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Experimental ecosystem and climate change research in controlled environments: lessons from the Biosphere 2 Laboratory 1996-2003

Barry Osmond[1]

[1]Visiting Fellow, School of Biochemistry and Molecular Biology, Australian National University, PO Box 3252 Weston Creek ACT 2611, Australia. Fax +61 2 6125 0313, email Barry.Osmond@anu.edu.au

Summary. It is clear from the project summaries below that the Biosphere 2 Laboratory (B2L) delivered handsomely as a controlled environment facility for experimental ecosystem and global climate change research. Ironically, the short and medium term experiments with model complex systems revealed that some of the most exciting and unexpected questions involved carbon cycling in benthic and soil metabolism, the very same processes that caused the first closed mission to fail, and eventually made the apparatus available for research. The effects of elevated [CO_2] on these processes in the marine and agriforest mesocosms was to stimulate flux and to reduce C-sequestration, by reduced carbonate deposition and enhanced metabolism of soil C reserves, respectively. The extent to which this and other themes that emerged from experiments were products of the initial conditions established in B2L model systems, or are general principles that prevail in natural ecosystems, remains to be seen.

Key words. Elevated [CO_2], C-cycles, Coral reefs, Tropical forests, Agriforests,

Introduction

Control of the physical and chemical environment during plant growth has been of paramount importance over the last 50 years in advancing the understanding of physiological, biochemical and genetic processes in individual plants as a foundation of crop and tree physiology, and for the emergence of plant ecophysiology as a discipline. Fritz Went pioneered the concept of phytotrons in the 1950s, and these then expensive controlled environment facilities soon became indispensable for environmental plant science research. In fact, the scale of commitment in 1960 for the Canberra Phytotron placed it in national competition for capital funding with radio telescopes (Evans 2003). As we now come down firmly to Earth and our need to understand the feedbacks between complexity in the biosphere and changing global climate systems, experimental facilities an order or more of magnitude larger than phytotrons, in size, sophistication and cost, will be needed. One such device, the $200 million Biosphere 2 facility at Oracle, Arizona (ironically, within sight of the telescopes on Kitt Peak), became available in 1996 as a prototype apparatus for large-scale experimental research with complex model ecosystems (mesocosms).

Harte (2002) pointed out that the polarization of research efforts into Newtonian and Darwinian camps has become a key obstruction to progress in earth systems science. The boundaries of the divide can be paraphrased as dynamic global climate models grounded in the laws of fluid dynamics on the one hand, and on the other, a fascination with biodiversity for its own sake, lists of organisms probed to the limits of molecular biology. If we are to bridge the Newtonian-Darwinian divide we must engage an expanded program of controlled experiments that will evaluate the significance of partial processes at all manageable scales (Harte 2002). Without experimental evidence it will be impossible to convince policy makers of the many dimensional responses of the biosphere to changing global climates. Indeed, can any discipline in natural science, no matter the scale or complexity, eschew the importance of controlled experiments indefinitely? In this context, the time for the Biosphere 2 Laboratory (B2L) had come (Marino and Odum 1999; Osmond et al 2004).

How B2L became available as an apparatus for experimental ecosystem and global change research

The original focus of B2L on human life support (Walford 2002) demanded a much higher standard of engineering, with redundancy in back-up environmental control systems far exceeding that normally encountered in other systems deployed for ecological research in laboratory and field studies. Perhaps the most tightly closed building ever constructed, B2L exchanged less than 8% of its original atmosphere each year of the original closed system experiment. The original human enclosure experiments revealed that the balance and composition of soil and plants was sub-optimal for long term closed system research, principally because the O_2 demand of soil metabolism was greater than the O_2 replacement capacity of the vegetation. This itself highlighted one of the least well understood components of the Earth system. Moreover, exposed fresh structural concrete in the enclosed system became an irreversible sink for CO_2 (as CO_3^-) and rapidly lead to atmospheric O_2 depletion (Severinghaus et al 1994). Subsequent reconfiguration of B2L into a series of separately controlled spaces for research gave a series of chambers that varied from 11,500 to 27,000 m^3, in which control and measurement of leaks, temperature and light gradients was better than in conventional growth chambers and gas exchange systems. Retrofitting for research projects in ocean, tropical forest, agriforest and wilderness mesocosms commenced immediately and within a few years distinctive programs were in place (Marino and Odum 1999; Walter and Lambrecht 2004).

Under the stewardship of the Earth Institute of Columbia University, the Biosphere 2 facility was made available in 1996 for large-scale controlled environment experiments with complex systems, as part of a research, education and public outreach effort in the context of an embryonic western campus of the University. The management contract with the owner was renewed in 2000, through 2010, with pledges of support for research leadership faculty appointments, start-up support through 2005, and a research laboratory, in the expectation that it would become self sufficient as a research facility 2006-2010. Following changes to the senior administration of the university in June 2002 it became clear that these commitments were not going to be met, and the apparatus was closed in December 2003. The site was listed for sale in January 2005. This paper illustrates the attributes of B2L (Table 1) with examples of the research done 1996-2003, and in the process also illustrates the potential in future for more specific, purpose built controlled environment systems in experimental ecosystem and global change research.

Table 1. Distinctive attributes of the Biosphere 2 Laboratory (B2L) for experimental ecosystem and climate-change research (Osmond et al 2004)

1) CONTROLLED PHYSICAL ENVIRONMENTS in the soil-plant-atmosphere continuum with respect to CO_2 (and other gas) concentration, temperature, precipitation, humidity and nutrients.

2) MASS AND ISOTOPE BALANCE with all inputs, outputs and flux rates of gases, isotopes and elements measured with precision in open flow or intermittent closure mode.

3) REPLICATION OF EXPERIMENTS IN TIME using synthetic, model complex mini-ecosystems (mesocosms) was achievable within the limits of the usually reliable high light environment of Oracle, AZ.

4) ACCELERATED TESTING OF IDEAS with data available on line and experiments replicated within days to weeks vs. seasons to years to obtain comparable data sets under field conditions.

5) ACCESS TO FOREST CANOPIES via the space frame of B2L for on the leaf measurements of processes with hand held instruments.

6) CALIBRATION OF NEW TECHNOLOGIES based on isotopes and remote sensing against whole system and process measurements.

7) REPLACEMENT AND SUCCESSION because the biological composition of mesocosms can be altered at will.

8) MODEL VALIDATION AND EXTRAPOLATION from synthetic model systems of B2L to natural ecosystems using sensor arrays and defined boundary conditions.

9) INFRASTRUCTURE SUPPORT ON-SITE with engineering, accommodation, and conference facilities commensurate with the role of an inclusive, multi-user facility.

Lessons from the B2L coastal marine mesocosm (CMM)

It is estimated that as much as half of the global flux of CO_2 into the biosphere occurs in marine ecosystems (Field et al 1998). Unlike the terrestrial mesocosms, the B2L ocean proved to have been constructed and to have settled in a self-sustainable condition, without the occurrence of algal blooms, and able to support a small coral and fish population with a minimum of maintenance. The CCM thus required the little modification to transform it into a model experimental inshore coral reef mesocosm, and researchers moved quickly with experiments that bridged some critical aspects of the Newtonian-Darwinian divide in this mesocosms.

Calcification in coralline organisms is inhibited by elevated [CO_2].

Field scale experiments in the CCM convincingly confirmed 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 CO_2 concentration expected mid 21st Century (Langdon et al. 2000, Marubini et al. 2001). Moreover, there was a good correspondence between controlled environment experiments and field observations (Broecker et al 2001). Some regard these observations as the first evidence for a direct deleterious effect of elevated CO_2 concentration on a key ecosystem process. When the facility was closed, Langdon was testing a new device capable of measuring coral growth rates with time resolution of hours rather than weeks.

Elevated [CO_2] accelerates biological C-influx with faster C-efflux.

System level studies using an extremely low level of $^{14}CO_3^-$ (only detectable by C-dating techniques) showed that although elevated CO_2 accelerated photosynthesis in the model coastal ecosystem, respiratory turnover was also immediately stimulated, and there was no change in organic C-sequestration (Langdon et al 2003). As above, the dominant effect of elevated [CO_2] on the carbon sink in this marine ecosystem was a 7-fold reduction of inorganic C-sedimentation. Although only a small component of total marine C- flux (Field et al 1998), these forms of C-sequestration are of critical significance in coastal, tropical marine ecosystems.

Wave motion accelerates nutrient uptake and facilitates CO_2 transfer into the ocean during rainfall.

The ability to control water flow, wave action and to simulate rainfall some 15m above the seawater surface facilitated another major line of enquiry in the B2L ocean. Demonstrations of the role of mixing in boundary layer limitation of nutrient delivery to corals were reported by Atkinson et al (2001) and Hearn et al (2001). Unique large-scale experimental evaluation of wave action and rain drop size on gas mixing, particularly of CO_2 transfer atmosphere-ocean surface, addressed one of the important unknowns of global models of CO_2 dynamics (Ho et al 2004). Further reports on this project, involving scientists from 8 laboratories across the US, are in preparation, and studies on the effects of marine biota on the chemistry of ocean derived aerosols had begun before the apparatus closed (J Allen, unpublished).

When coupled with the effects of warm water incursions on coral bleaching, it becomes clear that the sustainability of coral reefs is threatened by rising CO_2, ocean surface temperature and sea level change, suggesting potentially severe socio-economic consequences in coastal reef communities. As in most aspects of slowly unfolding global change, extreme events such as the December 26 2004 tsunami in the Indian Ocean, compress time scales and almost instantly transform present ecosystems into those we may have to confront in a few decades to come.

Lessons from the B2L tropical forest mesocosms (TFM)

Difficult of access, tropical forest canopies have been estimated to comprise 90% of the functional interface between Earth's terrestrial biomass and the atmosphere (Ozanne et al 2003). Tropical forests are thought to represent about half the global terrestrial C-sink (Field et al 1999; Malhi and Grace 2000), but there is concern that this sink may switch to a source of CO_2 in response to drought events in El Nino years. Over a decade, the model synthetic pan-tropical forest system in B2L became an excellent structural and functional approximation to a disturbed rainforest margin community (Arain et al 2000; G Prance 2003, unpublished).

Whole mesocosms responses to elevated [CO_2] validate the "big-leaf" model of tropical forest productivity.

Lin et al (1998, 1999), confirmed that the "big leaf" model of Lloyd et al (1995) fitted well with the CO_2 response curves measured in the whole mesocosms and flux measurements from B2L provide a strong basis for improved models of the C-sequestration capacity of tropical forest canopies as atmospheric [CO_2] continues to rise. Depending on assumptions about temperature responses of these processes, such models suggest that this sink-capacity is already, or soon will be, saturated (Lin et al 2001).

The TFM canopy responds rapidly, but reversibly, to month long droughts, but remains a net C-sink, possibly because of the functional diversity of responses among different dominant species.

A set of 4 drought treatments applied over 3 years showed that mesocosm C-influx declined by 32% within days of commencement of the drought, suggesting a rapid response to water loss in the soil surface layers. The water content of deep soil was unaffected, and leaf water status of most canopy dominants was only slightly reduced. These changes were reversible within weeks (Rascher et al 2004). Although stomatal closure reduced ecosystem conductance by 33%, individual trees responded differently and showed different levels of stress and mechanisms of stress avoidance. Taking full advantage of the space frame and climbing facilities in B2L, a team of 25 scientists from 8 institutions showed that leaf area declined by 10% due to a doubling of leaf fall and to reduction in leaf expansion growth by up to 60% in some species. Photosynthetic electron transport rate at light limitation declined by up to 70% in some species but was unaltered in others. This functional diversity introduces heterogeneity of response in the canopy with challenging implications for scaling leaf processes to ecosystem behavior.

Drought reduces the emission of the trace greenhouse gas N_2O and isoprene.

The enclosed TFM facilitated measurements of trace gases, showing that although N_2O emission declined with drought, flux from the soil was stimulated 5-20-fold in 24hr after re-watering, releasing a large proportion of N_2O that had not been emitted during the drought (vanHaren et al 2005). The glass enclosure of B2L minimized the UV-catalyzed destruction of isoprene and permitted accurate estimates of leaf and mesocosm emission rate and also facilitated detection of a soil sink for isoprene of about the same magnitude as the canopy efflux (Pegoraro et al 2005).

On-line monitoring of stable isotopes in the canopy atmosphere indicates changing C-flux processes during drought.

With net CO_2-influx of the entire system readily available the TFM was an attractive setting in which to integrate and identify component processes using stable isotopes and a ratio mass spectrometer with an automated sample processing system was installed on-line to obtain routine, well replicated estimates of C, O, and N isotope fractionation. The $\delta^{13}C$ value of respiratory CO_2 changed markedly from -25.2 ‰ before drought, to -24.4 ‰ during drought and -28.2 ‰ after re-watering (G Lin in Osmond et al 2004), indicating stomatal closure during the drought, and rapid respiration of more negative $\delta^{13}C$ substrates (perhaps fats and waxes in leaf litter) after re-watering.

Remote sensing of chlorophyll fluorescence parameters reveals functional diversity in canopy photosynthesis.

Canopy access with hand held instruments remains a limiting feature for assessment of the most of the global photosynthetic system. A novel fast repetition rate laser device was developed to analyze chlorophyll fluorescence transients and thereby evaluate stress responses of photosynthetic processes in the outer canopy (Ananyev et al 2005). Ultimately it may be possible to relate estimates of photosynthetic efficiency obtained by fluorescence (Ananyev et al 2005; Kolber et al 2005), or reflectance (Rascher et al 2005), to canopy C-flux measurements (Osmond et al 2004). Serendipitously, the arbitrary biodiversity of the TFM also facilitated evaluation of novel mechanisms of photoprotection of the photosynthetic apparatus from excess light (Matsubara et al 2005).

The policy implications of such insights may be still more uncertain than those associated with coral calcification, but the apparatus that was the B2L TFM clearly made an important contribution to the debate on the sustainability of tropical forest ecosystems in the face of global change. As the apparatus was closed, plans were on hand to harvest and replace elements of the TFM, such as the shade belt of banana and ginger trees, to assess their edge-effect contributions to total mesocosm CO_2-fluxes, and to replace dead palms and their deep soil with a walk-in root observation and soil monitoring facility with early successional species. One legacy of the research may be a new generation of flux-towers fitted for isotope collection for better understanding of respiratory C-efflux processes, and with fluorescence and reflectance monitoring and imaging devices that will improve understanding of photosynthetic C-influx processes.

Lessons from the intensive forest mesocosms (IFM) in B2L

Plantation forestry using rapidly growing trees has been widely touted as a means of mitigating CO_2 emissions and as energy forest substitutes for fossil fuels. The decision to replace the former food growing areas of Biosphere with three replicated *Populus deltoides* stands, each exposed to different atmospheric $[CO_2]$ (ambient, 2x and 3x ambient), committed this part of the apparatus to a medium term experiment of great potential. Coppiced annually and litter-free, coordination of projects in the TFM presented more problems than in the CMM and TFM, and was especially demanding of the on-site research support team.

Global warming increases temperature at night more than in the day, with differential effects on leaf photosynthesis and respiration.

Temperature and humidity control at the stand level in the IFM opened a new range of possibilities for exploring leaf level functions in the canopy (Griffin et al 2001) such as differential thermal effects on respiration and photosynthesis (Griffin et al 2002 a, b; Turnbull et al 2002, 2004; Engel et al 2004).

Elevated $[CO_2]$ inhibits isoprene emission but not in drought.

The highly reactive chemistry of this hydrocarbon stimulates local ozone production but levels of this and other reactive oxygen species in the atmosphere is minimized under glass in B2L, facilitating precise estimates of emission and uptake. Emission from *P. deltoides* is inhibited by elevated $[CO_2]$ (Rosenstiel et al 2003) but this effect is eliminated under drought (Pegoraro et al 2004).

System level measurements of stand photosynthesis and respiration differ from those projected from the leaf level.

Murthy et al (2003) first demonstrated the different effects of temperature on soil respiratory CO_2-efflux in the 500 m^3 soil blocks of the IFM compared with usual spot measurements. Subsequent experiments with a combination of atmospheric and soil water stress treatments, assessed by both leaf-level measurements and system-level CO_2-fluxes, revealed a transition from canopy light environment control of system C-influx to stomatal control of assimilation at the level-of the individual leaf as water stress progressed (Murthy et al 2005).

Elevated [CO_2] promotes leaf area development and this dominates system level responses aboveground.

As became obvious from greater leaf fall in response to soil and atmospheric water stress in the elevated [CO_2] treatment (Murthy et al 2005), leaf area development studies by Walter et al (2005) found larger canopy area in the elevated [CO_2] treatment was due to a larger population of more rapidly expanding leaves. The unusual diel pattern of expansion growth in poplar, and an afternoon depression of glucose availability under elevated [CO_2] may limit the extent of changes in the population distribution of growth rates.

Elevated [CO_2] promotes system respiration at all levels, increases fine root production, rhizodeposition of substrates, and accelerates decomposition of existing soil C and depletion of soil nutrients.

Barron-Gafford et al (2005) observed that although foliage was a large and variable proportion of aboveground biomass, fine root production and C-secretion belowground were key determinants of system respiration. Moreover, decoupling was evident in that stimulation of system level respiration by elevated [CO_2] carried over from coppicing to the next growing season initially, and was further exaggerated as the canopy developed. Soil microbial ecology was not significantly perturbed by elevated [CO_2], but the biomass of soil microbes increased (Lipson et al 2005). Trueman and Gonzalez-Meler (2005) used stable isotope to show that elevated [CO_2] not only accelerated fine root development during the growing season and accumulation of dead roots in the soil after coppicing, but also accelerated the respiration of “old carbon” residues in the soil. Total soil-C declined over the 3-4 year experiment, and there was no evidence for greater C-sequestration in this agriforest at elevated [CO_2].

Elevated [CO_2] enhances expression of genes of metabolism, especially those controlling the lignin formation and the chemical composition of wood.

After 3 cycles of growth at elevated [CO_2] with annual coppicing, *P. deltoides* leaves showed few significant changes in gene expression associated with photosynthesis or respiration. Stems showed marked enhancement of expression in genes associated with lignin biosynthesis, and repression of those associated with cell wall formation and growth (Druart et al 2005). The implications of these results for paper production, timber quality are clear. Furthermore they present potential opportunities to engineer less biodegradable wood that might enhance C-sequestration and assist mitigation of rising [CO_2].

Lessons from the wilderness mesocosms in B2L

The wilderness mesocosms in B2L were in the process of reconfiguration when the facility was closed. Part of the thorn scrub was cleared of invading grasses and because it was a region of particularly steady air flow, supported studies of elevated [CO_2] on oviposition behavior of moths with well developed CO_2-sensors (Abrell et al 2005). The response of moths to volatile chemical attractants was also explored in preparation for studies of interactions with elevated [CO_2] (Pophof et al 2005). A small sonoran desert ecosystem, dominated by succulent plants with nocturnal CO_2-fixation was set up in the original test module of B2L. Nobel and Bobich (2002) demonstrated that root growth following rain after drought consumed all the CO_2 fixed as well as drawing on reserves. At the system level, this mesocosm was unable to recapture all of the CO_2 lost by respiration of the native soil (Rascher et al (2005 b). This system was presented as a model of the experimental capabilities of B2L as part of the public outreach program.

Overview

It is clear from the above summaries of some high points of research at B2L that one objective for the apparatus, to operate in "telescope mode" with significant efforts from scientists at remote sites, was realized. The planned consolidation of this potential by research leadership faculty and facilities on-site was not achieved. Although dismayed by the manner and turn of events within the university that caused the above vision to fade, commitments to be withdrawn, and the facility to be closed, one hopes the experimental approaches that emerged from B2L might stimulate research on this scale elsewhere. Further insight into the interactions of temperature and elevated [CO_2] on system C- and nutrient fluxes can be expected, as well as experimental definition of trophic interactions. Integration may well follow from stable isotope, remote sensing and imaging methods explored in B2L.

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