Using a Closed Ecological System to Study Earth's Biosphere

Author(s): Mark Nelson, Tony L. Burgess, Abigail Alling, Norberto Alvarez-Romo, William F. Dempster, Roy L. Walford, John P. Allen

Source: *BioScience*, Vol. 43, No. 4 (Apr., 1993), pp. 225-236
Published by: University of California Press on behalf of the American Institute of Biological Sciences
Stable URL: http://www.jstor.org/stable/1312123

Using a Closed Ecological System to Study Earth's Biosphere

Initial results from Biosphere 2

Mark Nelson, Tony L. Burgess, Abigail Alling, Norberto Alvarez-Romo, William F. Dempster, Roy L. Walford, and John P. Allen

The idea of creating materially closed microbiospheres, including humans, to study ecological processes had its roots in several branches of research. One was the sealed microcosms and open, but boundary-defined, mesocosms that ecologists developed to study ecosystem processes. Another source was the experimental life-support systems designed for use in spacecraft and as prototypes for space habitations.

During the 1960s, H. T. Odum began advocating life-support research in sealed greenhouses that would rely on the ecological self-organizing properties of the enclosed soils, plants, and animals (Odum 1963). In 1971, Dennis Cooke wrote, "The fact that we are not now able to engineer a completely closed ecosystem that would be reliable for a long existence in space...is striking evidence of our ignorance of, contempt for, and lack of interest in the study of the vital balances that keep our biosphere operational. Therefore, future efforts to construct a life-support system by miniaturizing the biosphere and determining the minimum ecosystem for man is a goal that is as important for the quality of human life on Earth as it is for the successful exploration of the planets" (Cooke 1971).

Mark Nelson is chairman of the Institute of Ecotechnics, London, UK, and director of environmental applications, Space Biospheres Ventures (SBV), Oracle, AZ 85623. Tony L. Burgess is program coordinator of the Desert Laboratory, University of Arizona, Tucson, AZ 85621. Abigail Alling is director of research and marine ecosystems, Biosphere 2, SBV. Norberto Alvarez-Romo is director of Mission Center, SBV. William F. Dempster is director of systems engineering, SBV. Roy L. Walford is chief of medical operations, Biosphere 2, SBV. John P. Allen is vice president of biospheric development, SBV. Nelson, Alling, and Walford are also crew members inside Biosphere 2 for the initial closure experiment, 1991–1993.

Synthetic biospheres open the prospect for comparative biospherics

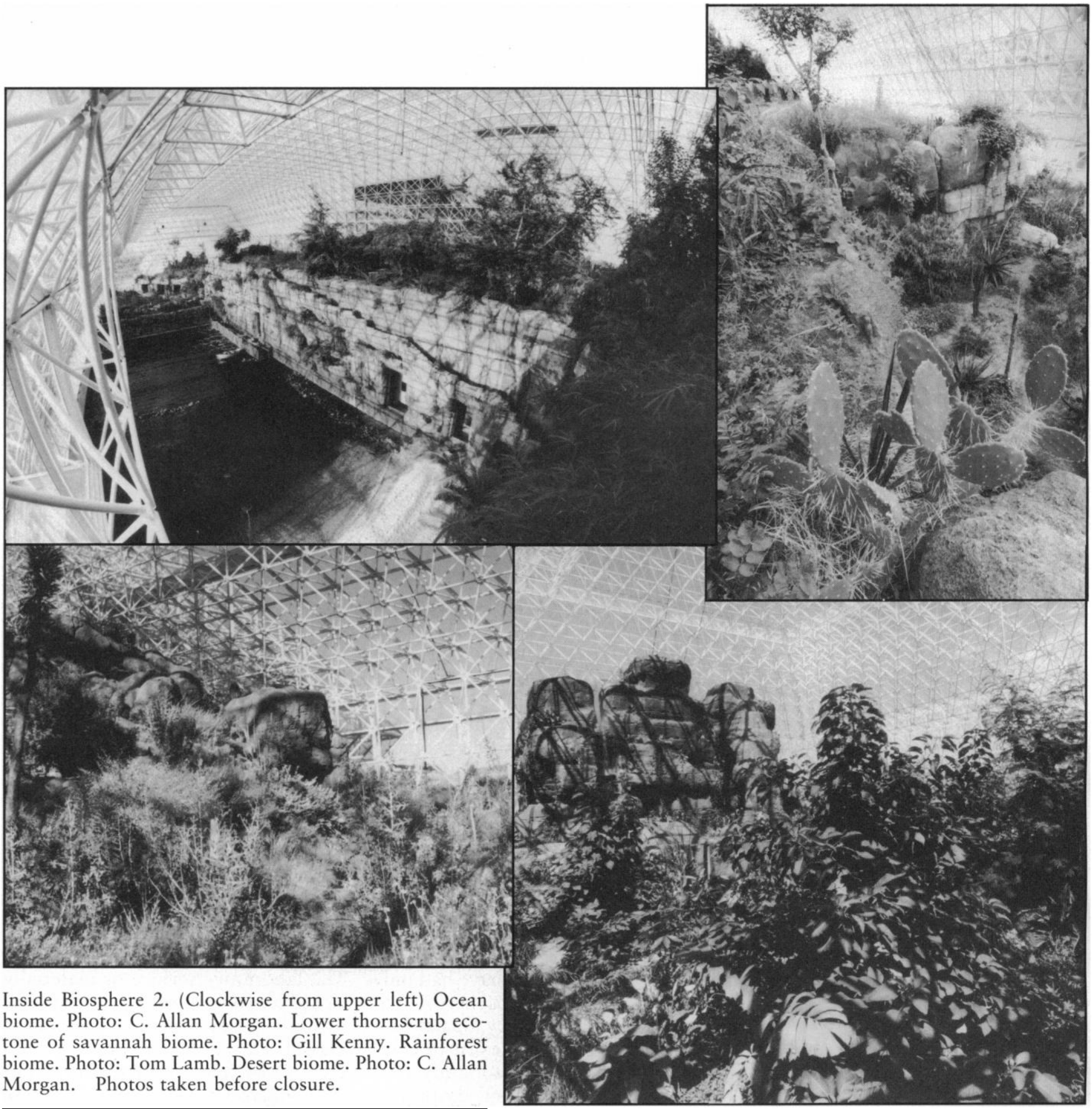
Biosphere 2 (so named to emphasize that previously we have had only Earth's biosphere, "Biosphere 1," to study) was designed by Space Biospheres Ventures (SBV), a private company started in 1984 to study processes and ecosystem dynamics analogous to those of the global biosphere (Allen 1991). Biosphere 2 also was planned to be an entrepreneurial venture to market closed life-system facilities, data management systems, and spin-off products such as air purifiers. Visitors and educational materials also generate income.

Biosphere 2 differs from previous laboratory microcosms and mesocosms in size, diversity of ecosystems, and degree of material closure. It is virtually materially sealed (currently less than 10% air exchange per year) and open to energy of sunlight, electricity, heat transfer, and information flow. The first closure experiment, of two years' duration, began in September 1991. Initial results indicate that the ecosystems in Biosphere 2 are maturing rapidly and functioning to maintain most introduced species. The humans are healthy and producing nearly all their nutritional requirements from the agricultural area. The cycling of nutrients such as carbon dioxide through the vegetation is operating with shorter periods and greater fluxes than in the global environment, atmospheric oxygen has shown an unanticipated decline, and some shifts in community dominance of the ecosystems are occurring.

Previous research in closed ecological systems

The laboratory science of materially closed ecosystems began with the work of Clair Folsome at the University of Hawaii. Folsome materially closed 1–5 liter flasks filled with ocean water, sand, microbes, algae, and air. These flasks have proved to be viable for prolonged periods if they contain sufficient metabolic diversity at closure and are provided with an adequate energy flow (Folsome and Hanson 1986). Some, closed as long ago as 1968, are still functional today. Other early researchers of materially closed systems (ecospheres) include Frieda Taub of the University of Washington, Joe Hanson of the Jet Propulsion Laboratory in Pasadena, California, and Basset Maguire of the University of Texas (Hanson 1982).

Previous closed ecological system facilities developed for space application focused on providing human life support and included either algae or



Inside Biosphere 2. (Clockwise from upper left) Ocean biome. Photo: C. Allan Morgan. Lower thornscrub ecotone of savannah biome. Photo: Gill Kenny. Rainforest biome. Photo: Tom Lamb. Desert biome. Photo: C. Allan Morgan. Photos taken before closure.

bacteria and sometimes agricultural crops as well. Research efforts in the 1950s and 1960s focused on systems based on green algae (*Chlorella vulgaris*). In 1961, Yevgeny Shepelev at the Institute of Biomedical Problems (IBMP) in Moscow became the first human to survive one day in a bioregenerative life-support system, which included some 30 liters of *Chlorella* that supplied all of his required air and water (Shepelev 1972). Jack Myers at the University of Texas was among early US experimenters to develop systems coupling mice with *Chlorella* (Eley and Myers 1964, Myers 1963).

Russian work on algae-based systems proceeded at IBMP in Moscow and at the Institute of Biophysics, Krasnoyarsk, Siberia, culminating in human closures of 15 and 30 days in the late 1960s and early 1970s. In the United States, early NASA-funded research conducted by scientists with Boeing Corporation also achieved human-occupied closures. But the early hopes of a completely regenerative system using only one companion species to support humans began to fade when it became apparent that *Chlorella* was not palatable as a human food. It became clear that the next step would be to include higher plants in the closed systems that could produce grains and vegetables for human nutrition (Galston 1992).

This step was taken at the Institute of Biophysics in the Bios-3 experiment. The test facility had a volume of more than 300 cubic meters divided among a chamber for algae tanks, a hydroponic cropping area, and a human living area that included food processing, medical, and control rooms, kitchen and dining areas, and separate apartments for the three crew members. The research, first led by Boris Kovrov, and, after Kovrov's death, by Josef Gitelson, used lettuce, wheat, potatoes, radishes, and beets grown hydroponically under artificial lighting to provide approximately half the nutrition for crews of two or three people. Experiments lasted as long as six months. Almost all air was regenerated, although catalytic burners were needed to oxidize trace gas buildups. More than 90% of water was recycled, the main mechanism being purification by plant transpiration and then condensation to provide drinking and irrigation water. Human wastes, aside from a portion of the urine, were not processed inside the facility, but were exported; some food, including dried meat for needed protein, was imported. Overall, health of the crew of Bios-3 was good, although some simplification of their intestinal microbiota occurred (Lebedev and Petrov 1971, Terskov et al. 1979).

In the United States, funding for bioregenerative life support experiments was drastically reduced when a 1966 conference to review the field made it apparent that simple systems using only one or two species of algae and bacteria would not be feasible. The meeting also dramatized two radically different strategies for further development: those who favored complex, multispecies systems modeled on natural communities and those who favored a more reductionist, engineered approach with a few species that could be manipulated for maximal productivity (Cooke 1971, NASA 1968).

In 1978, NASA reinstituted a program for the development of bio regenerative systems called CELSS (Controlled Ecological Life Support Systems). CELSS has funded research at a variety of universities and within NASA, principally at Ames Research Center, Johnson Space Center, and Kennedy Space Center to conduct basic investigation and explore engineering applications of the various components necessary for life support. Much work has focused on high-yield systems for biomass and food production. University work has included intensive hydroponic systems for growing some of the principal targeted food crops, including wheat, white and sweet potatoes, and soybeans (Bubenheim 1990, Bugbee and Monje 1992, Corey and Wheeler 1992, MacElroy et. al. 1987, Salisbury et. al. 1987, Schwartzkopf 1992).

In 1986, the CELSS Breadboard Project was started with a goal of scaling up from previous research prototypes to include the integration of food production, water recycling, and atmospheric gas control in its biomass production chamber. Support laboratories are investigating associated questions of waste recycling, food preparation, and overall data management. From this first phase it is anticipated that designs for further ground-based and ultimately space systems will emerge (Knott 1990).

Japanese and European programs in closed ecological systems for life support, although smaller, also are under way. The Japanese efforts, under the leadership of Keiji Nitta of the National Aerospace Laboratory in Tokyo, have concentrated on gas recycling systems involving oxygen and carbon dioxide separation and concentration, water recycling systems, plant and algae physiology and cultivation techniques, and animal physiology and breeding (Nitta 1987). European efforts have focused on microgravity effects on biological development essential for the successful translation of ground-based controlled ecological life support systems into space, and on basic physiological responses of plants (Andre et. al. 1989, Skoog 1987).

Biospheric research facility

Biosphere 2 differs from other research programs in that it is a system with diverse components that provide not only human life support but also maintain resilient, persistent, complex, and evolving ecosystems. This design philosophy contrasts with CELSS-type systems, which seek to integrate separate components into a tailored system. Such CELSS systems are focused on minimizing weights and volumes for launch. Biosphere 2, although employing specialist knowledge, has incorporated an approach that seeks to promote and ensure the self-organizing capabilities of living systems by deliberately replicating a typical range of tropical and subtropical environments with their associated diversity of life forms and metabolic pathways. Research using Biosphere 2 has focused on studies relevant to Earth's ecosystem and biospheric processes. Such studies also are expected to provide baseline data on the dynamics of complex life-support systems that eventually can be incorporated into systems for long-term habitation on the moon, Mars, and other space bases.

The design of Biosphere 2 employs the tendency of biological systems to self-organize: "the process by which ecosystems develop structure and processes from available energies...[to] improve the system's adaptation to external changes and variations" (Odum 1983).

> In appraising the potential costs of closed system design one has the alternative of paying for a complex ecosystem with self maintenance, respiration and controls in the form of multiple species as ecological engineering, or in restricting the production to some reduced system like an artificial algal turbidistat and supplying the structure, maintenance, controls and the rest of the functions as metallic-hardware engineering. Where the natural combinations of circuits and "biohardware" have already been selected for power and miniaturization for millions of years probably at thermodynamic limits, it is exceedingly questionable that better utilization of energy can be arranged for maintenance and control purposes with bulky, non-reproducing, non-selfmaintaining engineering.
>
> —Odum 1963

These hypotheses, as well as the theory that ecological systems have greater resilience to perturbations than monocultural systems, have not been tested extensively. In particular, such studies are pertinent to the question of determining how biodiversity affects stability of ecosystems and of our global ecology.

To foster its diversity, Biosphere 2 includes many microhabitats within each ecosystem type. It was deliberately over-packed with species to provide maximal diversity for self-organization and to compensate for unknown and potentially large initial species losses. Environmental technologies provide thermal control, water and wind flows, and substitutes for natural functions like waves and rain. But the facility would not function unless the biota fulfills its essential role of using energy flow for biomass production (including food from

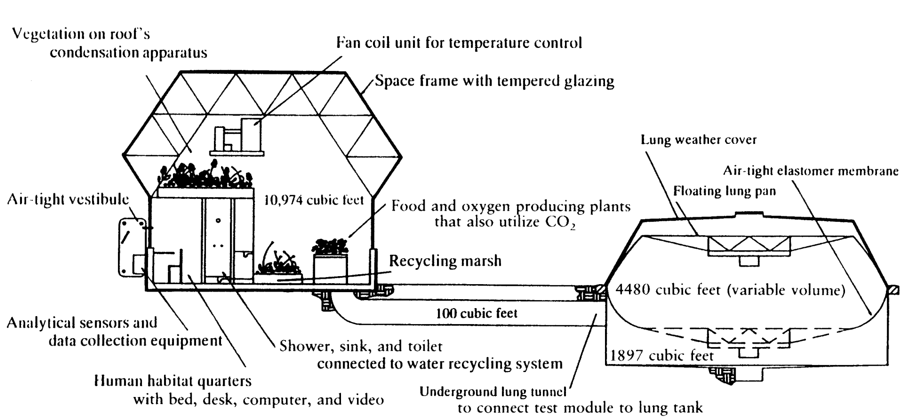


Figure 1. Schematic of Biosphere 2 test module showing its configuration during a series of human enclosure experiments conducted from 1988 to 1990. Its main structure is approximately 7 m on a side by 8 m tall, with a variable volume of approximately 480 m^3.

agricultural crops) and ensuring closure of essential biogeochemical cycles through diverse metabolisms. The design of Biosphere 2, which attempts to harmonize living systems with supporting environmental technologies, unites two historical approaches to life-support systems: the engineered and the ecological. In the Russian terminology from V. I. Vernadsky, this integration of "biosphere" and "technosphere" by man is called the "noosphere" (Vernadsky 1986).

A biosphere was defined in the design of Biosphere 2 as "an evolving, stable, complex, self-regulating system containing more than one ecosystem as well as all five kingdoms of life" (protoctists, prokaryotes, fungi, plants, and animals), capable of supporting humans and their technologies, open to energy and information flow, and essentially materially closed (Allen and Nelson 1988). Parameters for the life systems, engineering and mechanical systems, and information and analytical systems all have been developed to satisfy requirements flowing from this definition of a biosphere. The research program, which included four years of experiments in a closed ecosystem test facility, was developed to test how well these design parameters would succeed in creating a biosphere and to investigate mechanisms of biosphere operation.

Research and development in preparation for Biosphere 2

Since the commencement of the project in 1984, research and development objectives have been accomplished using the Biospheric Research and Development Center (BRDC) facilities at the project site near Oracle, Arizona. Experiments were conducted with the 480-cubic-meter Biosphere 2 test module (Figure 1) to test sealing technologies, as well as many other component technologies developed for Biosphere 2. Like Biosphere 2, the test module admits ambient sunlight through a laminated glass and steel spaceframe superstructure, and is sealed underground with a stainless steel liner. To avoid dangerous pressures from expansion or contraction of the air inside the tightly sealed structure, a variable volume chamber (lung) with a flexible membrane absorbs the volume changes. Inclusion of selected plant species from tropical ecosystems in test module experiments verified their ability to thrive in close proximity in a small, tightly sealed environment. The test module achieved air-exchange rates (leakage) as low as 24% per year.

Starting in 1988, there were test module experiments that included humans. These experiments were the first to seal a human into a system designed for bioregeneration of water, wastes, food, and air driven by natural sunlight for an extended period of time (Alling et al. 1990, in press, Nelson et. al. 1991a).

An air-purification system using soil bed reactors (Bohn 1972, Bohn and Bohn 1986, Carlson and Leiser 1966) was developed to metabolize and thus remove trace gas contaminants from outgassing of structural materials, plants, and humans. The reactors operate by forcing air through a plenum at the base of a soil container so that it diffuses through the biologically active soil, exposing trace gases to the wide range of metabolic pathways of a diverse suite of soil microbiota (Hodges and Frye 1990). Patents have been issued on new developments of this air purification technology.

The test program for the soil-bed reactors included laboratory bench-top replicate systems and trials in the test module. Potential problem gases such as ethylene, carbon monoxide, and methane could be effectively controlled in this manner. The field crop area for Biosphere 2 agriculture was designed as a soil-bed reactor. The entire volume of air in Biosphere 2 can be pumped upward through the soil in approximately one day if trace gas levels in the atmosphere require its operation (Glenn and Frye 1990, Nelson 1989). Throughout the first year of operation, the air has not required purification by means of the soil-bed reactor system. Individual food crops and cropping systems were tested for productivity, disease and pest resistance, and ease of harvest in BRDC and at the Environmental Research Laboratory (ERL) of the University of Arizona. Techniques of integrated pest management for biological control of pests and diseases were developed. The small buffering capacity and rapid cycling of air and water of Biosphere 2 precludes use of toxic pesticides and herbicides and demands that nutrients be returned to the soil to maintain intensive agricultural productivity (Leigh et al. 1987).

Aquatic plant and microbial systems for recycling human and animal wastes and domestic wastewater were developed and tested in experiments in which humans and other animals were enclosed for up to 21 days in the Biosphere 2 test module (Nelson et. al. 1991b). These waste treatment systems, developed with the consultation of B. C. Wolverton of the NASA Stennis Space Center, demonstrated the ability of human-made wetlands to process waste products and isolate potential chemical pollutants (Hammer 1989, Wolverton 1987).

An analytic laboratory system was designed to minimize outside consumable materials and to be sufficiently pollution-free so it can be incorporated inside a materially closed facility. A gas chromatograph–mass spectrometer (GCMS) system was developed that uses as a carrier gas hydrogen produced inside Biosphere 2. Also required was an apparatus for producing liquid nitrogen to be used in air and water analyses. A set of nearly reagent-free laboratory analytic techniques was devised in which the few chemical reagents required for analysis are neutralized or contained. Automated systems were developed for continuous air and water quality determinations as well as GCMS, ion chromatography, and atomic absorption techniques for more extensive analysis of soil, plant tissue, water, and air samples.

A five-level cybernetic system (nerve system) was developed by SBV and Hewlett-Packard to automate much of the technical interface with the life systems and to archive and process information from approximately 1900 data points distributed throughout Biosphere 2. The nerve system is distributed both inside Biosphere 2 and in the nearby Mission Center building, and it is linked together by a computer network.

In preparation for building the Biosphere 2 marsh ecosystem, SBV and the Marine Systems Laboratory at the Smithsonian Institution created two small estuarine systems, ecological mesocosms, in Washington, DC. The first was modeled on the Chesapeake Estuary, a temperate system; the second was an Everglades system (Adey and Loveland 1991, Finn and Adey 1991). These mesocosms were able to establish a gradient of environmental conditions analagous to the natural ones, such as salinity and tidal flow, and they have thus far maintained a high level of biodiversity.

Creation of Biosphere 2

During the design phase, from 1984 to 1988, there was close collaboration among ecologists, engineers, and architects[1] as ecological requirements were translated into construction plans, and technologies were employed to ensure maintenance of appropriate temperatures, water flows, and other ecological parameters. Two contrasting ecological approaches for selecting species were developed by terrestrial and marine system designers. The terrestrial team favored a strategy that targeted particular species for inclusion. This iterative process, for example, integrated pollinators with host plant requirements and canopy structure as total species lists were evaluated. Selection criteria for Biosphere 2 plant assemblages took into account life support for animal consumers, taxonomic diversity, life-form spectra, envelopes of physical parameters within Biosphere 2, as well as ethnobotanical utility and aesthetic interest.

Animal food requirements introduced several biases into the selection of plant species. The African bushbaby (*Galago garnetii*) needed fruits and acacia gum. Bees would be most reliably supported by Compositae flowers. Because many plant species would take several years to reach peak flowering capacity, fast-growing support species were introduced to allow rapid production of animal foods during initial stages of closure.

During construction, tight controls were not maintained to prevent local organisms from entering the structure, because it was felt that rigorous sterilization and biocide applications would be more likely to induce explosive reproduction of undesirable organisms than would accidental inclusion of local species. To build up invertebrate and microbiota diversity and biomass, soils installed in Biosphere 2 were inoculated with natural soil cores and mycorrhiza, waters from natural ecosystems were imported, and flying insects attracted to lights were collected and introduced. Species survyes, except for soil microbiota, were conducted before closure and indicated that approximately 3000 species were included.

The other design approach, used to create the marsh, ocean, and streams inside Biosphere 2, favored the diversity of crucial microbiota by bringing intact chunks (extracted homologues) from the natural ecosystems and, in addition to the collection of particular species, installing community samples in Biosphere 2. For example, the marsh biome was constructed of 3.5-cubic-meter marsh modules consisting of boxed soil with plants transported intact from Florida Everglades wetlands. The strategy taken in the design and development of the marsh was to replicate as closely as possible the natural environment (Finn and Adey 1991). Mechanical systems were designed to generate tides, currents, waves, and rain, as well as to help control salinity gradients and nutrient cycling. Inoculation of the ocean inside Biosphere 2 to ensure a diversity of ocean plankton was accomplished by transporting 20% of the approximately 900,000-gallon ocean volume from Scripps Institution in La Jolla, California, as well as a small amount of sea water that accompanied the shipment of corals from the Caribbean and the Yucatan Peninsula. The remainder was made up of local well water mixed with aquarium salt.

Agricultural regulations governing imports into Arizona necessitated the use of soil materials predominately from southern Arizona. Soil horizons with appropriate physical and chemical characteristics were installed as deep as 5 meters to permit adequate space for root maturation over an extended time. For the marine systems, local limestone was used as the base of both the marsh and reef systems, whereas additional aragonite Bahamian sand, reef rock, aragonite clam shell, oyster shell, and silica sand were included to supply required chemical constituents.

After closure, it was anticipated that there would be species losses that would decline as food webs became

[1]The team of ecological designers of Biosphere 2, given specifications and coordinated by the SBV research staff, included staff from the Royal Botanical Gardens at Kew and New York Botanical Gardens on rainforest design and operation; the Environmental Research Laboratory at the University of Arizona on intensive agriculture and some of the environmental engineering; Smithsonian's Marine Systems Laboratory for marsh and ocean design; Tony Burgess of the Desert Laboratory, Tucson, AZ, for desert and thornscrub; Peter Warshall, an independent consultant working with the Office of Arid Land Studies, University of Arizona, for savannah and vertebrate species selections; and Scott Miller of the Bishop Museum in Honolulu, HI, to coordinate a team of entomological consultants. The Institute of Ecotechnics (UK), a small, private research company that has worked on developing the theory and practice of integrating appropriate technology with ecological restoration projects, was the consultant on management of the designed ecosystems. SARBID, now Biospheric Design, Inc., coordinated overall physical design to provide the required number of habitats, as well as temperature, humidity, wind, wave, tide, and rain controls.

Table 1. Dimensions and volumes of Biosphere 2.

Section	Dimensions (meters) N-S E-W height	Areas (square meters)	Volumes (cubic meters)	Soil (cubic meters)	Water (cubic meters)	Air (cubic meters)
Agriculture	41 54 24	2000	38,000	2720	60	35,220
Habitat	22 74 23	1000	11,000	2	1	10,997
Rainforest	44 44 28	2000	35,000	6000	100	28,900
Savannah/ocean	84 30 27	2500	49,000	4000	3400	41,600
Desert	37 37 23	1400	22,000	4000	400	17,600
West lung	48 48 15	1800	15,000	0	0	15,000
South lung	48 48 15	1800	15,750	0	750	15,000

Lungs were measured at one-half inflation.

more integrated and canopy structure matured. To allow for the Darwinian process to operate and to compensate for extinctions, communities were initially stocked with a greater diversity of plant species than would probably be supportable. In most habitats, plants were installed in fairly equal abundances to allow a hierarchy of dominance to emerge and to evaluate how species thrived relative to one another. To allow tracking of plant community changes, each perennial in the terrestrial and marsh biomes was mapped and its canopy diameter measured before closure. Subsamples are remeasured periodically, and a complete resurvey is scheduled in September 1993 after the initial two-year closure period.

Ecosystem changes since closure

Biosphere 2 is designed to be as materially closed as engineering could ensure to prevent exchanges with the outside atmosphere and underlying soil. It is energetically open, allowing both incident sunlight through its glass spaceframe and the import of electricity in addition to heat transfer by means of heated or chilled water, which regulates internal temperature. It also is informationally open, connected with the outside for exchange of data and communications via computer systems, telephone, video, and television.

The 1.28-hectare airtight area, approximately 180,000 m^3 in volume (Table 1), is sealed above ground with laminated glass mounted on a spaceframe and below ground with a stainless steel liner. Two variable volume chambers are connected to the main structure. Experimentation with various pressures during September 1991–January 1992 established a relation between leak rate and pressure that extrapolates to an estimated leak rate of 6% per year at the currently maintained operating pressure. In addition, measurement of the progressive dilution of a marker trace gas (SF_6) confirms that the leak rate is not larger than 10% per year. During the initial four-month experimental period, approximately 10% of the air was lost and a corresponding 10% was injected during a one-time operation in December 1991. Previous systems, such as Bios-3 and the Breadboard Facility, have had leak rates in the range of 1–10% per day (Knott 1990).

The ecosystems of Biosphere 2 are housed in two wings (Figure 2) that share water and air circulation. Screens prevent flying insects and other animals from moving between the anthropogenic biome wing (agricultural and human habitat) and the wilderness biome wing (rainforest, savannah, desert, marsh, and ocean). Like the global biosphere, Biosphere 2 is composed of various biomes with differing soils, climate regimes, and vegetation. Five areas patterned on a tropical to subtropical climatic gradient are housed in the eastern wing, which is 165 meters long and 30–44 meters wide.

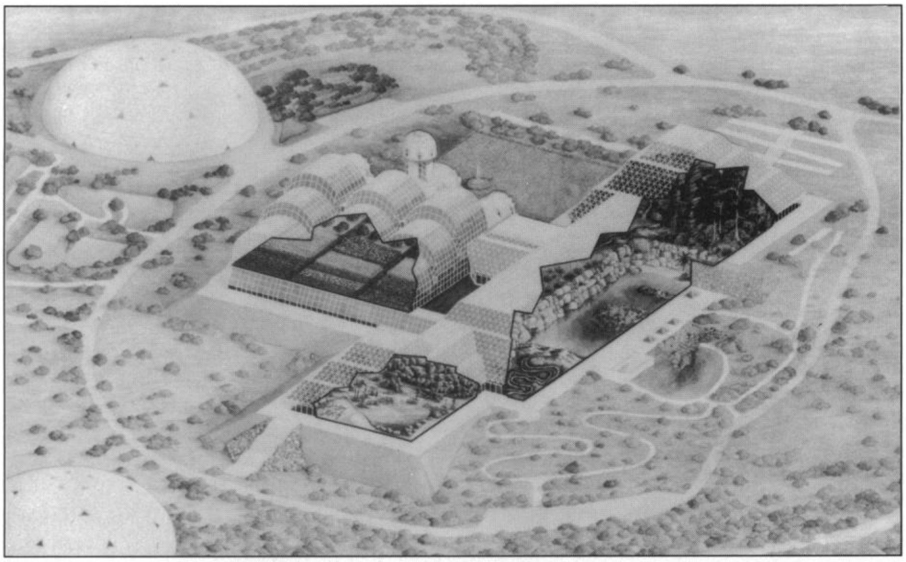
A tropical rainforest with neotropical, predominantly Amazonian species, occupies the humid end of the gradient. Rainforest habitats include cloud forest, flood plain, stream, and lowland rainforest. Along three sides of the rainforest, a dense growth of plants in the order Zingiberales (the ginger belt) protects the inner rainforest from strong lateral sunlight; a bamboo planting between the rainforest and the ocean is intended to reduce salt aerosol intrusion. The lowland rainforest has a quick-growing canopy of light-loving trees such as *Cecropia peltata*, white popinac (*Leuceana glauca*), and horseradish tree (*Moringa oleifera*). These trees probably will gradually be replaced by the slower-growing trees more characteristic of the mature rainforest such as mahogany (*Swietenia macrophylla*), rubber trees (*Hevea brasiliensis*), kapok (*Ceiba pentandra*), tree ferns, and palms. There are more than 300 species of higher plants in the Biosphere 2 rainforest, with initial biomass less than 10% of that expected at full growth. Thus, the succession can be studied.

Biomass increased approximately 50% in the rainforest from the time it was planted in November 1990 until it was resurveyed in July 1991 (Petersen et al. 1992). Since closure, the canopy structure has continued to develop rapidly, with some *Leuceana* trees now 12–18 meters tall requiring pruning back from the frame. Occasional treefall occurs, allowing faster growth of previously shaded trees, analogous to what occurs under natural rainforest conditions. The ginger belt also has developed vigorously, performing its role of sidelight screen. The crew has replaced understory plantings to overcome soil trampling and plant loss occasioned by construction activities.

A savannah with species from Australia, South America, Africa, and Florida occupies the central terrestrial corridor. Habitats within the savannah include a gallery forest (with African acacia trees), two seasonally flooded ponds (billabongs), a small stream (modeled on a Florida Everglades stream), and a grassland with 35 grass species, as well as associated legumes and shrubs. The major grass herbivore is the leopard tortoise (*Geochelone pardalis*). An ecotone modeled on the thornscrub areas of Sonora, Mexico, and Malagasy separates the savannah from the desert biome. Since closure, a number of grasses have spread by stoloniferous growth, especially para grass (*Brachiaria mutica*), Rhodes grass (*Chloris guyana*), and *Paspalum conjugatum*, whereas Vasey grass *(Paspalum urvillei)* has increased through seedling establishment. These are C4 plants, and their accelerating dominance within Biosphere 2 in the first ten months contrasts with predictions made on the basis of the previously measured, competitive disadvantage of C4 photosynthesis under low light and elevated carbon dioxide levels (Ehleringer 1978).

A coastal fog desert area patterned on those found in the Vizcaino region of Baja California and similar climates in other continents occupies the lower elevation, south end of the eastern wing. Its habitats include bajada, sand dune, granite boulders and slope, clay pan, and salt flat. The vegetation includes columnar species such as boojum tree (*Fouquieria columnaris*), cardon cactus (*Pachycereus pringlei*), and datil (*Yucca valida*) and shrubs such as cholla cactus (*Opuntia molesta*, *Opuntia prolifera*), century plants (*Agave* spp.), creosote bush (*Larrea tridentata*), and lavender (*Lavandula pubescens*).

The Biosphere 2 desert was designed to simulate a community transitional between open desert scrub with a diverse life-form spectrum and a denser, more uniform coastal scrub, approximating an ecotone between Vizcaino desert scrub (Turner and Brown 1982) and Vizcaino coastal succulent scrub (Westman 1983). Since closure, dense canopies have formed in some sites, suppressing smaller plants, especially succulents, to form a vegetation more closely resembling coastal sage scrub, drought-deciduous thicket, or batha (Zohary 1962). This change was associated with the management strategy of watering the desert biome to keep it actively growing for an extended period (November 1991 through March 1992) to assist in lowering atmospheric carbon dioxide concentrations during the first winter. Unlike other parts of the desert biome, the sand dune has shown a dramatic increase in perennial grass cover, dominated by *Eragrostis lehmanniana* and *Sporobolus contractus*. This increase conforms with a general tendency for sandy soils to favor perennial grasses in arid climates (Shmida and Burgess 1988).



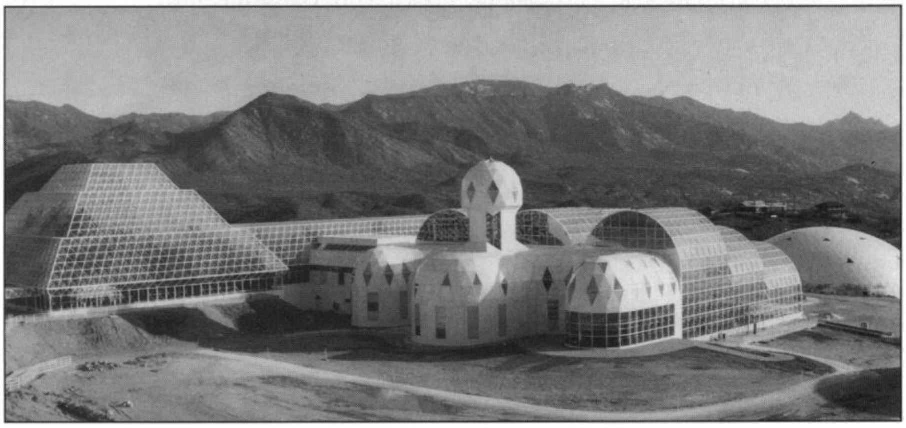


Figure 2. a. The areas within Biosphere 2. Isometric drawing by Elizabeth Dawson. **b.** Biosphere 2, human habitat in foreground. Photo by Gill Kenney.

A salt- and freshwater marsh modeled on the wetlands of the Florida Everglades has six habitats on a gradient from freshwater to progressively more saline water. The freshwater marsh includes Everglades cattails (*Typha* spp.) and other tall emergent plants (*Canna* spp.); the oligohaline marsh is dominated by a variety of grass species such as wild millet (*Setaria geniculata*) and large ferns such as *Acrofticbum* spp.); the salt marsh has *Spartina* grasses and fiddler crabs (*Uca* spp.); the black mangrove area has *Avicennia germinans*; an oyster bay area; and a red mangrove (*Rhizophora mangle*) marsh area adjoins the ocean ecosystem. The mangroves have grown rapidly, with many individuals now more than 5 meters tall, and there has been new seedling establishment since closure. Under the lower light (there is 40–50% of ambient light after transmission through the glass and structural shading) and reduced wind (the air handling system generally produces only mild air movements), the mangroves and some other plants have become somewhat leggy and etiolated, with markedly greater internode lengths than occur in nature. Observations of the marsh biome phenology and biomass are assisted by Matt Finn of the Smithsonian Institution.

A coral reef ecosystem modeled on the Caribbean coral reef biome is part of the ocean biome. There are four habitats: beach with edible coconut palms (*Cocos nucifera*) and Everglades beach community grasses and other halophytes; a shallow lagoon area with sea grasses (*Thallasia testudinum*), conch (*Strombus gigas*), and red-banded shrimp (*Stenopus hispidus*); a coral reef collected off the Yucatan Peninsula and from the Bahamas with soft and hard corals, including sea fans (*Gorgonia* spp.) and brain corals (*Diploria* spp.); and a sandy bottomed eight-meter-deep ocean. More than 40 species of coral and a similar number of fish species were introduced.

Since closure, overall reef system health has been good, with only one known loss of a coral species, represented by one individual. Tissue death of some individuals and a few cases of white band disease were noted in some brain corals commencing in early spring of 1992. Algae scrubbers designed for maintenance of required low nutrient levels in the ocean (Adey and Loveland 1991) have been supplemented and eventually may be replaced by protein-skimmers fabricated from fiberglass tubing inside Biosphere 2, which remove dissolved organic molecules and acids by aeration. Coral health and vitality is being tracked through analysis of underwater videos by Phil Dustan of the College of Charleston in Charleston, South Carolina, who has developed color photographic techniques for long-term monitoring of natural coral reefs (Dustan 1985, Dustan and Halas 1987). Studies conducted by Donald Spoon of Georgetown University in the year between creation of the ocean system and closure indicated that a high diversity of microbiota was being maintained (Spoon and Alling 1991). Robert Howarth of Cornell University is collaborating on studies of Biosphere 2 ocean chemistry.

Vertebrates in Biosphere 2 include the prosimian bushbaby (*G. garnetii*) from Africa, Australian blue-tongued skink (*Tiliqua scindoides*), prehensile skink (*Corucia zebrata*), and more than a dozen frog and lizard species. There are approximately 150 insect species, including several dozen species raised in the Biosphere 2 insectary. The insects provide a variety of functions, including that of enhancing food webs. Mapping and calculation of food chains and striving for redundancy through alternate pathways to offset species extinctions was important preparatory research in the design of Biosphere 2.

Since closure, there has been a sharp reduction in the number of flying insects and loss of two bird species: the emerald hummingbird (*Amazilla amazilla*) and the red-cheeked cordon bleu finch (*Uraeginthus bengalus*).

Table 2. Energetics of Biosphere 2.

Energy	Peak	Average
Electrical	1000 KW	800 KW
(External support)	2000 KW	1200 KW
Heating	11×10^6 kj/hr	5×10^6 kj/hr
Cooling	35×10^6 kj/hr	20×10^6 kj/hr
Solar flux	27×10^6 kj/hr	6×10^6 kj/hr
Photosynthetic active radiation	$30\ e \cdot m^{-2} \cdot day^{-1}$	$20\ e \cdot m^{-2} \cdot day^{-1}$

Cactus wrens (*Campylorhynchus brunneicapillus*) and rock wrens (*Salpinctes obsoletus*) were evicted before full closure, but a single curve-billed thrasher (*Toxostoma curvirostre*) and several English sparrows (*Passer domesticus*) eluded capture. The thrasher has since died, but English sparrows are still resident in both wilderness and agriculture areas. A baby galago was born, and fighting between the dominant and subordinate adult female galago has required caging of the latter to avoid serious injury.

Viability of small plant and animal populations is being studied through several genetic assays. The assays were developed after a workshop in September 1991, convened by Stephen O'Brien of the National Cancer Institute and Michael Clegg of the University of California–Riverside, to explore the research potential of Biosphere 2. Biosphere 2 offers an opportunity to examine in detail founder effects on small populations. With limited breeding pools, to what extent will genetic bottlenecks develop and what strategies can be used to increase genetic variation to mitigate the problem? A few initial studies are under way and longer-term studies are being developed.

Since initial installation of the ecosystems, humans have intervened, assuming the role of keystone predators (Paine 1966) to control weed and pest outbreaks and to maintain biodiversity. Lobsters and large parrotfish have been culled in the ocean when food chain stress was evident. Without deliberate keystone predators (humans), biological diversity would have been reduced during the initial operating period of Biosphere 2.

The western wing of Biosphere 2 includes the two human-dominated biomes. One is an agricultural area (including rice paddies, which also rear fish; fodder plants; tropical orchard; chickens; goats; pigs; and vegetable and grain systems) that provides a complete diet for the eight-person crew (Glenn et al. 1990) and supports the recycling systems for the human and domestic animal waste products and inedible biomass. The agricultural system operates without biocides, and it employs a host of beneficial insects as well as sprays (e.g., soap, sulfur, and *Bacillus thuringensis*) for controlling pests and diseases.

The Biosphere 2 agricultural system is soil-based to minimize consumables (e.g., chemical fertilizers or hydroponic nutrient chemicals) and make return of nutrients more feasible than in a hydroponic system. Moreover, the soil was designed to function as a soilbed reactor to reduce trace gas buildups.

At closure, there was an initial supply of some three months' food previously grown in Biosphere 2. The goal is to supply the crew's nutrition during this initial two-year closure and leave a similar amount for the next crew. Waste recycling is accomplished by composting animal wastes and inedible crop residues and through use of an aquatic plant lagoon system for human wastewater treatment. The remaining nutrients in the water in these lagoons go back into the fields during crop irrigation. A separate system that condenses water from the atmosphere supplies potable water.

Since closure, the agricultural system has provided, on average, 90% of the nutritional needs for the crew of eight, supplemented by food previously grown in Biosphere 2. The diet is calorie-restricted (2000 calories/day on average through the first ten months, gradually rising to the current 2200 calories), thus facilitating the first study of humans in a nutrient-dense, low-calorie regime, which has been extensively studied in laboratory animals (Weindruch and Walford 1988). Responses in the Biosphere 2 crew include weight loss, a sizable decrease in blood cholesterol level (from an average of approximately 195 to approximately 125), reduction of blood pressure and white blood cell count, and other physiologic changes previously noted in laboratory experiments with mice, which also showed a slowing of aging processes and marked prolongation of lifespan (Walford et. al. 1992).

A human habitat with living and working areas for the crew adjoins the agricultural area. Plant photosynthesis is powered by ambient sunlight, but technical systems, including those required for thermal control, are powered by external co-generating natural gas electrical generators (Table 2). Heated, chilled, or evaporatively cooled water passes through Biosphere 2 isolated in closed-loop piping into air-handler units, where energy exchange for thermal control takes place (Dempster 1988, 1989). Evaporative water towers outside Biosphere 2 dissipate rejected heat. The air handlers can circulate air up to 600 m^3/sec throughout Biosphere 2. Velocities range from 5 m^3/sec at a few localized discharge ducts to nearly imperceptible in many areas. Temperature parameters have been set in accordance with normal tolerances of the biomes, generally ranging from 15 to 35 °C and kept at comfortable levels in the human habitat (Dempster 1989).

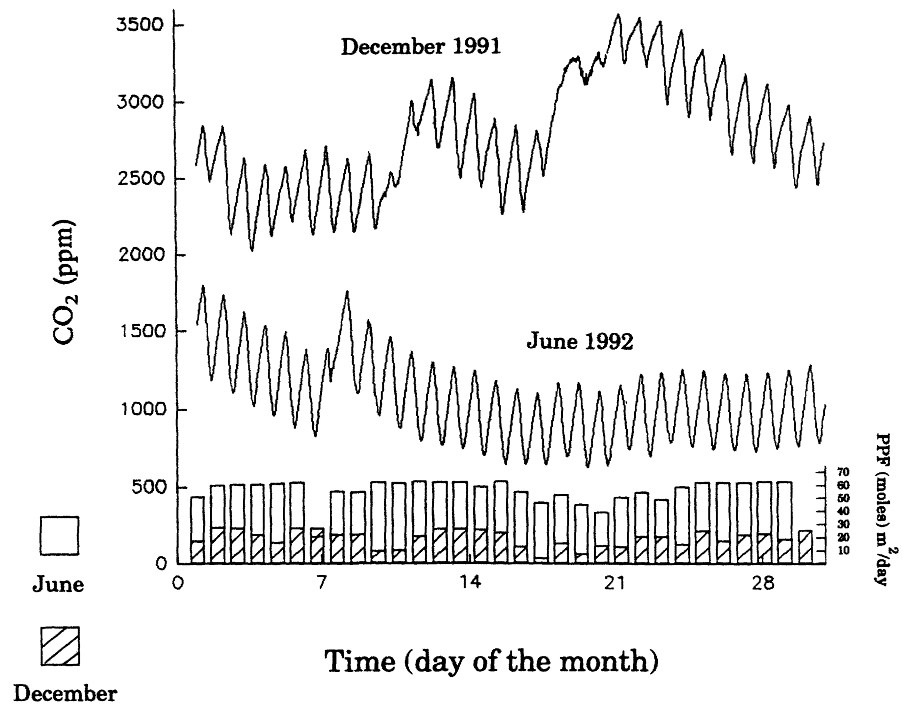


Figure 3. Atmospheric CO_2 dynamics within Biosphere 2 during December 1991 and June 1992. The overlapped bar values given for photosynthetic photon flux (PPF) are for total daily incident sunlight at the project site; internal light levels vary depending on location in the facility but average 40–50% of ambient sunlight. The large diurnal and seasonal fluxes are the result of the smaller atmospheric and oceanic buffers and denser concentrations of plant and soil biota than are found in Earth's atmosphere. Cloudy days have a large impact on CO_2 dynamics, and normal day/night variations are large, because photosynthesis dominates during daylight hours, drawing CO_2 levels sharply down, and soil and plant respiration at night lead to large rises.

Dynamics of carbon dioxide and oxygen since closure

Rates of biogeochemical cycles are greatly accelerated in small, closed ecological systems because there is an absence of the large reservoir buffers available in Earth's biosphere and because the ratios of living material to inorganic substrate are much greater. Even in a facility as large as Biosphere 2, the mean residence time for atmospheric CO_2 is only 1–4 days, whereas in Earth's atmosphere it is approximately 3 years (Schlesinger 1991).

To comprehend these profound scale differences, it is useful to point out that a 1500 ppm concentration of CO_2 in the Biosphere 2 atmosphere (approximately four times Earth's CO_2 concentration) equals approximately 100 kg of carbon. This amount is dwarfed by the quantities of carbon in living biomass and organic carbon in its soils.

Biosphere 2 has an approximate 100:1 ratio of carbon in living biomass to atmospheric carbon, whereas the earth's ratio is 1:1. Organic carbon in Biosphere 2 soils has a more than 5000:1 ratio with atmospheric carbon, compared to approximately 2:1 in Earth's biosphere (Bolin and Cook 1983).

Calculation and modeling of these dynamics, plus experience with atmospheric cycling in the Biosphere 2 test module, led project designers to anticipate the strong diurnal and seasonal CO_2 fluxes that have been seen in Biosphere 2 (Figure 3). Daily CO_2 can fluctuate as much as 700–800 ppm, although the fluctuation is usually 500–600 ppm and sometimes slightly lower, because the life system is active photosynthetically during the day and respiration is dominant during the night. During December 1991, when photosynthetic photon flux (PPF, sunlight available for photosynthesis) reached its lowest annual value of 16.8 moles · m^{-2} · day^{-1}, Biosphere 2 averaged 2466 ppm of atmospheric CO_2. By contrast, during June 1992, Biosphere 2 recorded its lowest monthly average for CO_2 of 1060 ppm at the highest daily PPF, 53.7 moles · m^{-2} · day^{-1}, since closure.

Several options have been pursued to manage CO_2 levels inside Biosphere 2 within acceptable limits for ecosystem and human health, including a CO_2 precipitator and recycling chemical system, adjustments of ecosystem growing periods, and buffering of ocean waters. This challenge is anticipated to be greatest during the early years of operation because living plant biomass is projected to increase to as much as five times the initial amount and because respiration of the new soils was probably greatest at the beginning of the enclosed experiment.

To help buffer the system during winter low-light months in its first years as biomass increases in Biosphere 2, a CO_2 recycling system was installed that first sequesters CO_2 into calcium carbonate by the reactions:

$$CO_2 + 2NaOH \longrightarrow Na_2CO_3 + H_2O$$

$$Na_2CO_3 + Ca(OH)_2 \longrightarrow CaCO_3 + 2NaOH$$

The second reaction returns the NaOH for reuse in the first. Subsequent heating of the $CaCO_3$ to 950 °C in a furnace will dissociate

$$CaCO_3 \longrightarrow CaO + CO_2$$

returning the CO_2 to the atmosphere and regenerating CaO which, with water, provides $Ca(OH)_2$ to be reused in the second reaction. Failure of the furnace inside Biosphere 2 has thus far prevented the scheduled return of the CO_2 into the atmosphere. During the first fall and winter, some 53,880 moles (equivalent to 9450 ppm) of CO_2 was deposited as $CaCO_3$ through the periodic use of this physicochemical CO_2 system between October 1991 and January 1992. This deposition also indirectly accounts for a nearly 1% decrease in atmospheric oxygen through oxidation of organic carbon and subsequent sequestering in calcium carbonate. By contrast, the addition of 10% ambient air in December 1991 to compensate for leak rate tests made a small impact—a momentary reduction of CO_2 levels by 200 ppm, approximately one-third of normal diurnal variations.

In addition, management of life systems was undertaken during the critical low-light season. Biosphere 2 had been originally designed with the savannah active during spring and summer months and the desert active during the winter. Reduced sunlight would slow savannah grass growth during winter months, and some habitats, for example thornscrub, should be kept dry during late winter or spring to simulate their typical moisture regimes and to accommodate daylength responses of some species. It was expected that during winter the ratio of soil respiration to canopy photosynthesis would increase in the savannah. The desert biome was designed to have its peak growth during cooler months to help offset possible CO_2 efflux from the savannah.

Understanding how vegetation responses could be tailored to atmospheric regulation has been a major goal; observing how plant phenologies are correlated with temperature and soil moisture is an important research activity. But during this first winter, rainfall was continued in the savannah to keep it actively growing, and the desert was brought out of dormancy, by irrigating earlier, to assist in uptake of anticipated high CO_2 levels. Nighttime temperatures were reduced to minimize soil and plant respiration, savannah grasses, marsh cattails, and ginger-belt plants in the rainforest were pruned to stimulate rapid regrowth while the cut biomass was stored to slow its decomposition. Compost-making was largely suspended in the agricultural area from November to January to minimize its release of CO_2, and the crew made additional plantings to promote understory development in the ecosystems and use additional incident light.

Another area of potential concern because of the elevated CO_2 levels was the ocean coral reef. Because atmospheric CO_2 comes to equilibrium with the dissolved CO_2 in ocean water, it was expected that rising CO_2 would tend to increase the acidity of marine water. To buffer the expected influx of CO_2 in the ocean, additions of sodium carbonate and bicarbonate have been made on several occasions since closure with the goal of maintaining pH above 7.7.

Oxygen dynamics have proved surprising. Since closure, oxygen has declined from Earth's ambient level of 20.94% to slightly lower than 14.5% (middle of January 1993). On medical recommendation, when this level was reached, pure oxygen was injected into Biosphere 2 over a period of several weeks to increase its atmospheric concentration to 19%. Much of the decline occurred during the first four months after closure. By the end of January 1992, it had reached 18%. Since the end of April 1992, the decline in oxygen has been fairly linear at a rate of approximately 0.25% per month. Investigations of oxygen dynamics are being carried out in a collaborative study headed by William Dempster and Wallace Broecker of the Lamont-Doherty Laboratory, using several methods, including studying the distribution of oxygen isotopes in Biosphere 2.

Biosphere 2 offers an opportunity to do sophisticated modeling of biogeochemical cycles and to test them experimentally. SBV researchers and Kristina Vogt, Daniel Vogt, and Tom Siccama of the Yale University School of Forestry and Environmental Studies have begun collaborative work aimed at tracking the carbon budget of Biosphere 2—the distribution of carbon at initial closure throughout the system and studying its dynamics over time (Petersen et. al. 1992).

Biosphere 2 also provides an opportunity to accurately measure the metabolism of a complex ecosystem for an extended period of time. Prior determinations of terrestrial ecosystem metabolism have usually involved short-term measurements taken on small components of ecosystems (Golley et. al. 1962, McKellar 1977, Odum and Jordan 1970). Currently, carbon cycle modeling is under way with a group that includes Daniel Botkin of the University of California, Santa Barbara, and Robert Frye of the University of Arizona. Nutrient cycles (e.g., nitrogen, phosphorus, and sulfur) are to be added as total systems models of Biosphere 2 are developed.

Research opportunities

Significant research opportunities are offered by a facility like Biosphere 2, which has been designed for a lifetime of 100 years. Because the system is so tightly closed, it permits tracking of major nutrient cycles through ecosystems, atmosphere, and water systems. No specific replicate for the entire experiment could be made, given its large size and cost, but comparative work can be done with similar ecosystems outside Biosphere 2.

The greenhouses in BRDC have been transformed into areas housing ecosystems paralleling those inside Biosphere 2, with many of the same species. In addition, comparative studies can be conducted on a sequential basis as daily, seasonal, and yearly cycles recur in Biosphere 2. The small atmospheric reservoir (compared to Earth's biosphere) greatly enhances its sensitivity to biogeochemical processes. The previously noted changes in oxygen and CO_2, as well as variations in biogenic trace gases, are examples of opportunities for investigation.

The Biosphere 2 test module can also provide subsystem analogues to Biosphere 2. In the test module experiments, there has been an examination of the consequences of key variables such as ratios of biogeochemical reservoirs, effects of soil disturbance, human and plant adaptation to lower light/elevated CO_2, and dynamics of trace gases.

The study of the component microbiomes in Biosphere 2 should advance knowledge of ecosystem function, restoration ecology strategies, biological dynamics of atmospheric gases such as methane and CO_2, biological effects of the exclusion of UV light, response of ecosystems to different light regimes than those of their natural habitat, and viability of small plant and animal populations. The Biosphere 2 agricultural system may be of greatest applicability to tropical, developing countries that at present are food impoverished, least able to afford high-input agriculture, and which have great problems with waste recycling from human populations. The detailed study of these integrated cropping techniques, waste recycling systems, air purification, and biological control of pests is especially timely in light of the reexamination of alternative agriculture systems called for in the recent National Resource Council report (NAS 1989).

Biomes (called in the Russian tradition bio[geo]coenoses) play a key role in the structural organization of the biosphere. The Russian biologist M. M. Kamshilov recognized their "ability to withstand various external effects...[due to their] homeostasis or buffering power. There seems to be a direct relationship between the complexity of [a] biocoenosis and its ability to withstand diverse external effects...greater resistance not only to intrusion of individual species from different ecosystems but also to abiotic factors....The stability of the biosphere as a whole, and its ability to evolve, depends, to a great extent, on the fact that it is a system of relatively independent biogeocoenoses...[which] compete for habitat, substance and energy provides optimal conditions for the evolution of the biosphere as a whole" (Kamshilov 1976).

In Biosphere 2, one can study the interrelationship of biomic areas and how their interplay affects overall system balances. The relation of diversity to stability and resilience in ecosystems is an issue that generates considerable controversy and theoretical interest. Biosphere 2 offers the opportunity to study changing species demography and community dominance in response to environmental perturbations in both terrestrial and aquatic ecosystems.

Summary: a new type of research facility

A new type of research tool has been developed with the first microbiosphere, Biosphere 2. It has operated successfully since its initial closure in September 1991, maintaining the overall health of its diversity of internal ecosystems and a large proportion of its species. Biogeochemical cycles are operating, at least on the short term, with strong daily and seasonal fluxes of atmospheric CO_2, although atmospheric oxygen is showing a decline in concentration. Overall system biomass continues to increase, with woodland canopies rapidly developing in rainforest, savannah, and marsh. The Biosphere 2 desert biome has shown a community dominance shift to subshrubs/annuals since closure.

Such a human-made biosphere may offer unique opportunities for advancing understanding of fundamental components and processes of Earth's biosphere. These opportunities include tracking in great detail the dynamics of land and water ecosystems and of biotic interaction with the atmosphere, evaluating human impact on complex ecologies, and developing technologies compatible with sustaining the biosphere. Studying such a biospheric system may provide a unique testing ground for evaluation of its self-regulatory functions. This study is intended to help evaluate the hypothesis that a biosphere regulates its environment by means of an ecological feedback process involving its microbial, plant, fungal, and animal communities. SBV is exploring a number of collaborative studies with researchers to further enrich the scientific information the facility can yield. The long-term design of the project offers wide scope for potential investigations, including those that would commence after the first two-year closure.[2]

Though human-made biospheres such as Biosphere 2 differ in significant ways from the global system, the intensive study of their nutrient cycles may shed great insight into the key mechanisms of global ecology. Indeed, one problem in developing a science of the biosphere is that Earth's biosphere is unique. Because there are, as yet, no other natural biospheres known for comparison, synthetic biospheres open prospects for comparative biospherics. These studies should deepen understanding of the nature of the global biosphere just as comparative planetology has sharpened understanding of Earth as a planet.

[2]SBV is receptive to research proposals for topics of mutual interest from private, university, or federal laboratories.

References cited

Adey, W. H., and K. Loveland. 1991. *Dynamic Aquaria: Building Living Ecosystems.* Academic Press, New York.

Allen, J. 1991. *Biosphere 2: The Human Experiment.* Penguin Books, New York.

Allen, J., and M. Nelson. 1988. *Space Biospheres.* Synergetic Press, Oracle, AZ.

Alling, A., L. Leigh, T. MacCallum, and N. Alvarez-Romo. 1990. Biosphere 2 test module experimentation program. Pages 23–32 in M. Nelson and G. A. Soffen, eds. *Biological Life Support Technologies.* Synergetic Press, Oracle, AZ.

Alling, A., M. Nelson, L. Leigh, R. Frye, N. Alvarez-Romo, T. MacCallum, and J. Allen. In press. Experiments on the closed ecological system in the Biosphere 2 test module. Appendix chapter in R. J. Beyers and H. T. Odum, eds. *Ecological Microcosms.* Springer-Verlag, New York.

Andre, M., F. Cotte, A. Gerbaud, D. Massimino, J. Massimino, and C. Richaud. 1989. Effect of CO_2 and O_2 on development and fructification of wheat in closed systems. Pages 17–28 in R. D. MacElroy, T. W. Tibbitts, B. G. Thompson and T. Volk, eds. *Natural and Artificial Ecosystems.* Pergamon Press, Oxford, UK.

Bohn, H. L. 1972. Soil adsorption of air pollutants. *J. Environ. Qual.* 1: 372–377

Bohn, H. L., and R. K. Bohn. 1986. Soil bed scrubbing of fugitive gas releases. *J. Environ. Sci. Health Part A Environ. Sci. Eng.* 21: 561–569.

Bolin, B., and R. B. Cook, eds. 1983. *The Major Biogeochemical Cycles and their Interactions.* John Wiley & Sons, New York.

Bubenheim, D. 1990. CELSS research and development program. Pages 53–59 in M. Nelson and G. A. Soffen, eds. *Biological Life Support Systems.* Synergetic Press, Oracle, AZ.

Bugbee, B., and O. Monje. 1992. The limits of crop productivity. *BioScience* 42: 494–502.

Carlson, D. A., and C. P. Leiser. 1966. Soil beds for the control of sewage odors. *J. Water Pollut. Control Fed.* 38: 829–840.

Cooke, G. D. 1971. Ecology of space travel. Pages 498–509 in E. P. Odum. *Fundamentals of Ecology.* Saunders College Publ., Philadelphia.

Corey, K. A., and R. M. Wheeler. 1992. Gas exchange in NASA's biomass production chamber. *BioScience* 42: 503–509.

Dempster, W. F. 1988. Biosphere II: design of a closed manned terrestrial ecosystem. SAE Technical Paper Series #881096, 18th Intersociety Conference on Environmental Systems. SAE, Warrendale, PA.

______. 1989. Biosphere II: technical overview of a manned closed ecological system. SAE Technical Paper Series #891599, 19th Intersociety Conference on Environmental Systems, SAE, Warrendale, PA.

Dustan, P. 1985. The bio-optics of coral reefs. Pages 189–198 in M. L. Reaka, ed. *The Ecology of Coral Reefs.* NOAA Undersea Research Program, Rockville, MD.

Dustan, P., and J. Halas. 1987. Changes in the reef-coral community of Carysfort reef, Key Largo, Florida, 1974 to 1982. *Coral Reefs* 6: 91–106.

Ehleringer, J. 1978. Implications of quantum yield differences on distribution of C3 and C4 grasses. *Oecologia (Berlin)* 31: 255–267.

Eley, J. H. Jr., and J. Myers. 1964. Study of a photosynthetic gas exchanger: a quantitative repetition of the Priestley experiment. *Texas J. Sci.* 16: 296–333.

Finn, M., and W. H. Adey. 1991. Mesocosms: encapsulated ecosystems on display. *Sea Technol.* 32: 85–88.

Folsome, C. E., and J. A. Hanson. 1986. The emergence of materially closed system ecology. Pages 269–288 in N. Polunin, ed. *Ecosystem Theory and Application.* John Wiley and Sons, New York.

Galston, A. W. 1992. Photosynthesis as a basis for life support on Earth and in space. *BioScience* 42: 490–493.

Glenn, E. P., and R. Frye. 1990. Soil bed reactors as endogenous control systems of CELSS. Pages 41–58 in *Workshop on Artificial Ecological Systems.* Proceedings of a meeting in Marseilles, France, October 1990, sponsored by DARA and CNES. DARA, Berlin.

Glenn, E., C. Clement, P. Brannon, and L. Leigh. 1990. Sustainable food production for a complete diet. *HortScience* 25: 1507–1512.

Golley, F. B., H. T. Odum, and R. F. Wilson. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* 43: 9–19.

Hammer, D., ed. 1989. *Constructed Wetlands for Wastewater Treatment: Municipal, Industrial and Agricultural.* Lewis Publ., Boca Raton, FL.

Hanson, J. 1982. Workshop on closed system ecology. Summary report. Jet Propulsion Laboratory Publication 82-64, Pasadena, CA.

Hodges, C., and R. Frye. 1990. Soil bed reactor work of the Environmental Research Lab of the University of Arizona in support of the Biosphere 2 project. Pages 33–40 in M. Nelson and G. A. Soffen, eds. *Biological Life Support Systems.* Synergetic Press, Oracle, AZ.

Kamshilov, M. M. 1976. *The Evolution of the Biosphere.* Mir Publ., Moscow, Russia.

Knott, W. M. 1990. The CELSS Breadboard Project: plant production. Pages 47–52 in M. Nelson and G. A. Soffen, eds. *Biological Life Support Systems.* Synergetic Press, Oracle, AZ.

Lebedev, K. A., and R. V. Petrov. 1971. Immunological problems of closed environments and gnotobiology. JPRS 54331, National Technical Information Service, Springfield, VA.

Leigh, L., K. Fitzsimmons, M. Norem, and D. Stumpf. 1987. An introduction to the intensive agriculture biome of Biosphere II. Pages 76–81 in B. Faughnan and G. Maryniak, eds. *Space Manufacturing 6: Nonterrestrial Resources.* Biosciences and Space Engineering, AIAA, Washington, DC.

MacElroy, R. D., J. Tremor, D. T. Smernoff, W. Knott, and R. P. Prince. 1987. A review of recent activities in the NASA CELSS program. Pages 53–58 in R. D. MacElroy and D. T. Smernoff, eds. *Controlled Ecological Life Support Systems.* Pergamon Press, Oxford, UK.

McKellar, H. N. 1977. Metabolism and model of an estuarine bay ecosystem affected by a coastal power plant. *Ecol. Modell.* 3: 85–118.

Myers, J. 1963. Space biology: ecological aspects; introductory remarks. *Am. Biol. Teach.* 25: 409–411.

National Academy of Sciences (NAS). 1989. *Alternative Agriculture.* Committee on the Role of Alternative Farming Methods in Modern Production Agriculture, Board on Agriculture, National Research Council, National Academy Press, Washington, DC.

National Aeronautics and Space Administration (NASA). 1968. *Bioregenerative Systems.* Proceedings of a conference in Washington, DC, 15–16 November 1966. NASA-SP-165, Science and Technical Information Division, OTA, NASA, Washington, DC.

Nelson, M. 1989. The biotechnology of space biospheres. Pages 185–200 in G. Malacinski, ed. *Fundamentals of Space Biology.* Springer-Verlag, New York.

Nelson, M., L. Leigh, A. Alling, T. MacCallum, J. Allen, and N. Alvarez-Romo. 1991a. Biosphere 2 test module: a ground-based sunlight-driven prototype of a closed ecological system. Pages 151–158 in R. D. MacElroy, M. M. Averner, T. W. Tibbitts, B. B. Bugbee, G. Horneck, and E. H. Dunlop, eds. *Natural and Artificial Ecosystems.* Pergamon Press, Oxford, UK.

Nelson, M., J. P. Allen and W. Dempster. 1991b. Biosphere 2, prototype project for a permanent and evolving life system for a Mars base. Pages 211–218 in R. D. MacElroy, M. M. Averner, T. W. Tibbitts, B. B. Bugbee, G. Horneck, and E. H. Dunlop, eds. *Natural and Artificial Ecosystems.* Pergamon Press, Oxford, UK.

Nitta, K. 1987. An overview of Japanese CELSS research activities in controlled ecological life support systems. Pages 95–104 in R. D. MacElroy and D. T. Smernoff, eds. *COSPAR Advances in Space Research.* vol. 7(4). Pergamon Press, Oxford, UK.

Odum, H. T. 1963. Limits of remote ecosystems containing man. *Am. Biol. Teach.* 25: 429–443.

______. 1983. *Systems Ecology.* Wiley-Interscience, New York.

Odum, H. T., and C. F. Jordan. 1970. Metabolism and evapotranspiration of the lower forest in a giant plastic cylinder. In H. T. Odum and R. F. Pigeon, eds. *A Tropical Rainforest.* National Technical Information Service, Technical Information Extension Service, Washington, DC.

Paine, R. T. 1966. Food web diversity and species diversity. *Am. Nat.* 100: 65–75.

Petersen, J., A. Haberstock, T. Siccama, K. Vogt, D. Vogt, and B. Tusting. 1992. The making of Biosphere 2: frontiers in synthetic ecology. *Restoration and Management Notes* 10: 158–168.

Salisbury, F., B. Bugbee, and D. Bubenheim. 1987. Wheat production in controlled environments. Pages 123–132 in R. D. MacElroy and D. T. Smernoff, eds. *COSPAR Advances in Space Research.* vol. 7(4). Pergamon Press, Oxford, UK.

Schlesinger, W. H. 1991. *Biogeochemistry: An Analysis of Global Change.* Academic Press, New York.

Schwartzkopf, S. H. 1992. Design of a controlled ecological life support system. *BioScience* 42: 526–535.

Shepelev, Yevgeny Y. 1972. Biological life support systems. Pages 274–308 in M. Calvin and O. Gazenko, eds. *Foundations of Space Biology and Medicine.* vol. 3. Academy of Sciences USSR, Moscow, Russia, and NASA, Washington, DC.

Shmida, A. and T. L. Burgess. 1988. Plant growth form strategies and vegetative types in arid environments. Pages 211–241 in N. J. A. Werger, P. J. M. van der Aart, H. J. During, and J. A. Verhoeven, eds. *Plant Form and Vegetation Structure.* S. P. Academic Publ., The Hague, Netherlands.

Skoog, A. I. 1987. Progress in European CELSS activities in controlled ecological life support systems. Pages 7–10 in R. D. MacElroy and D. T. Smernoff, eds. *COSPAR Advances in Space Research.* vol. 7(4). Pergamon Press, Oxford, UK

Spoon, D., and A. Alling. 1991. Preclosure survey of aquatic microbiota of Biosphere 2. Paper presented at the Third East Coast Conference on Protozoa, Mount Vernon College, VA, 21–22 May 1991.

Terskov, I. A., et al. 1979. *Closed System: Man-Higher Plants (Four Month Experiment).* Translation of Nauka Press, Siberian Branch, Novocibirsk, publication. NASA-TM-76452, Washington, DC.

Turner, R. M., and D. E. Brown. 1982. Sonoran desertscrub. *Desert Plants* 4: 181–221.

Walford, R. L., S. B. Harris, and M. W. Gunion. 1992. The calorically restricted low-fat nutrient-dense diet in Biosphere 2 significantly lowers blood glucose, total leukocyte count, cholesterol, and blood pressure in humans. *Proc. Natl. Acad. Sci.* 89: 11,533–11,537.

Weindruch, R., and R. L. Walford. 1988. *The Retardation of Aging and Disease by Dietary Restriction.* Charles C. Thomas, New York.

Westman, W. E. 1983. Xeric Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. *Vegetation* 32: 3–19.

Wolverton, B. C. 1987. Aquatic plants and wastewater treatment (an overview). Pages 3–15 in K. Reddy and W. H. Smith, eds. *Aquatic Plants for Water Treatment and Resource Recovery.* Magnolia Publ., Orlando, FL.

Vernadsky, V. I. 1986. *The Biosphere.* Synergetic Press, Oracle, AZ.

Zohary, J. 1962. *Plant Life of Palestine.* Ronald Press, New York.