate-limiting mechanisms in global carbon budgets have been addressed with models derived from extensive observations on natural systems (Cao & Woodward, 1998) but have yet to be linked with controlled experiments at appropriate spatial scales. It is essential that ecosystem processes be properly represented in these models, and although the predictive capacity of ES models has been advanced by improved representation of ecosystem processes (Sellers *et al.*, 1996; Berry *et al.*, 1997), most ES models have a limited experimental basis, and often rely on a few laboratory-scale studies to parameterize processes over vast areas such as the Amazon rainforest.

As with the coral calcification studies described above, large-scale experiments with a complex (approximately 100 species), contained and controlled synthetic model tropical forest mesocosm (TFM) in B2L, are yielding mechanistic insights to ecosystem-level

Table 2 Effects of drought on net ecosystem respiration and the $\delta^{13}\text{C}$ signature of respired CO_2 in the tropical forest mesocosm of B2L during the experiment shown in Fig. 3

Date	Treatment	Ecosystem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$\delta^{13}\text{C}$ (‰) of respired CO_2
June 1, 2002	Wet	-6.13	-25.2
June 15, 2002	Dry	-4.85	-24.4
June 29, 2002	Re-wet	-5.82	-28.2

B2L, Biosphere 2 Laboratory.

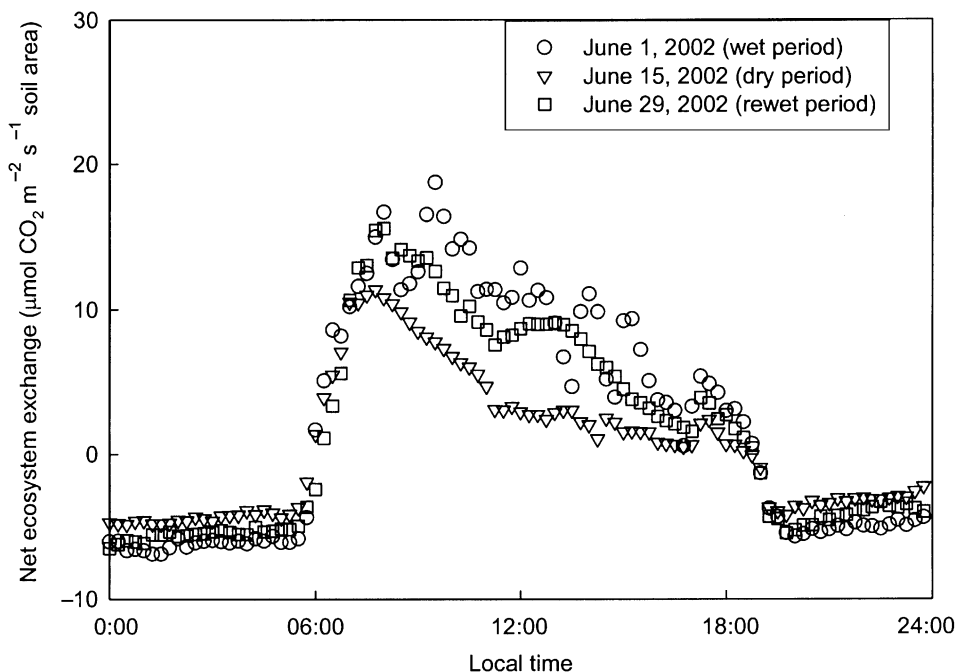


Fig. 3 Changes in net ecosystem influx and efflux of CO_2 in the Biosphere 2 Laboratory tropical forest mesocosm in response to drought. The CO_2 evolved in the dark period showed $\delta^{13}\text{C}$ signatures (Table 2) indicative of different carbon sources for respiration (data of G. Lin *et al.*, unpublished results).

processes. Good correspondence between modeled and measured ecosystem productivity has been established (Lloyd *et al.*, 1995; Lin *et al.*, 1998), and daily carbon fluxes measured in the TFM (Fig. 3) closely correspond to those now reported from flux tower observations in the Amazon (Andreae *et al.*, 2002). Four replicated experiments conducted over 3 years show that although drought decreases ecosystem carbon influx, model projections that suggest tropical forests switch from a sink to a source of CO₂ have not been confirmed in the TFM. This experimental finding also seems to be confirmed by flux tower observations in the Amazon. As emphasized above, predictions of catastrophic ecosystem responses to sustained climate change (Cox *et al.*, 2000) need to be much more better informed by large-scale assessments of stomatal feedbacks, both in response to high temperature and to buffering by the within-canopy environment. Controlled environment experimental facilities such as B2L can be used to assess these feedbacks at appropriate scales, and improve confidence in model predictions.

Models also suggest that atmospheric CO₂ concentrations on Earth are approaching those at which the terrestrial CO₂ influx is rate limited by photosynthetic processes. The sink capacity of temperate forests has been investigated in field experiments using FACE techniques under mid-21st Century treatments. Nutrient limitations (Oren *et al.*, 2001), acclimation of assimilatory processes and soil responses to warming (Melillo *et al.*, 2002) all accelerate the time at which the sink capacity of forests will be saturated. Controlled environment experiments in the tropical forest ecosystem show that, depending on the model chosen and assumptions as to the relationships between rising CO₂ concentration and global warming, the sink capacity of the TFM in B2L may saturate mid-21st Century (Lin *et al.*, 2001).

The large ratio of leaf biomass to chamber volume of the TFM provides high signal-to-noise ratios and excellent sensitivity for diurnal profiles of net ecosystem CO₂ flux at present and future atmospheric CO₂ concentrations (Lin *et al.*, 2001). In addition to net flux measurements, the isotopic composition of CO₂ efflux from this system shows large changes before, during and after the drought treatments (Table 2) that are sufficient to partition the CO₂ sources among soil, root, litter and aboveground fractions. These signatures will give better insights into the effects of temperature and drought on ecosystem CO₂ efflux. In the course of a day, stable isotope signatures associated with diffusion, evaporation, carboxylation and other processes occurring during the assimilation of CO₂ and the respiration of assimilates in plants and soils can be evaluated in the atmosphere of the 37 000 m³ chamber with 10 greater sensitivity and 100 × more rapidly

than the interannual variation of these signatures in planetary atmosphere (Fig. 1). When extended to include the isotopes of N, these methods hold great promise for mechanistic evaluation of carbon and nutrient fluxes in ecosystems (Griffiths *et al.*, 1999).

Much progress has been made in understanding regulatory interactions in complex systems through application of control theory (Kacser, 1987) and it is believed that 'similar principles for control exist at vastly different levels of organization. The principles of control are analogous at the ecosystem, population, organism, and even at the enzyme reaction level' (Schulze *et al.*, 1994). Containment and control mean that the formal requirements for flux analysis can be met in the mesocosms of B2L. In principle, there is every reason to suppose that this approach will serve well to untangle flux analyses in synthetic, model ecosystems. The 'new stable points' at which an ecosystem functions after changes in environmental conditions presumably depend on the 'pathway' to this new stability, and the 'pathway' presumably depends on the kinetics of the pools as the conditions change, as well as on the frequency and intensity of the change. More complex adaptive behavior can be expected in ecosystems than in a linear metabolic pathway, and control analysis will need to embrace nonlinear properties of the system (such as kinetic properties of impacts). Such experiments might reveal phases of the system that are more important than others, and these can be assessed by sensitivity analysis of kinetic properties of the system, thereby revealing functional biodiversity. Some of the experimental questions that can be explored in this way include:

- How does the CO₂ fertilization response scale from plants to ecosystems? Does the CO₂ concentration at which CO₂ fertilization saturates vary between ecosystems and if so, for what reasons?
- How do respiratory mechanisms and responses differ among ecosystem components at different scales and with environmental variables?
- How do ecosystem carbon fluxes respond to the frequency and magnitude of stress events (abiotic: temperature, water, nutrients; biotic: herbivory, pathogens)?
- Can we determine how episodic events shape the structure and function of ecosystems by measuring responses to the changing frequency and magnitude of events at differing CO₂ concentrations, temperatures and precipitation regimes?
- How does cyclic environmental behavior (wet-dry cycles, multiyear droughts, etc.) impact ecosystems in climatic change contexts?

- Do time delays arising from perturbations affect ecosystem responses to changing climates?
- How does covariance of key parameters, such as the projected more rapid increase in night vs. day temperatures, affect carbon cycling in the soil–plant–atmosphere continuum?

Improving the mechanistic understanding of ecosystem processes in ESs science

Large-scale experiments in expensive facilities are of more value if they are supported by measurement technologies that eventually can be applied more generally in the field. It has been clear for more than two decades that scaling up of plant biosphere responses to global climate change will be facilitated by integrative technologies that report on the dark and light reactions of photosynthesis. Scaling up the dark reactions through the use of stable isotopes was highlighted above. Leaf-level photosynthetic activities, formerly measured by CO₂ exchange, are now routinely inferred from chlorophyll fluorescence (Schreiber *et al.*, 1994) and reflectance techniques (Field *et al.*, 1995) in the laboratory and in the field. Unlike other current methods (such as Normalized Difference Vegetation Index (NDVI)) that use surrogate, optically sensed parameters to empirically estimate biomass, we can now expect more progress through focusing on biophysical signals that report on the process of photosynthesis itself. These techniques can be scaled up to support experiments that will bridge the Newtonian–Darwinian divide through remote sensing and calibrated against net carbon fluxes in B2L.

Field *et al.* (1995) pointed out that ‘Extending small-scale techniques to large spatial scales involves a number of challenges that can only be addressed with theoretical and empirical studies at a range of scale. ... The advances of the past have come from studies at a range of spatial scales and especially from studies in which the analysis of remote sensing data is combined with analysis of data from other sources. This paradigm provides a blueprint for future progress’. Thus, we can construct instruments in which signals from primary processes with small relaxation times (10⁻⁴s) can be used to monitor much slower processes (diurnal patterns of photosynthesis; 10⁴s), and can be used remotely to give process-level insights into leaf and canopy processes with relaxation times of weeks to years (10⁶–10⁸s). Such methods will facilitate a functional understanding of biodiversity between the canopy and the atmosphere; Ozanne *et al.* (2003) emphasize that the forest canopy is the functional interface between 90% of the Earth’s terrestrial biomass

and the atmosphere. The well-proven fast repetition rate fluorescence (FRRF) laser-induced fluorescence transient (LIFT) method used to evaluate photosynthetic efficiency of phytoplankton in water columns (Kolber *et al.*, 1998) has been adapted for remote sensing in canopies. With appropriately placed light sensors, these data can be used to estimate photosynthetic electron transport in the canopy. The ‘functional biodiversity’ in this canopy at this time is evident in the different patterns of photosynthetic electron transport, measured at 12–15 m, in leaves of two adjacent canopy dominant trees to net ecosystem CO₂ exchange in the TFM (Fig. 4).

Although chlorophyll fluorescence imaging techniques now reveal unexpected details of physiological limitations (Rascher *et al.*, 2001) and stress phenomena (abiotic and biotic) in leaves and tissues, they remain difficult to apply in canopies. However, the well-established correlation (Gamon *et al.*, 1997) between leaf reflectance, xanthophyll pigment composition and the wastage of absorbed light as heat (and hence the efficiency of light use) scales well in canopies. Helicopter-borne measures of the photosynthetic reflectance index (PRI) correlates well with pigment composition and flux tower estimates of photosynthetic efficiency (Nichol *et al.*, 2002). Experiments in B2L show that it may be possible to achieve even better scaling with PRI imaging systems (U. Rascher and C.J. Nichol, unpublished results). A pixel is a pixel, and the algorithms developed at one scale in space or time can be applied to answer relevant questions up or down scale. We do not underestimate the complexities of dealing with the diverse and diffuse light environment of the canopy (Méthy, 2000). Nevertheless, we expect that:

- measurement and modeling of canopy light environments with distributed sensors of direct and diffuse radiation, will permit integration with remotely sensed images of canopy architecture and chlorophyll fluorescence;
- miniaturized chlorophyll fluorescence/light sensors can be networked for *in situ* spot assessment of photosynthesis in different vegetation types and integrated with remotely sensed reflectance and chlorophyll fluorescence;
- remotely sensed photosynthetic data can be calibrated using radiative transfer, leaf chemistry and physiological process models, with independently measured fluxes of CO₂ and isotopes;
- an open ecological observatory (OEO), analogous to an astronomy observatory, with on-line access to instruments and data streams can provide unrestricted access for a qualified community of specialists is needed to fast track these approaches. It could also

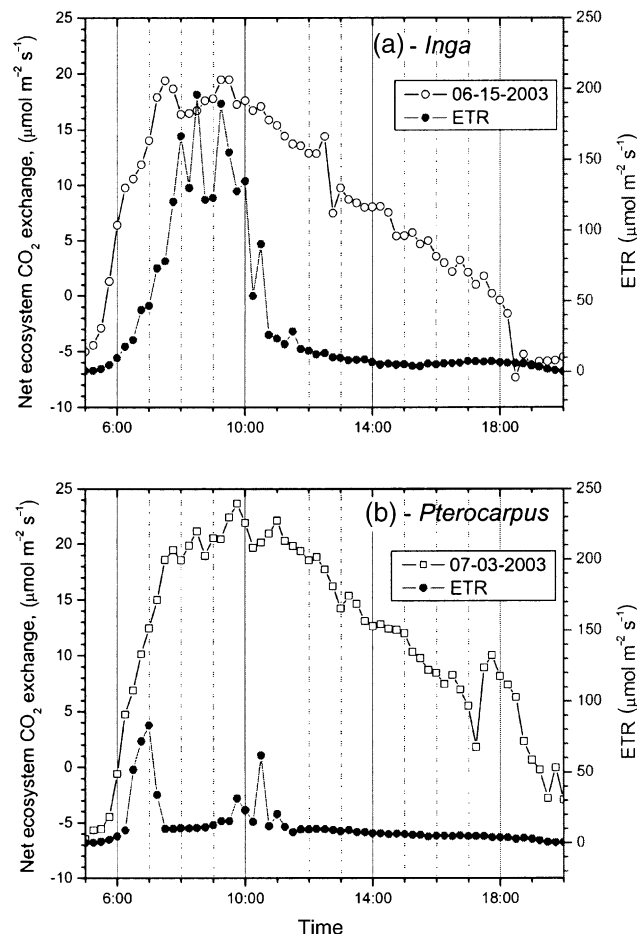


Fig. 4 Remote sensing of canopy photosynthetic electron transport rate (ETR) measured at 12 m with laser-induced fluorescence transient techniques. Calculated according to Genty *et al.* (1989) from photosystem II efficiency and incident light, ETRs (closed symbols) in the sun exposed canopy of *Inga sapindoides* (a) and *Pterocarpus indicus indicus* (b) are superimposed on measurements of net ecosystem CO₂ exchange (open symbols) in the Biosphere 2 Laboratory-tropical forest mesocosm (data of G. Ananyev *et al.*, unpublished results).

provide real-time observation for education programs explaining the role, vision, instrumentation, and ecological significance of the above measurements.

If it is imagined that CO₂ emissions policies may soon include carbon credits that will be traded in a futures market, verification technologies will have to be rather more precise than those currently available (Tans & Wallace 1999). Compliance may initially have to rest on remotely sensed NDVI, a surrogate for green leaf area that correlates well with the pool of woody biomass in Northern Forests (Myneni *et al.*, 2001). However, year-to-year changes in the biomass estimated from this index are some two orders of magnitude smaller than estimates obtained from flux towers, and more sensitive process-based sensing methods are needed. In particular, methods that detect stochastic stress events and anticipate the subsequent decline in the strength of a carbon sink, may come to assume an important role in assessing compliance and

projecting futures trading. The development and calibration of these devices at the mesocosm scale under controlled conditions is an important contribution from experimental ecosystem science to bridging the Newtonian-Darwinian divide.

Quo Vadis?

Given contemporary political realities, for the foreseeable future, greenhouse gas-driven global climate change seems inexorable for several human generations at least. So we need to begin now to deal with the full spectrum of ecosystem responses to changing climates. It may well be possible to devise sequestration technologies that scrub the atmosphere of CO₂ on a huge scale (Lackner, 2003). In future, it may be possible to engineer sequestration crops that store assimilated carbon in slowly released pools. It may be possible to engineer food crops that retain yield in the face of more stochastic and stressful environments. It may be

possible to devise migration corridors for preservation of threatened ecosystems. Also, it may be that global change is irreversible. We are headed for a future in which it will not be enough to have convincingly demonstrated that climate has changed, but one in which we must mobilize all the creativity and ingenuity of natural sciences and engineering, of the social sciences and economics. As distinguished climate modelers have made abundantly clear: 'The economic stakes are very high. To attain maximum credibility we will need all the experimental approaches mentioned. The observational task is demanding. It is not too soon to start the development of such methods now' (Tans & Wallace, 1999). Indeed it may soon be too late.

We can ill afford to indulge ourselves in business as usual, or to parade chauvinisms on either side of the Newtonian–Darwinian divide. We must seize the opportunity to bridge the divide with experiments and, in the tradition of natural sciences, learn as much from our errors as from our achievements as we guide the scaling of past knowledge from the leaf to the landscape, from the molecule to the biosphere. Although B2L has already proven to be a useful apparatus for experimental ecosystem science, it is but a small part of the arsenal that has to be developed. Perhaps eminently practical engineers, respecting the achievements of the engineered environments in B2L, and familiar with the breakthroughs made possible with simulators such as wave tanks and wind tunnels, are better placed to use the facility and build the bridge between the insular towers of ecological complexity and simplified simulation.

Gifted to the research community, but evidently beyond the capacity of a single institution to sustain, future attempts to realize the potential of B2L will demand consortium development, with peer endorsement at all levels of the complex infrastructure of private and public support of science. As with other projects ahead of their time, peer endorsement has been slow to mobilize, the promised private institutional support has been terminated prematurely, and the enterprise has foundered. Whether the opportunity can be restored will depend to a significant extent on persuading agencies responsible for facilities such as telescopes, research vessels and the apparatus for particle physics research, that ES science cannot eschew the experimental approach. In the next 50 years, we can expect interests to move beyond the questions listed above to problems of sustaining ecosystem 'goods and services'; to biogeochemical insights that are scarcely discernable today. The need for large-scale closed systems with controlled environments is already recognized in Japan, in Europe and elsewhere as more optimal iterations of B2L are being explored.

In summary, we face huge uncertainties. Our present understanding of climate change impacts on ecosystem processes is limited and incomplete, especially as to feedbacks, and is largely based on observation and modeling. It is poorly supported by mechanistic insights from experiments at scales approximating those of ecosystems. By analogy with the response to another global threat, the HIV-AIDS pandemic, we can ask where would we be in controlling the epidemic today if we had left the response to epidemiologists alone? Just as the full arsenal of experimental biomedical research has been mobilized to address the pandemic, so we need now to mobilize the whole arsenal of experimental capabilities in natural sciences and engineering in support of climate change science, from the molecule to the biosphere.

We have to build Harte's bridge and cross the Newtonian–Darwinian divide, and this bridge needs to be constructed on a sound experimental basis. Only by this means can we expect to reduce uncertainty, understand sustainability, improve predictability, evaluate mitigation technologies, gain credibility with policy makers, and strengthen political will. If we as experimentalists, observers and modelers fail now to engage in this way, global change may well be inexorable, and become irreversible over the next two to five human generations.

Acknowledgements

We thank Dr Paul Falkowski for his interest and inputs to this manuscript. This article and the data reported could not have been assembled without the sustained private support of Mr Edward P. Bass, the owner of B2L, and of Columbia University, as realized through the vision of Dr Michael Crow, 1996–2003. This paper is dedicated to them.

References

- Allen J (1991) *Biosphere 2. The Human Experiment*. Viking Penguin, New York.
- Andreae MO, Artaxo P, Brandão C *et al.* (2002) Biogeochemical cycling of carbon, water, energy trace gases, and aerosols in Amazonia: the LBA-EUSTACH experiments. *Journal of Geophysical Research*, **107**, 8066.
- Battle M, Bender ML, Tans PP *et al.* (2000) Global carbon sinks and their variability inferred from atmospheric O₂ and δ¹³C. *Science*, **287**, 2467–2470.
- Beerling DJ, Royer DL (2002) Fossil plants as indicators of the Phanerozoic global carbon cycle. *Annual Reviews of Earth and Planetary Sciences*, **30**, 527–556.
- Berry JA (1992) Biosphere, atmosphere, ocean interactions: a plant physiologist's view. In: *Primary Productivity and Biogeochemical Cycles in the Sea* (eds Falkowski PG, Woodhead AD), pp. 441–454. Plenum Press, New York.

- Berry JA, Sellers PJ, Randall DA (1997) SiB2, a model for simulation of biological processes within a climate model. In: *Scaling-up, from Cell to Landscape. SEB Seminar Series 63* (eds van Gardingen P, Foody G, Curran P), pp. 347–369. Cambridge University Press, Cambridge.
- Björkman O, Demmig-Adams B (1994) Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. In: *Ecophysiology of Photosynthesis* (eds Schulze E-D, Caldwell MM), pp. 17–47. Springer-Verlag, Berlin.
- Broecker WS (1997) Thermohaline circulation, the Achilles heel of our climate system. Will man-made CO₂ upset the current balance? *Science*, **278**, 1582–1588.
- Broecker W, Langdon C, Takahashi T *et al.* (2001) Factors controlling the rate of CaCO₃ precipitation on Grand Bahama Bank. *Global Biogeochemical Cycles*, **15**, 589–596.
- Broecker WS, Takahashi T (1966) Calcium carbonate precipitation on the Bahama Banks. *Journal of Geophysical Research*, **71**, 1575–1602.
- Buchmann N (2002) Plant ecophysiology and forest response to global change. *Tree Physiology*, **22**, 1177–1184.
- Caldwell MM, Matson PA, Wessman C *et al.* (1993) In: *Scaling Physiological Process from the Leaf to the Globe* (eds Ehleringer J, Field CR), pp. 223–230. Academic Press, San Diego.
- Chambers JQ, Higuchi N, Tribuzy ES *et al.* (2001) Carbon sink for a century. *Nature*, **410**, 429.
- Cao M, Woodward FI (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, **393**, 249–252.
- Cornford FM (1908) *Microcosmographica Academica*. Bowes and Bowes, Cambridge.
- Cox PM, Betts R, Jones CD *et al.* (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.
- Drake BG, Raschke K, Sailsbury FB (1970) Temperatures and transpiration resistances of Xanthium leaves as affected by air temperature, humidity and wind speed. *Plant Physiology*, **46**, 324–330.
- Falkowski PG (1992) Molecular ecology of phytoplankton photosynthesis. In: *Primary Productivity and Biogeochemical Cycles in the Sea* (eds Falkowski PG, Woodhead AD), pp. 47–67. Plenum Press, New York.
- Falkowski P, Scholes RJ, Boyle E *et al.* (2000) The global carbon cycle: a test of our knowledge of Earth as a system. *Science*, **290**, 291–296.
- Field CB, Gamon JA, Penuelas J (1995) Remote sensing of terrestrial photosynthesis. In: *Ecophysiology of Photosynthesis* (eds Schulze E-D, Caldwell MM), pp. 511–527. Springer Verlag, Berlin.
- Field CB, Behrenfeld MJ, Randerson JT *et al.* (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**, 237–240.
- Gamon JA, Serrano L, Surfás JS (1997) The photochemical reflectance index: an optical indicator of photosynthetic radiation use efficiency across species, functional types and nutrient levels. *Oecologia*, **112**, 492–501.
- Genty B, Briantis JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica Biophysica Acta*, **180**, 302–319.
- Griffiths H, Borland A, Gillon J *et al.* (1999) Stable isotopes reveal exchanges between soil, plants and the atmosphere. In: *Advances in Physiological Plant Ecology* (eds Press MC, Scholes JC, Baker M), pp. 415–441. Blackwell, Oxford.
- Goldenfield N, Kadanoff LP (1999) Simple lessons from complexity. *Science*, **284**, 87–89.
- Harte J (2002) Towards a synthesis of the Newtonian and Darwinian world views. *Physics Today*, **55**, 29–37 <http://www.aip.org/pt/vol-55/iss-10/p29.html>.
- Hoffert MI, Caldeira K, Benford G *et al.* (2002) Advanced technology paths to global climate stability: energy for a greenhouse planet. *Science*, **298**, 981–987.
- Houghton JT, Ding Y, Griggs DJ *et al.* (eds) (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Isebrands JG, McDonald EP, Kruger E *et al.* (2001) Growth responses of *Populus tremuloides* clones to interacting elevated carbon dioxide and tropospheric ozone. *Environmental Pollution*, **115**, 359–371.
- Kacser H (1987) Control of metabolism. In: *Biochemistry of Metabolism*, Vol. 11 (ed. Davies DD); *The Biochemistry of Plants* (eds Stumpf PK, Conn EE), pp. 39–67. Academic Press, New York.
- Kamen MD (1964) *Primary Processes in Photosynthesis*. Academic Press, New York.
- Körner C, Arnone JA (1992) Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science*, **257**, 1672–1675.
- Kolber ZS, Prasil O, Falkowski PG (1998) Measurements of variable chlorophyll fluorescence using fast repetition rate techniques. I. Defining methodology and experimental protocols. *Biochimica Biophysica Acta*, **1367**, 88–106.
- Kuhn TS (1960) *The Structure of Scientific Revolutions*, 2nd edn, pp. 5–6. The University of Chicago Press, Chicago.
- Lackner KS (2003) A guide to CO₂ sequestration. *Science*, **300**, 1677–1678.
- Langdon C, Broecker W, Hammond D *et al.* (2003) Effect of elevated CO₂ on the community metabolism of an experimental coral reef. *Global Biogeochemical Cycles*, **17**, 1–14.
- Langdon C, Takahashi T, Marubini F *et al.* (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles*, **14**, 639–654.
- Leclercq N, Gattuso J-P, Jaubert J (2000) CO₂ partial pressure controls the calcification rate of a coral community. *Global Change Biology*, **6**, 329–334.
- Lin G, Berry JA, Kaduk J *et al.* (2001) Sensitivity of photosynthesis and carbon sinks in world tropical rainforests to projected atmospheric CO₂ and associated climate changes. In: *Proceedings of the 12th International Congress on Photosynthesis*. CSIRO Publishing, Melbourne, www.publish.csiro.au/ps2001
- Lin G, Marino BDV, Wei Y *et al.* (1998) An experimental and model study of the responses in ecosystem exchanges to increasing CO₂ concentrations using a tropical rainforest mesocosm. *Australian Journal of Plant Physiology*, **25**, 547–556.
- Lovelock J (1990) *The Ages of Gaia*. Bantam, New York.
- Lloyd J, Grace J, Miranda AC *et al.* (1995) A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Plant Cell and Environment*, **18**, 1129–1145.

- Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *TREE*, **15**, 332–337.
- Matamala R, Gonzalez-Meler MA, Jastrow JD *et al.* (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science*, **302**, 1385–1387.
- Marubini F, Barnett H, Langdon C *et al.* (2001) Interaction of light and carbonate ion on calcification of the hermatypic coral *Porites compressa*. *Marine Ecology Progress Series*, **220**, 153–162.
- May RM (1999) Unanswered questions in ecology. *Philosophical Transactions of the Royal Society, London B*, **354**, 1951–1959.
- Melillo JM, Steudler PA, Aber JD *et al.* (2002) Soil warming and the carbon-cycle feedbacks to the climate system. *Science*, **208**, 2173–2176.
- Méthy M (2000) Analysis of photosynthetic activity at the leaf and canopy levels from reflectance measurements: a case study. *Photosynthetica*, **38**, 505–512.
- Murthy R, Griffin KL, Zarnoch SJ *et al.* (2003) Response of carbon dioxide efflux from a 550 m³ soil bed to a range of soil temperatures. *Forest Ecology and Management*, **178**, 311–327.
- Myneni RB, Dong J, Tucker CJ *et al.* (2001) A large carbon sink in the woody biomass of Northern forests. *Proceedings of the National Academy of Sciences (USA)*, **98**, 14784–14791.
- National Assessment Synthesis Team (NAST) (2001) *Climate Change Impacts on the United States: The Potential Consequences of Climate Variability and Change*. US Global Change Research Program, Washington, DC.
- Nichol CJ, Lloyd J, Shibistova O *et al.* (2002) Remote sensing of photosynthetic light use efficiency of Siberian boreal forest. *Tellus*, **54B**, 677–687.
- Norby RJ, Wullschlegel SD, Gunderson CA *et al.* (1999) Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell and Environment*, **22**, 683–714.
- Ohde S, van Woesik R (1999) Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bulletin of Marine Science*, **65**, 559–576.
- Oren R, Ellsworth DS, Johnsen KH *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature*, **411**, 469–472.
- Osmond CB (1989) Photosynthesis from the molecule to the biosphere. In: *Photosynthesis* (ed. Briggs W), pp. 5–17. AR Liss, New York.
- Osmond CB, Anderson JM, Ball MC *et al.* (1999) Compromising efficiency: the molecular ecology of light resource utilisation in terrestrial plants. In: *Advances in Physiological Plant Ecology* (eds Press MC, Scholes JC, Baker M), pp. 1–24. Blackwell, Oxford.
- Osmond B, Yakir D, Giles L *et al.* (1994) From corn shucks to global greenhouse: stable isotopes as integrators of photosynthetic metabolism from tissue to planetary scale. In: *Regulation of Atmospheric CO₂ and O₂ by Photosynthetic Carbon Metabolism* (eds Tolbert NE, Preiss J), pp. 249–265. Oxford University Press, New York.
- Ozanne CMP, Anhuif D, Boulter SL *et al.* (2003) Biodiversity meets the atmosphere: a global view of forest canopies. *Science*, **301**, 183–186.
- Randall DA, Shao O, Moeng C-H (1992) A second-order boundary layer model. *Journal of Atmospheric Science*, **49**, 1903–1923.
- Rascher U, Hütt M-T, Siebke K *et al.* (2001) Spatio-temporal variation of metabolism in a plant circadian rhythm: the biological clock as an assembly of coupled individual oscillators. *Proceedings of the National Academy of Sciences (USA)*, **98**, 11801–11805.
- Raven JA (1998) Extrapolating feedback processes from the present to the past. *Philosophical Transactions of the Royal Society of London B*, **353**, 19–28.
- Root TL, Price JT, Hall KR *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Rosenstiel T, Potosnak M, Griffin KL *et al.* (2003) Elevated CO₂ uncouples growth and isoprene emission in a model agriforest ecosystem. *Nature*, **421**, 256–259.
- Sage RF, Monson RK (1999) *C₄ Plant Biology*. Academic Press, San Diego.
- Schimel DS, House JI, Hibbard KA *et al.* (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature*, **414**, 169–172.
- Schreiber U, Bilger W, Neubauer C (1994) Chlorophyll fluorescence as a noninvasive indicator for rapid assessment of *in vivo* photosynthesis. In: *Ecophysiology of Photosynthesis* (eds Schulze E-D, Caldwell MM), pp. 49–70. Springer Verlag, Heidelberg.
- Schulze E-D, Beck E, Steudle E *et al.* (1994) Flux control in biological systems: a comparative view. In: *Flux Control in Biological Systems* (ed. Schulze E-D), pp. 471–485. Academic Press, San Diego.
- Sellers PJ, Bounoua L, Collatz GJ *et al.* (1996) Comparisons of radiative and physiological effects of doubled atmospheric CO₂ on climate. *Science*, **271**, 1402–1406.
- Severinghaus JP, Broecker W, Dempster W *et al.* (1994) Oxygen loss in Biosphere 2. *Transactions of the American Geophysical Union*, **75**, 35–37.
- Shaw MR, Zavaleta ES, Chiariello NR *et al.* (2002) Grassland responses to global environmental changes suppressed by elevated CO₂. *Science*, **298**, 1987–1990.
- Snow CP (1959) *The Rede Lecture 1959. The Two Cultures*. The University Press, Cambridge.
- Tans PP, Wallace WR (1999) Carbon cycle research after Kyoto. *Tellus*, **51B**, 562–571.
- Taylor K (1999) Rapid climate change. *American Scientist*, **87**, 320–327.
- Tian HQ, Melillo JM, Klighter W *et al.* (1998) The effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature*, **396**, 664–667.
- Tingey DT, McVeety BD, Wachsmann R *et al.* (1996) A versatile sun-lit controlled-environment facility for studying plant and soil processes. *Journal of Environmental Quality*, **25**, 614–625.
- US Climate Change Science Program (CCSP) (2002) Draft strategic plan, November 11. www.climatechange.gov
- Walford RL (2002) Biosphere 2 as a voyage of discovery: the serendipity from inside. *BioScience*, **52**, 259–263.
- Walther G-R, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Yakir D, Sternberg LSL (2000) The use of stable isotopes to study ecosystem gas exchange. *Oecologia*, **121**, 297–311.