ELSEVIER

Ecological Engineering 13 (1999) 65–93

ECOLOGICAL ENGINEERING

Tropical rainforest biome of Biosphere 2: Structure, composition and results of the first 2 years of operation

Linda S. Leigh [b,*], Tony Burgess [a], Bruno D.V. Marino [a,c], Yong Dan Wei [a]

[a] *Biosphere 2 Center, Inc. P.O. Box 689, Oracle, AZ 85623, USA*
[b] *Systems Ecology and Energy Analysis Program, Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL 32611, USA*
[c] *Department of Earth and Planetary Sciences, Harvard University, 20 Oxford St., Cambridge, MA 02138, USA*

Received 27 August 1997; received in revised form 12 January 1998; accepted 20 January 1998

Abstract

The tropical rainforest biome in the Biosphere 2 mesocosm was managed with rainfall and temperature conditions to simulate a natural rainforest typical of the new world tropics. The establishment of the biome was based on the introduction of excessive numbers of species allowing self-organization of an ecologically unique rainforest. Over 282 species of plants from rainforest areas were planted within the topographically diverse rainforest biome (area of 1900 m^2, volume of 35000 m^3), just before the Biosphere 2 closure in 1991. Approximately 61% of these species survived when counted in 1993, representing a plant species richness reduction to 172 species in 0.19 hectare. Rank order graphs show that a high diversity community resulted not unlike insular rainforests. The plants of the rainforest mesocosm, however, grew under anomalous conditions of soil (amended desert grassland soil), atmospheric composition (CO_2 up to 4500 ppm by volume (ppmv)) and rainwater composition (high salinity and nutrients). Stem growth rates of a dominant canopy tree, *Cecropia*, were up to four times higher but had reduced diameter at breast height compared to natural counterparts. Human intervention in plant succession was also an important factor in shaping the ecology of the rainforest biome of Biosphere 2.

Keywords: Biosphere 2; Rainforest; Mesocosm

* Corresponding author. Present address: Drylands Institute, 2509 North Campbell Ave, #405, Tucson, AZ 85719, USA. Tel.: +1 520 825-6755; fax: +1 520 8180911; e-mail: lleigh@nervm.nerdc.ufl.edu

0925-8574/99/$ - see front matter
PII S0925-8574(98)00092-5

1. Introduction

The tropical rainforest biome in Biosphere 2 was designed to be functionally analogous to planetary rainforests. One of five ecological systems of Biosphere 2 collectively called the ‘wilderness’ (Fig. 1a, b), it was built and its climate managed to emulate the general structure and function of a new world tropical rainforest. There were four design goals of the rainforest: (1) to produce a sustainable system that would help manage the atmosphere of Biosphere 2; (2) to contribute to the diversity of the Biosphere 2 laboratory; (3) to provide occasional food and other extras (cacao, flavors, medicines) to the inhabitants, and (4) to provide an attractive landscape for the inhabitants. The rainforest was excessively species-packed for self-organization over time under minimal influence of human management, with the expectation that new ecosystems would emerge representing ‘signatures’ of interactions among the physical properties of the system and the biota, including human residents. It was hypothesized that the rainforest structure would change over time from that of a recently cleared ecosystem to a complex primary forest (Prance, 1991). Details of other areas in the wilderness and the agricultural area are given by Petersen et al. (1992), Finn (1996), Silverstone and Nelson (1996), Atkinson et al. (1999) and Marino et al. (1999).

The conceptual design for the rainforest biome began in 1985; plant collections were made from 1986–1991; planting began in 1989; and a total survey and mapping of every plant was completed prior to the first material closure, which lasted from September, 1991 through September, 1993. A total re-survey of plants

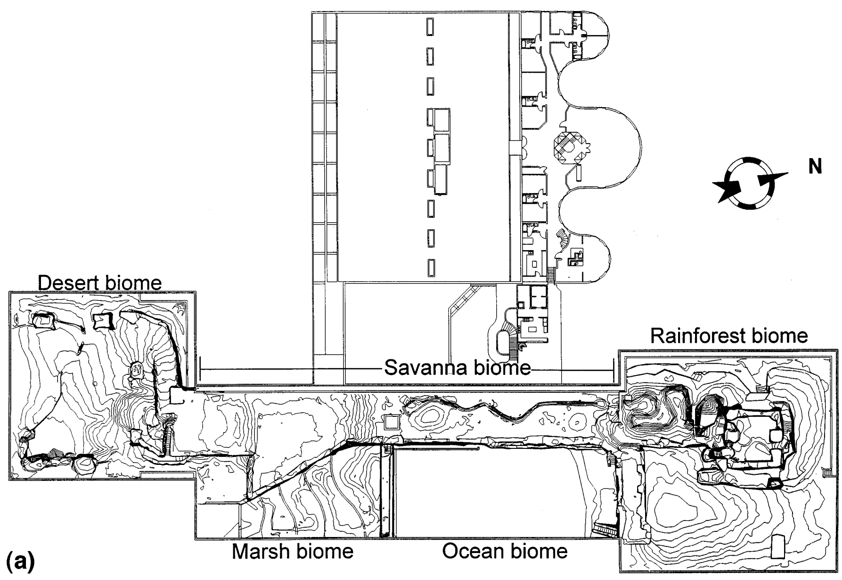

Fig. 1. Biosphere 2 layout showing (a) wilderness systems and (b) Detailed layout of rainforest biome showing habitats.

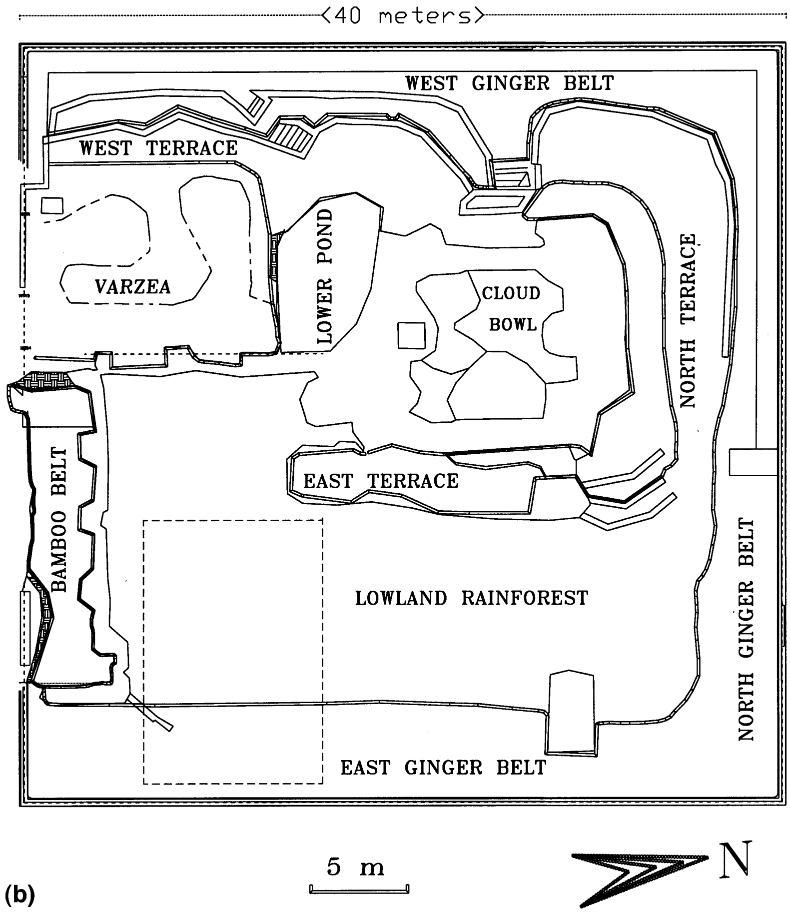

Fig. 1. (*Continued*)

in the rainforest was made after the 2 year closure and again in 1996. This paper describes the rainforest area, its habitats, the species planted, and the characteristics of the ecosystem that developed.

2. System description

A tropical rainforest climate was created by control of rain, temperature and humidity so as to support plant species from various humid tropical regions. The climate differed from a planetary tropical rainforest in that the annual changes in day length were much greater in Biosphere 2, and temperature and atmospheric CO_2 ranges were greater on both a daily and annual basis (Fig. 2). Eight separate habitats were delineated in the rainforest biome. Although Amazonian plant species dominated, species from other rainforests of the world were also planted. The soils were created from local desert grassland materials.

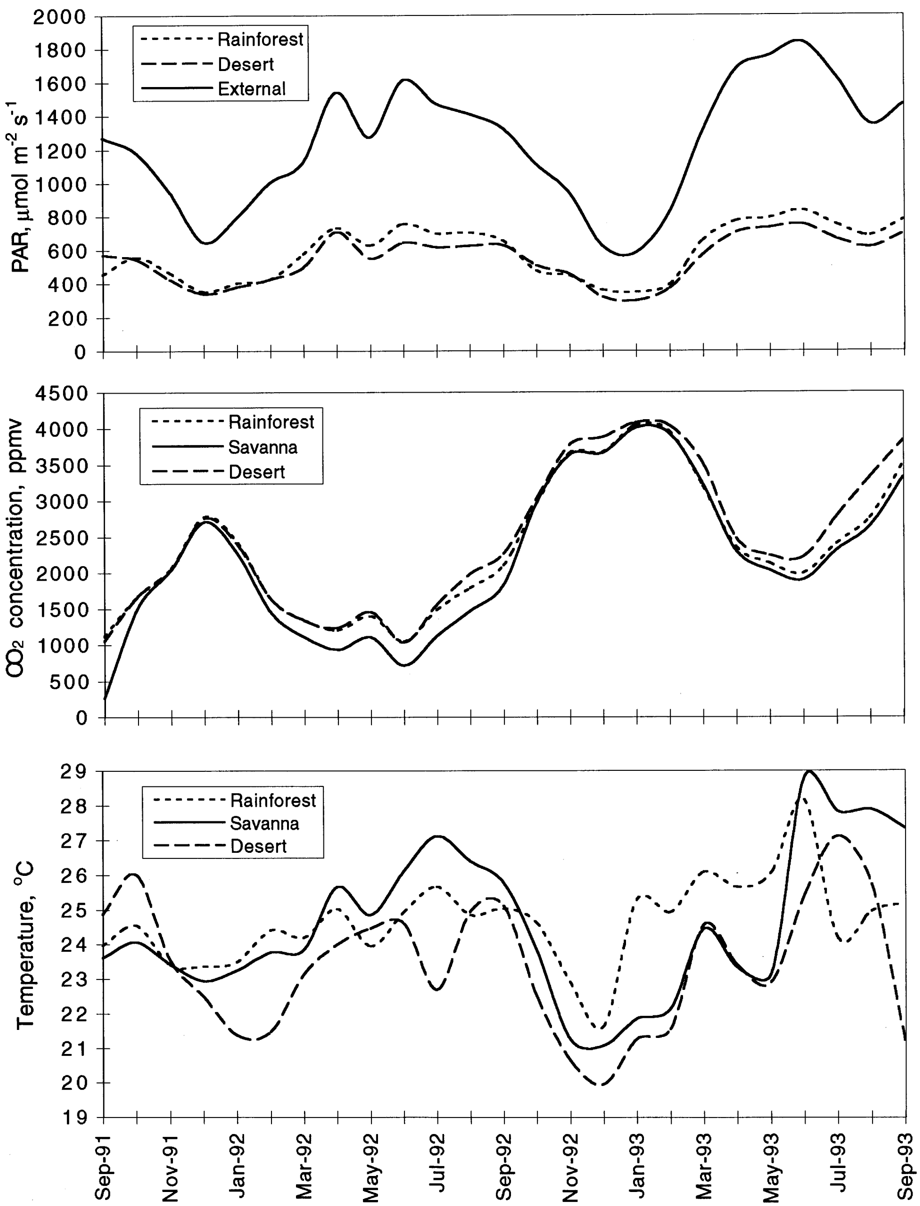

Fig. 2. Climatology for the wilderness biomes showing monthly averages of temperature, light, and CO_2 concentrations.

The rainforest biome shared its atmosphere and water with the other wilderness biomes, the agricultural area and human habitat. Temperatures, rainfall regimes and humidities were maintained locally within each biome (Fig. 2), whereas the atmospheric chemistry was a global phenomenon within Biosphere 2.

The interaction of the rainforest biome with the atmosphere of the larger scale system has been modelled by Engel and Odum (1999).

The footprint of the rainforest biome is 1900 m^2. The highest point of the pyramidal glass structure enclosing it was 22 m, measured from the soil surface in the lowland rainforest. The total volume of the rainforest is about 35000 m^3 (Dempster 1993), nearly 17% of the total Biosphere 2 volume.

2.1. Biome design and assembly

The design objectives for the rainforest soils were to produce a functional equivalent of tropical rainforest soils, to allow soils to develop in place, and to provide a horticulturally adequate substrate. Over time, the formation of humic and fulvic acids was expected to reduce the soil pH, similar to a planetary rainforest. The soils were designed to be deep enough to allow expansion of roots needed to stabilize aboveground canopy expansion and to contain elements necessary for 100 years of growth. Soils for the rainforest biome were obtained locally.

The soils were constructed in two parts, topsoil and subsoil. The subsoil was a layer of uniform composition but variable thickness that was built up in the shape of the final topography. The subsoil selected was a rocky, pebbly, very sandy loam extracted from a local quarry. The thickness of the subsoil layer in the rainforest varied from 0 to about 5 m. Criteria for subsoil selection were good downward percolation of water after repeated wettings, radon emissions not greater than background crustal emissions, low heavy metal content, price-competitiveness, and proximity to the Biosphere (Scarborough, 1994).

The topsoils were imported and/or blended into horticultural specifications and applied on top of the subsoil. The topsoil used for each habitat of the rainforest consisted of a mix of a local desert grassland silt loam soil with organic and/or gravelly sand amendments. The organic amendment was compost made from various organic materials, including forest mulch, alfalfa hay, cotton gin trash, and manure. Four different combinations of these materials formed the major volume of topsoil in the rainforest (800 m^3), with small amounts of three additional mixes (15 m^3) used for more specialized habitats. Topsoil types in the rainforest biome roughly follow the habitat boundaries (Fig. 1b). Depending upon the materials mixed and loading methods used, the degree of homogeneity obtained in the topsoils varied considerably. The clay fraction tended to stay aggregated as cohesive 'peds' of variable size (1–13 cm diameter). Thus these soils tended to have 'pockets' of pure clay soil, mixed with sandy or rocky pockets (Scarborough, 1994). To increase species richness in the soil biota, inocula from local sources were introduced in the form of litter and humus from 'wild' ecosystems, along with earthworms.

Starting in 1986, plants, seeds, and other propagules were grown in greenhouses located near Biosphere 2. Plant accessions were acquired from botanic gardens, plant nurseries and private collections; and from field collections in Puerto Rico, Belize, Venezuela and Brazil. Permits were acquired for exportation from countries of origin and for importation to the USA and Arizona; state and federal quarantine and inspection protocols were followed. Following soils placement in the rainforest biome, plant accessions were transplanted from greenhouses into Biosphere 2. Each plant was mapped by standard survey methods (Thompson 1992), using different symbols to represent plant growth forms (Fig. 3). Measurements such as basal diameter, crown width, and stem length were made. Each plant was assigned a unique number, and data on location, geographic origin, size, and phenology were recorded. Thus a history of every plant in the rainforest biome could be tracked through time. Of the initial 1833 plants, 1292 were identified in 282 species, 235 genera, and 99 families. To date, not all of the plants in the rainforest have been identified to species nor all identifications verified; specimens are maintained in herbarium cabinets on location at the Biosphere 2 Center, and some are in the herbarium of New York Botanical Garden.

The plant survey was completed prior to the first material closure, which lasted from September, 1991 through September, 1993. A total re-survey of plants in the rainforest was made after the 2 year closure and repeated in 1996.

2.2. Rainforest biome habitats

The initial design (Prance, 1991) created eight habitats within the rainforest biome. The habitats were named lowland rainforest, ginger belt, várzea, cloud bowl, surface aquatic systems, bamboo belt, mountain terraces, and cliff faces (Fig. 1b). Fig. 4 shows a sectional diagram across several of the habitats. Since no biotic introductions were to be made during the study period after the initial closure in 1991, initial planting had to include all of the species for succession and mature development. In contrast, an unconfined rainforest experiences continuing immigration during successional changes. A much larger number of species was planted than could survive, letting extinction occur as a natural process in the system while making every effort to ensure the survival of certain key species.

The challenge was to consider diversity across scales of population, community, and ecosystem as well as functional diversity. Each habitat had a different suite of species, including canopy plants, ground cover, shrubs and intermediate level life forms, as well as epiphytes and vines. Initial plantings of fast colonizers and secondary forest species (*Clitoria racemosa*, *Carica* spp., *Leucaena* spp., *Cecropia schreberiana*) provided shade and structure to the emerging and more characteristic primary rainforest species.

2.2.1. Lowland rainforest

The concave topography of the lowland rainforest area centered in the southeast quadrant of the rainforest allowed trees to reach a height sufficient for a layered canopy. The topsoil mixed for the lowland rainforest was 50% loam, 25% gravelly

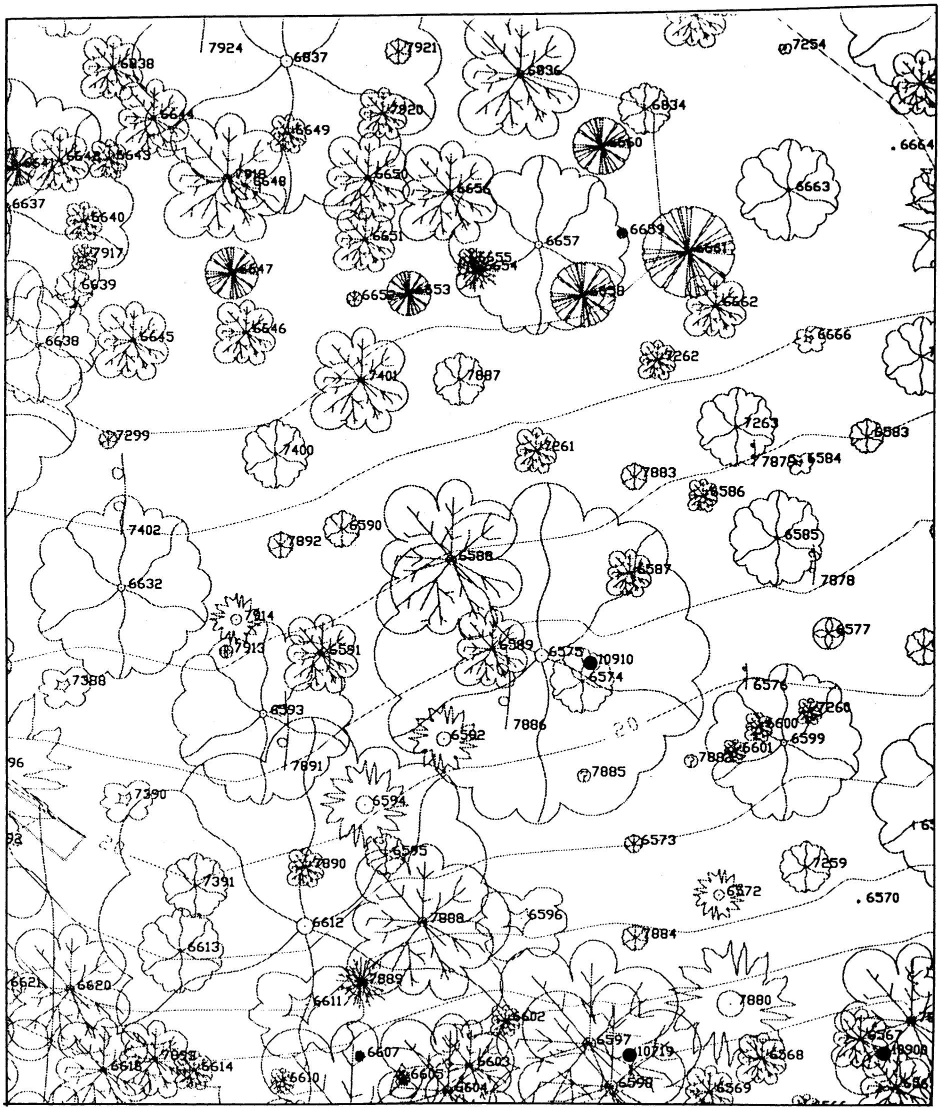

Fig. 3. Plant map of a section of the rainforest biome. Numbers refer to survey points used to track individual plants. A rectangle in the lower left of Fig. 1(b) locates the map within the rainforest.

sand, and 25% coarse organic material. After the first 2 years of closure, the species forming the canopy in the lowland rainforest were *Ceiba pentandra*, *Hura crepitans*, *Cecropia schreberiana*, *Arenga pinnata*, and *Clitoria racemosa*. There were lianas, epiphytes, and many broad leaved trees.

2.2.2. Ginger belt

The ginger belt surrounded the rainforest on all sides bounded by glass, excluding only the south edge which abutted the beach and the upper savanna (Fig. 1b). Its purpose was to shield the forest understory from excessive light. Studies on isolated patches of planetary rainforests show that the typical understory vegetation is altered for some distance beyond the forest edge in part by light penetration (Bierregaard et al., 1992). Thus this peripheral dense belt of vegetation was planted to filter the light and allow the interior of the forest to develop the shaded conditions that would foster an understory more typical of extensive rainforests.

Ginger belt topsoils were a mix of 80% loam and 20% compost. Soil depth was about 60–90 cm on the northwest and west side where no subsoil underlies the topsoil, and 1 m on the northeast, east and southeast sides, where it was underlain by a subsoil of variable thickness. The ginger belt ranged from about 1 to 4 m wide. Plants in the Order Zingiberales dominated the ginger belt. Plants in these genera were most abundant: *Musa*, *Heliconia*, *Alpinia*, *Strelitzia*, and *Costus*.

2.2.3. Várzea

The várzea habitat was designed to resemble a forest that is seasonally flooded. It featured a tightly meandering stream that ran from the pond to the edge of the savanna biome. The stream course was made by first filling the regular topsoil layers to the specified level; then excavating the stream courses; and then lining them with concrete and thick PVC. The várzea topsoil was 60% loam and 40% coarse peat. The várzea was not flooded during the study period. It was planted with *Phytolacca dioica*, *Pachira aquatica*, *Pterocarpus indicus*, and palms.

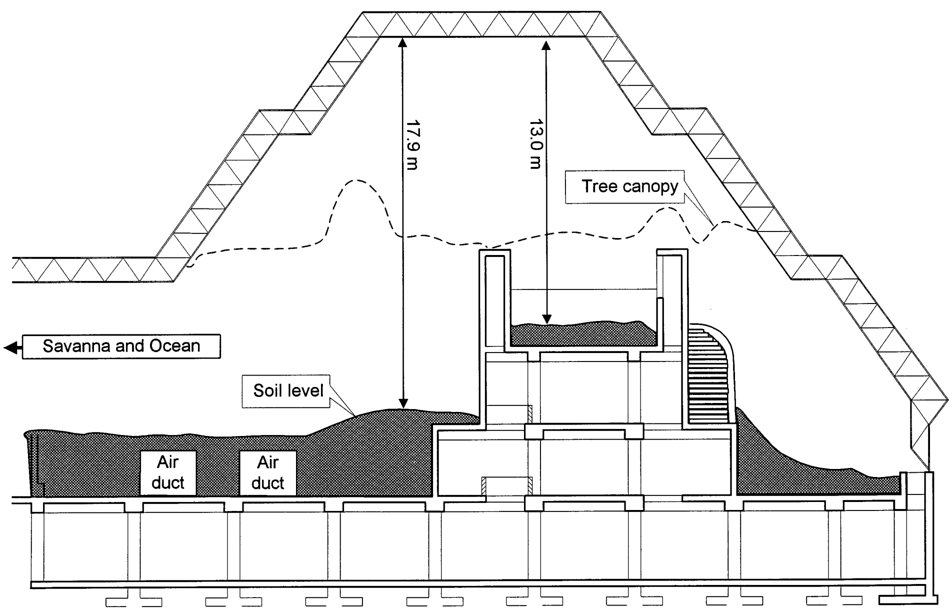

Fig. 4. South to north cross-section of the rainforest biome with structural dimensions.

2.2.4. Cloud bowl

Suggested by the tepui sandstone formation from eastern Venezuela, the central mountain 'cloud bowl' was managed as a cooler and more humid microclimate. The soil was less than 1 m deep. It was a mix of 40% Canadian sphagnum moss, 50% coarse peat moss, and 10% loam. Soil in the planter pockets extended all the way to the bottom of the mountain. Bryophytes, carnivorous plants, and aquatic plants were introduced to this habitat.

2.2.5. Surface aquatic habitats

Surface aquatic habitats in the rainforest biome were hydrologically connected. The moss seep and upper pond in the cloud bowl spilled over a cut in the edge of the cloud bowl, creating a waterfall. The waterfall poured into a splash pool, which overflowed into the larger, lower pond and then into the várzea stream (Fig. 1b). At the bottom of the stream water flowed over a weir into a sump, from which the water was pumped back to the lower pond. Another pump moved water back to the cloud bowl. The water systems were underlain with a thick PVC liner beneath a concrete layer.

2.2.6. Bamboo belt

A bamboo belt was constructed along the south edge of the rainforest to baffle any airborne salt particles from the forest interior. Soils of the bamboo belt were 50% loam, 25% gravelly sand, and 25% coarse organic material, varying between 30–90 cm deep and laying over air delivery plenums. There was no subsoil beneath the topsoil in the bamboo belt. *Bambusa multiplex*, *B. tuldoides* and other species of bamboo formed the major structure of this habitat.

2.2.7. Mountain terraces

The mountain terraces skirted the rainforest mountain on the east, north, and west sides, extending to the west side of the lower pond. Flagstone walls were in place around the periphery of the terraces, separating them from the ginger belt habitat on the west and north sides and from the lowland rainforest habitat on the east. The flagstone was placed during construction to prevent soil from eroding down the somewhat steep grade from the mountain to the ginger belt. The topsoil mix for the mountain terraces was 50% loam, 25% gravelly sand, and 25% coarse organic material. The soils to the west and north of the mountain were about 0.3–3 m deep, and those east of the mountain were about 0.3–6 m deep. The plants on the terraces included *Carica papaya*, *Clitoria racemosa*, *Coffea arabica*, *Carludovica palmata*, *Inga* sp., *Hibiscus rosa-sinensis*, *Strelitzia nicolai*, and *Manihot esculenta*.

The cliff faces of the mountain had pockets of soil to support vines and other plants that were to cloak its surface. Plants from the Araceae, Passifloraceae, and Vitaceae families and ferns were planted in the cliff face planter pockets. Rhyolite pumice chunks were blended at 10–15% of the total soil volumes. The high porosity of the pumice provides water-holding capacity and releases trace nutrients as it weathers.

3. Operation and management

3.1. Hydrologic cycle

The three terrestrial wilderness biomes of Biosphere 2—desert, tropical savanna, and tropical rainforest—vary substantially with regard to their ecological responses to hydrologic factors, and water management within each system varied accordingly. In contrast to the desert and savanna biomes, the rainforest plants were active continuously; dormancy was not part of the yearly cycle. In the tropical rainforest biome, water applied as rainfall flowed through and exited the soil profile throughout the year. Fig. 5 shows the water flows and reservoirs of the rainforest biome.

Rain was distributed to much of the rainforest biome through overhead sprinklers mounted in the space frame; other areas were irrigated with ground sprinklers or a drip irrigation system. Water vapor evaporated from soil, rain, or surface waters, transpired from plants, or delivered through a misting system could subsequently have been condensed from the air using the air handlers located in the rainforest basement. Water condensate that collected on the inside surface of the windows during late autumn, winter and early spring was an additional, seasonal source of condensate. Water from both of these sources was re-used in the wilderness biomes, and was one of the sources of rainwater.

The major water reservoirs in the rainforest were atmosphere (humidity), soil, water storage tanks, the surface aquatic habitats, and plants and other biota. The major water flows among reservoirs in the rainforest were rainfall and irrigation, subsoil drainage, reverse osmosis system flow, condensation, mist, evaporation, root uptake, transpiration, and diffusion as water vapor to other areas (Fig. 5).

Some of the rain and irrigation water percolated through the entire soil profile. This subsoil water, carrying substances leached from the soils, was collected and stored in a storage tank for future use. The subsoil water in the biosphere was reused either as-is or after removal of dissolved solids by a reverse osmosis system. The remaining rain and irrigation water was either held in the soil pores by matric forces, taken up by plants and retained, or diffused back into the atmosphere via evaporation and transpiration. The average monthly relative humidity was over 65% year-round in the rainforest biome, with daily minima above 50%.

3.2. Air handling system and climate control

Seven air handlers in the rainforest basement were operated to regulate temperatures, extract condensate from the air, and to create air movement. Temperature was controlled by a heat exchange between a water coil and circulating air in the handler. Three temperature classes of water originating externally to the Biosphere were circulated in the coils of the system: heating water, cooling tower water, and chilled water which reached the lowest temperatures. The rate of the air flow through an air handler was controlled by opening or closing an 'econodisc' located inside each of the air handlers. Though normally controlled remotely, they were

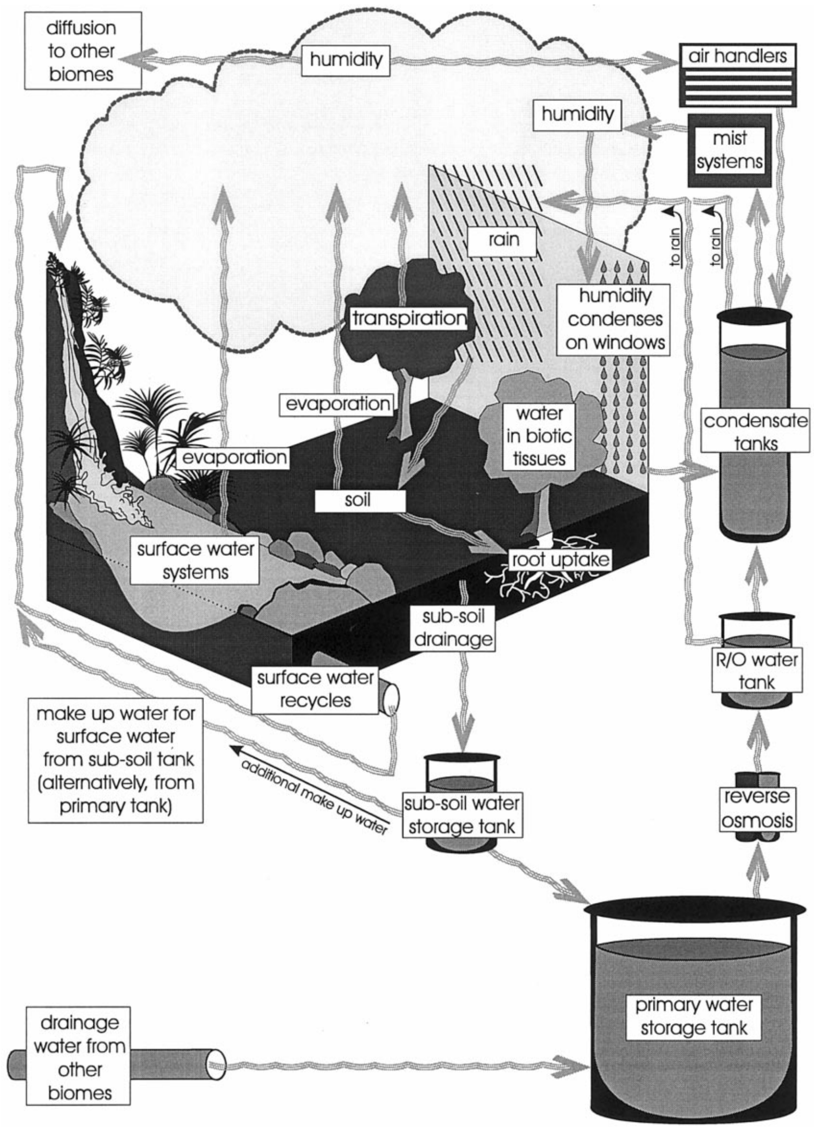

Fig. 5. Diagram of the rainforest hydrologic cycle as a subsystem of Biosphere 2.

also controlled manually from inside the air handler. Air from the air handlers circulated through a system of plenums, ducts and openings from the basement into the rainforest. The air returned through gratings on the west and northwest periphery of the rainforest, where it entered the basement and was again pulled through the air handlers and over the heating coils. The daily maximum and minimum operating temperatures and relative humidity values for the first 2 years of operation are shown in Fig. 6.

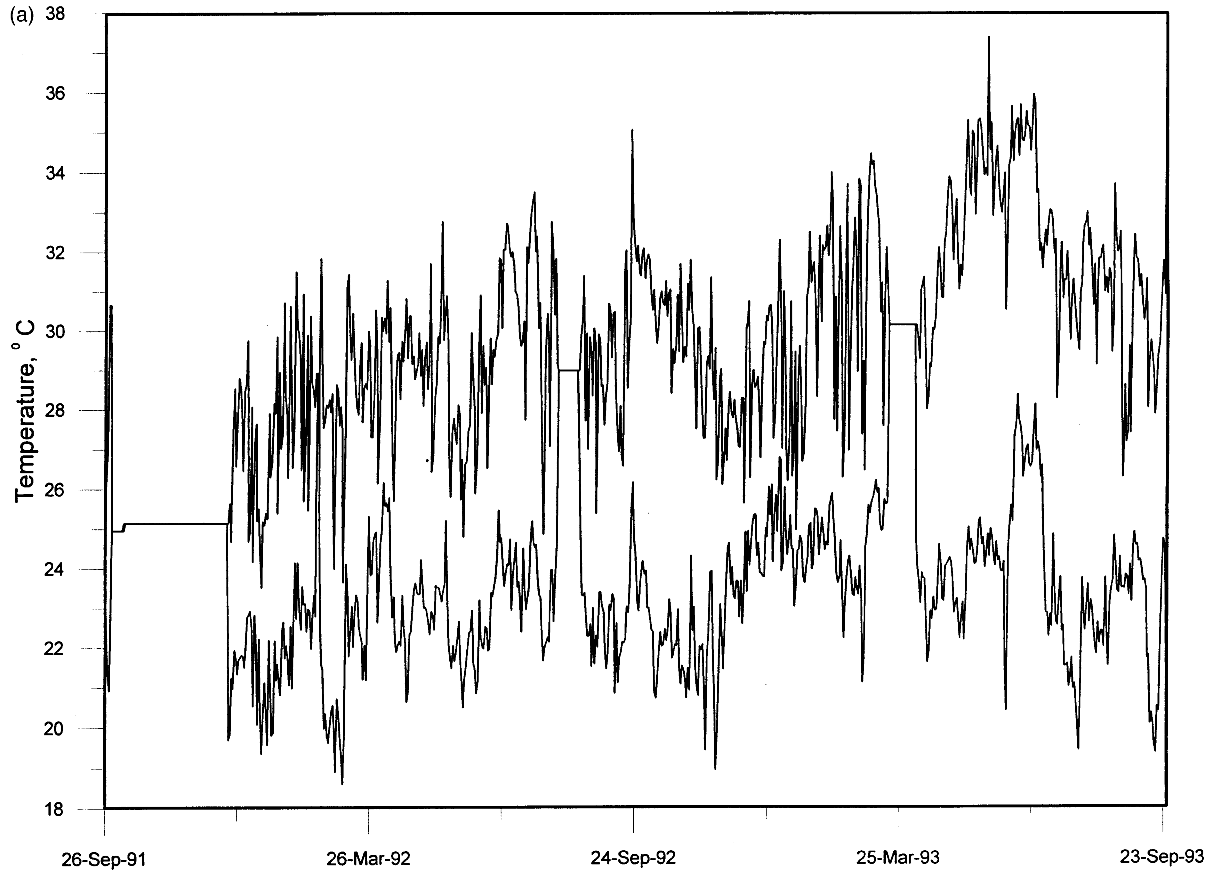

Fig. 6. Daily minimum and maximum (a) temperature and (b) relative humidity in the rainforest biome based on histories from single sensors. Flat lines are periods with no sensor data.

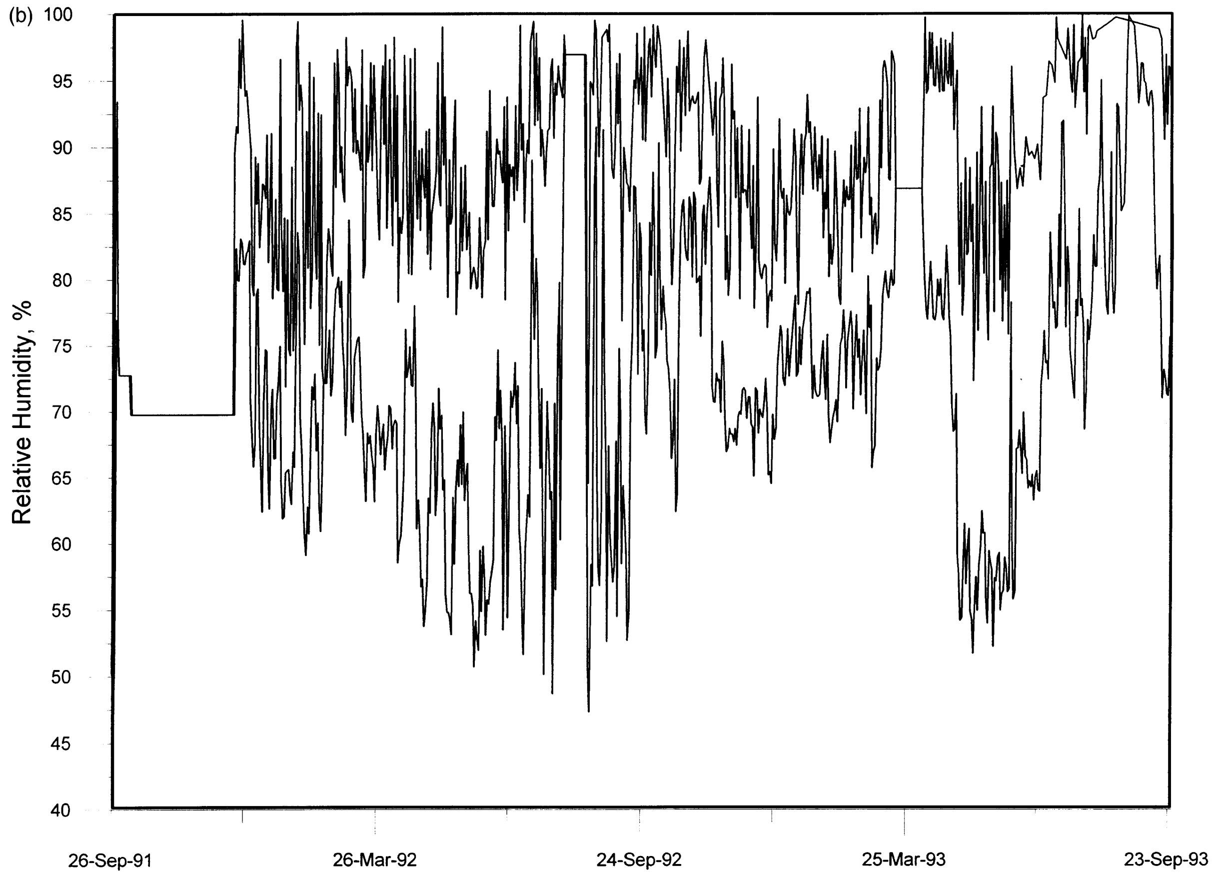

Fig. 6. (*Continued*)

3.3. Human intervention

During the 2 year closure of the system (1991–1993) certain herbaceous plants in the rainforest biome were extensively managed for two reasons. The first reason was to arrest primary succession. Early successional species were pruned so that the later successional species would survive. These selective harvests decreased the competitive advantage of high net-producers (e.g. *Ipomoea* and *Passiflora* vines) over species important for the long-term structure of the rainforest, particularly the larger trees. The second reason for management was an attempt to increase sequestration of CO_2 and to increase O_2 production. High levels of CO_2 were thought to be decreasing the ocean pH, and oxygen concentrations eventually decreased to the point of affecting the health of the human inhabitants. To meet these goals, plants were propagated in an attempt to cover vertical surfaces with photosynthetic biomass. Growth of high net-producing species (*Ipomoea* sp., *Passiflora edulis*) and herbaceous plant species in the circumferential ginger belt habitat was encouraged by judicious pruning in areas where they would not overwhelm other species, given the constraint of diversity maintenance.

The pruned biomass was removed from the rainforest, dried to retard respiration, and stacked in the basement. A small percentage of the material was used for fodder for domestic livestock. Of the three terrestrial wilderness biomes, the rainforest required the most time to manage for regulation of the atmosphere, while seeking to maintain species richness.

4. Results

4.1. Soils

An inspection of rainforest soils in December, 1993, showed differentiation with depth from the surface, and in particular, extensive soil homogenization of the upper 30–40 cm mostly due to earthworm activity. At the same time, soil pits revealed discontinuous soils next to plant sites where the original soils of the potted plants had not yet been mixed with surrounding soils (Scott, 1994). Average percent carbon and nitrogen ranged from about 3 to 2.3%, and from about 0.3 to 0.2%, respectively, for the upper and lower strata of soil pits in the rainforest (Scott, 1994). Recent analyses of the rainforest soils based on two pedons (1995, G. Kelly, personal communication), suggest that carbon and nitrogen content for the soils has decreased to about 2, and 0.1%, respectively, additional analyses are needed to confirm these trends. Based on flux measurements made in 1995 using static chambers, the rainforest soils were the largest source of N_2O among all the biomes within Biosphere 2. Values from a variety of locations ranged from 0.5 E-2 to 2.0 E-2 μmol m^{-2} s^{-1} (Mohapatra and Marino, report on file).

4.2. Flora

Table 1 lists all plant species and the number of individuals per species in 1991 and 1993. In the 1991 inventory, 1833 individual plants were recorded. By 1993, a total of 829 (45%) of the original plants were still alive. Of the original plants, 1292 were recorded to the level of species, representing 282 species in 99 families. In the 1993 inventory 588 (45%) of the original plants identified to species were alive, representing 172 (61%) of the original species in 59 families. The distribution of plants within species for both inventory years reveals a decline in both numbers of species as well as number of individuals per species (Fig. 7).

A third survey was made in 1996, and 528 (29%) of the original plants were alive. Of the originally identified species, 130 (45%) of the original species remained in 41 families. All or most of the plants in the following groups died during the 2 year study period: Adiantaceae, Aspleniaceae, Blechnaceae, Cyatheaceae, Orchidaceae, Polypodiaceae, Selaginellaceae, and most Bromeliaceae; *Sagittaria*, *Pontederia*, *Typha*, *Nymphaea*, and *Lycopodium*. This included almost all of the herbaceous and tree ferns, fern allies, epiphytes and aquatic plants. The large herbaceous species planted largely in the peripheral ginger belt thrived, spreading clonally. These included the following taxa: Musaceae, Marantaceae, Zingiberaceae, and Strelitziaceae.

Most of the introduced pollinators died by the second year of closure. However, the following plant species set fruit at least once during the 2 years: *Basella alba*, *Bixa orellana*, *Pachira aquatica*, *Carica papaya*, *Canna edulis*, *Coffea arabica*, *Ficus buxifolia*, *Moringa oleifera*, *Leucaena* spp., *Ricinus communis*, *Ipomoea* sp. Seedlings of the following species were observed: *Coffea arabica*, *Pachira aquatica*, *Canna edulis*, and *Leucaena* spp.

4.3. Habitats

By the end of the second year, the lowland rainforest had begun to display the structure of a rainforest, with an almost continuous canopy cover beneath emergent trees. However, a thermocline formed by restricted vertical airflow prevented cooling at higher altitudes and arrested tree growth above about 15 m. Fig. 8(a, b, and c) are photographs of the lowland rainforest during the first planting of trees (1989), during the first total plant survey (1991), and after almost 2 years of closure (1993).

In the ginger belt, many of the smaller species were crowded out or overshaded by the larger. *Phytolacca dioica* grew to dominate the várzea area. In the cloud bowl area few of the bryophytes, carnivorous plants and aquatic plants that were introduced survived, largely due to the higher temperature and lower humidity than parameters that were specified; and time constraints to manage weed competition. The inside of the cloud bowl became dominated with *Cyperus involucratus* and *Ipomoea* sp. In 1992, *Ficus pumila* cuttings and sugar cane were planted in the planter pockets at the top of the mountain, where they survived for several years.

Table 1
Plant species and change in numbers of individuals per species between 1991 and 1993 censuses in the rainforest biome of Biosphere 2

Family	Species	1991	1993
Acanthaceae	*Justicia californica*	1	0
	Justicia pectoralis	2	0
	Ruellia brevifolia	1	0
	Sanchezia speciosa	11	8
	Thunbergia mysorensis	15	2
Adiantaceae	*Adiantum raddianum*	5	0
	Pellaea viridis	1	0
	Polytaenium feei	5	0
	Pteris cretica	5	0
	Pteris longifolia	3	0
Alismataceae	*Sagittaria graminea*	1	0
	Sagittaria lancifolia	1	0
	Sagittaria latifolia	6	0
	Sagittaria rubrum	2	0
Amaryllidaceae	*Eucharis grandiflora*	7	6
	Hymenocallis sp.	1	0
Anacardiaceae	*Anacardium occidentale*	1	1
	Mangifera indica	5	2
	Spondias mombin	1	1
Annonaceae	*Annona muricata*	12	10
	Annona sp.	1	0
	Cananga odorata	1	0
	Rollinia mucosa	2	2
Apiaceae	*Eryngium foetidum*	1	0
	Hydrocotyle asiatica	3	0
	Hydrocotyle verticillata	1	0
Apocynaceae	*Allamanda cathartica*	8	4
	Catharanthus roseus	1	0
	Plumeria rubra	1	1
	Tabernaemontana divaricata	1	0
Aquifoliaceae	*Ilex paraguariensis*	2	1
Araceae	*Acorus calamus*	5	0
	Aglaonema crispum	2	2
	Aglaonema sp.	4	4
	Anthurium digitatum	2	1
	Colocasia antiquorum	9	4
	Colocasia esculenta	1	1
	Colocasia sp.	8	8
	Dieffenbachia sp.	20	19
	Dracunculus canariensis	2	2
	Monstera deliciosa	5	6
	Philodendron angustatum	7	0
	Philodendron erubescens	7	0

Table 1 (Continued)

Family	Species	1991	1993
	Philodendron glanduliferum	1	1
	Philodendron grazielae	3	0
	Philodendron rubens	10	8
	Philodendron selloum	9	7
	Philodendron tripartitum	3	0
	Philodendron wendembi	5	4
	Philodendron sp.	18	11
	Scindapsus aureus	14	8
	Spathiphyllum sp.	2	2
	Syngonium podophyllum	2	1
	Xanthosoma sagittifolium	25	11
	Xanthosoma sp.	1	1
	Zamioculcas zamiifolia	2	2
Arecaceae	*Archontophoenix sp.*	2	2
	Areca catechu	3	1
	Arenga pinnata	5	5
	Arenga sp.	1	1
	Bactris gasipaes	6	4
	Chamaedorea microspadix	9	4
	Chrysalidocarpus lutescens	4	3
	Cocos nucifera	2	2
	Elaeis guineensis	3	2
	Euterpe sp.	8	2
	Jessenia bataua	4	1
	Mauritia flexuosa	7	1
	Oenocarpus bacaba	2	1
	Oenocarpus mapora	2	1
	Phoenix roebelenii	4	2
	Prestoea montana	1	0
	Rhapis excelsa	2	0
	Roystonea regia	3	3
	Socratea exorrhiza	1	1
	Verschaffeltia splendida	5	4
	Wodyetia bifurcata	2	1
Asclepiadaceae	*Asclepias curassavica*	4	0
Asparagaceae	*Asparagus densiflorus*	2	0
Aspleniaceae	*Asplenium daucifolium*	1	0
	Asplenium nidus	5	1
	Diplazium l'herminieri	1	0
Asteraceae	*Baccharis halimifolia*	3	0
Basellaceae	*Basella alba*	4	0
Begoniaceae	*Begonia sp.*	2	0
Bignoniaceae	*Crescentia cujete*	5	3
	Pandorea pandorana	10	3
	Pithecoctenium sp.	5	2
	Spathodea sp.	1	1

Table 1 (Continued)

Family	Species	1991	1993
	Tabebuia heterophylla	3	3
Bixaceae	*Bixa orellana*	8	6
Blechnaceae	*Blechnum brasiliense*	1	0
	Blechnum occidentale	1	0
	Blechnum orientale	2	0
	Doodia caudata	1	0
Bombacaceae	*Ceiba pentandra*	6	6
	Pachira aquatica	16	15
Boraginaceae	*Cordia alliodora*	2	0
Bromeliaceae	*Aechmea orlandiana*	1	0
	Ananas sp.	2	1
	Billbergia pyramidalis	1	1
	Guzmania berteroniana	1	0
	Guzmania monostachia	2	1
	Guzmania sp.	1	1
	Tillandsia sp.	12	0
Buddlejaceae	*Buddleja diversifolia*	1	0
Cactaceae	*Rebutia sp.*	1	0
	Rhipsalis baccifera	5	0
Cannaceae	*Canna edulis*	11	5
	Canna generalis	11	5
	Canna indica	15	9
	Canna sp.	2	0
Capparaceae	*Capparis spinosa*	1	1
Caricaceae	*Carica papaya*	12	9
	Carica pentagona	4	0
	Carica sp.	6	5
Cecropiaceae	*Cecropia schreberiana*	11	6
Clusiaceae	*Clusia sp.*	13	1
	Garcinia tinctoria	1	1
	Garcinia sp.	3	3
Combretaceae	*Buchenavia capitata*	2	0
Commelinaceae	*Callisia fragrans*	14	3
	Commelina tuberosa	2	0
	Dichorisandra thyrsiflora	12	4
	Palisota schweinfurthii	1	0
	Tradescantia pallida	7	0
Convolvulaceae	*Ipomoea batatas*	8	1
Cyatheaceae	*Cnemidaria horrida*	1	0
	Cyathea arborea	3	0
	Cyathea cooperi	11	0
	Cyathea sp.	2	0

Table 1 (Continued)

Family	Species	1991	1993
Cyclanthaceae	*Carludovica palmata*	3	3
Cyperaceae	*Cyperus alternifolius*	20	17
	Cyperus hasperis	1	0
Davalliaceae	*Davallia solida*	1	0
	Nephrolepis exaltata	32	4
Dilleniaceae	*Dillenia indica*	2	0
Dioscoreaceae	*Dioscorea alata*	3	0
	Dioscorea sp.	1	0
Ebenaceae	*Diospyros digyna*	1	1
Elaeagnaceae	*Elaeagnus philippensis*	2	1
Ephedraceae	*Ephedra sp.*	2	0
Equisetaceae	*Equisetum hyemale*	2	0
Euphorbiaceae	*Aleurites moluccana*	7	6
	Breynia disticha	4	4
	Croton sp.	2	1
	Hevea brasiliensis	2	0
	Hura crepitans	3	3
	Manihot esculenta	10	9
	Phyllanthus pulcher	1	1
	Ricinus communis	5	4
Fabaceae	*Bauhinia sp.*	5	0
	Caesalpinia sp.	5	3
	Cajanus cajan	1	0
	Calopogonium mucunoides	13	0
	Canavalia ensiformis	1	0
	Ceratonia siliqua	2	0
	Clitoria racemosa	11	11
	Copaifera sp.	1	0
	Derris elliptica	2	2
	Enterolobium cyclocarpum	2	2
	Hymenaea courbaril	2	1
	Inga feuillei	1	1
	Inga sp.	6	4
	Leucaena glauca	26	19
	Leucaena leucocephala	7	5
	Leucaena sp.	12	12
	Pisum sativum	23	2
	Pterocarpus indicus	5	2
	Schotia latifolia	1	0
	Tamarindus indica	1	0
Gesneriaceae	*Sinningia regina*	1	0
Gnetaceae	*Gnetum sp.*	1	0
Heliconiaceae	*Heliconia bicolor*	10	2

Table 1 (Continued)

Family	Species	1991	1993
	Heliconia bourgaeana	2	2
	Heliconia caribaea	8	5
	Heliconia longiflora	7	5
	Heliconia mutisiana	1	0
	Heliconia psittacorum	12	3
	Heliconia sp.	7	2
Iridaceae	*Dietes bicolor*	1	1
	Dietes grandiflora	1	0
Lamiaceae	*Coleus blumei*	5	0
	Pogostemon cablin	2	0
	Pogostemon heyneanus	4	0
	Salvia divinorum	3	0
Lauraceae	*Cinnamomum zeylanicum*	1	1
	Persea americana	10	3
Lecythidaceae	*Barringtonia asiatica*	2	2
	Couroupita amazonica	1	1
	Couroupita guianensis	1	1
	Lecythis zabucajo	3	1
Lycopodiaceae	*Lycopodium cernuum*	2	0
Lythraceae	*Heimia salicifolia*	11	4
	Heimia sp.	1	1
Malpighiaceae	*Malpighia emarginata*	1	1
	Malpighia glabra	3	1
Malvaceae	*Hibiscus calyphyllus*	3	3
	Hibiscus elatus	2	2
	Hibiscus rosa-sinensis	4	4
Marantaceae	*Calathea gigantea*	2	2
	Calathea louisae	4	1
	Calathea panamensis	3	3
	Calathea violacea	4	2
	Calathea zebrina	1	1
	Maranta sp.	1	1
	Stromanthe amabilis	1	1
	Thalia geniculata	3	2
Marcgraviaceae	*Marcgravia rectiflora*	5	1
	Marcgravia sintenisii	1	1
	Norantea guianensis	1	0
Marsileaceae	*Marsilea mutica*	1	0
Melastomataceae	*Tibouchina interomalla*	2	0
Meliaceae	*Cedrela odorata*	1	1
	Cedrela sp.	6	6
	Guarea trichilioides	3	2

Table 1 (Continued)

Family	Species	1991	1993
	Melia azedarach	4	3
Moraceae	*Artocarpus heterophyllus*	2	2
	Ficus buxifolia	1	1
	Ficus pumila	19	7
Moringaceae	*Moringa oleifera*	2	0
	Moringa sp.	1	1
Musaceae	*Musa paradisiaca*	4	2
	Musa sapientum	1	1
	Musa textilis	5	4
	Musa sp.	31	24
Myristicaceae	*Myristica fragrans*	5	0
Myrtaceae	*Eugenia aggregata*	3	1
	Eugenia boqueronensis	6	0
	Myrciaria cauliflora	1	1
	Psidium guajava	8	3
	Syzygium jambos	7	5
Nymphaceae	*Nymphaea sp.*	9	0
Oleaceae	*Phillyrea angustifolia*	2	1
Onagraceae	*Ludwigia octovalvis*	1	1
	Ludwigia sp.	1	1
Orchidaceae	*Brachionidium sp.*	1	0
	Spathoglottis plicata	3	0
	Vanilla sp.	1	0
Oxalidaceae	*Averrhoa carambola*	5	2
Passifloraceae	*Passiflora coccinea*	1	0
	Passiflora coriacea	8	1
	Passiflora edulis	5	3
	Passiflora maliformis	5	0
	Passiflora mollissima	29	0
	Passiflora quadrangularis	7	2
	Passiflora trifasciata	1	0
Phytolaccaceae	*Phytolacca dioica*	8	7
Piperaceae	*Peperomia sp.*	1	0
	Piper nigrum	1	0
	Piper sp.	5	5
Poaceae	*Andropogon sp.*	1	0
	Arundinaria pygmaea	1	0
	Bambusa glaucescens	1	1
	Bambusa multiplex	17	9
	Bambusa oldhamii	1	1
	Bambusa tuldoides	8	7
	Bambusa vulgaris	1	1

Table 1 (Continued)

Family	Species	1991	1993
	Bambusa sp.	2	2
	Panicum sp.	2	0
	Paspalum plicatulum	1	1
	Phalaris arundinacea	1	0
	Saccharum officinarum	6	6
	Setaria palmifolia	6	5
	Spartina sp.	3	1
Polygonaceae	*Antigonon leptopus*	1	0
Polypodiaceae	*Platycerium superbum*	3	1
	Polypodium aureum	1	0
	Polypodium crassifolium	6	0
	Polypodium punctatum	2	0
Pontederiaceae	*Pontederia cordata*	7	0
Pteridaceae	*Acrostichum aureum*	1	0
Rosaceae	*Aphanes caryotaefolia*	2	2
	Prunus tomentosa	2	0
	Rubus sp.	2	0
Rubiaceae	*Coccocypselum herbaceum*	2	1
	Coffea arabica	18	17
	Coffea dewevrei	1	1
	Hamelia patens	1	0
	Palicourea sp.	1	0
	Psychotria sp.	1	1
Rutaceae	*Casimiroa edulis*	4	0
Sapindaceae	*Paullinia sp.*	2	0
Sapotaceae	*Manilkara zapota*	2	1
Sarraceniaceae	*Sarracenia purpurea*	4	0
Scrophulariaceae	*Bacopa monnieri*	1	0
Selaginellaceae	*Selaginella versicolor*	5	0
	Selaginella victoriae	1	0
	Selaginella sp.	3	0
Simaroubaceae	*Quassia amara*	1	0
Solanaceae	*Brugmansia suaveolens*	11	11
	Brunfelsia americana	1	1
	Brunfelsia jamaicensis	3	1
	Brunfelsia undulatum	2	1
	Capsicum sp.	6	0
	Datura stramonium	1	0
	Lycianthes rantonnetii	1	1
	Solandra maxima	4	2
	Solandra nitida	1	1
	Withania somnifera	5	0

Table 1 (Continued)

Family	Species	1991	1993
Sterculiaceae	*Theobroma cacao*	11	3
Strelitziaceae	*Phenakospermum guyanense*	14	14
	Strelitzia nicolai	5	2
	Strelitzia reginae	22	19
	Strelitzia sp.	3	3
Theaceae	*Camellia sinensis*	4	1
Thelypteridaceae	*Thelypteris sp.*	1	0
Typhaceae	*Typha angustifolia*	2	0
	Typha domingensis	1	0
Urticaceae	*Pellionia daveauana*	1	0
Verbenaceae	*Tectona grandis*	2	0
Vitaceae	*Cissus gongylodes*	2	1
	Cissus rhombifolia	1	1
	Cissus sicyoides	3	2
Zamiaceae	*Zamia fischeri*	2	2
	Zamia furfuracea	7	4
Zingiberaceae	*Alpinia purpurata*	4	3
	Alpinia sanderae	9	3
	Alpinia zerumbet	8	8
	Brachychilum horsfieldii	1	0
	Costus barbatus	1	0
	Costus elatus	3	1
	Costus globosus	1	1
	Costus scaber	2	1
	Costus sp.	27	22
	Curcuma domestica	10	3
	Curcuma longa	1	0
	Curcuma roscoena	4	0
	Etlingera elatior	4	2
	Globba sp.	5	0
	Hedychium aurantiaca	5	0
	Hedychium cornatum	4	2
	Hedychium coronarium	19	13
	Hedychium sp.	5	2
	Kaempferia decora	1	0
	Kaempferia elegans	1	0
	Kaempferia pulchra	6	1
	Kaempferia rotunda	7	3
	Renealmia alpinia	2	0
	Renealmia battenbergiana	1	0
	Zingiber officinale	6	3
	Zingiber spectabile	5	4
	Unidentified	262	85
	Total individuals	1833	829

The pH of the water in the surface aquatic systems was 8.5 during July 1996. Most of the aquatic plants died by 1993. In 1992 the west side of the pond on the mountain terrace was replanted with food species for the residents and with ground cover species to alleviate erosion. The bamboo belt grew well over the period. Most of the original plants placed in planter pockets of the cliff faces of the cloud bowl mountain perished as a result of an inadequate irrigation and/or high temperatures.

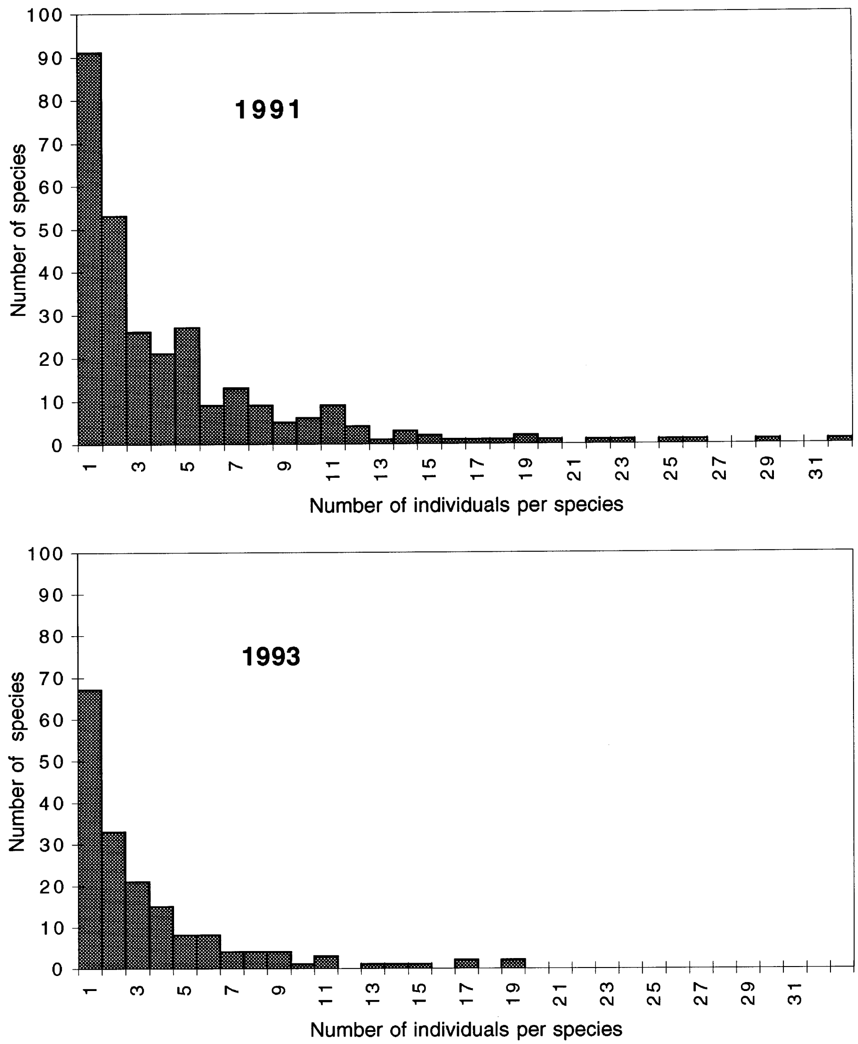

Fig. 7. Distribution of individuals within species for 1991 and 1993 surveys in the rainforest biome of Biosphere 2.

(a)

Fig. 8. (a) Lowland rainforest in the initial planting phase, 1989. (b) Lowland rainforest during the first complete plant survey, 1991. (c) Lowland rainforest in May 1993 after almost 2 years of material closure.

4.4. Plant growth

Growth rate data for the tree species *Cecropia schreberiana* are shown in Fig. 9. Fig. 9(a) illustrates the change in diameter at breast height (dbh) as a function of time, covering the period 1990–1997. Fig. 9(b) shows data for growth versus dbh for *Cecropia* from the rainforest biome as well as comparative data for related species of *Cecropia* in natural rainforests (Alvarez-Buylla and Martinez-Ramos, 1992; Korning and Balslev, 1994) The *Cecropia* growth rate was about four times their natural counterparts.

(b)

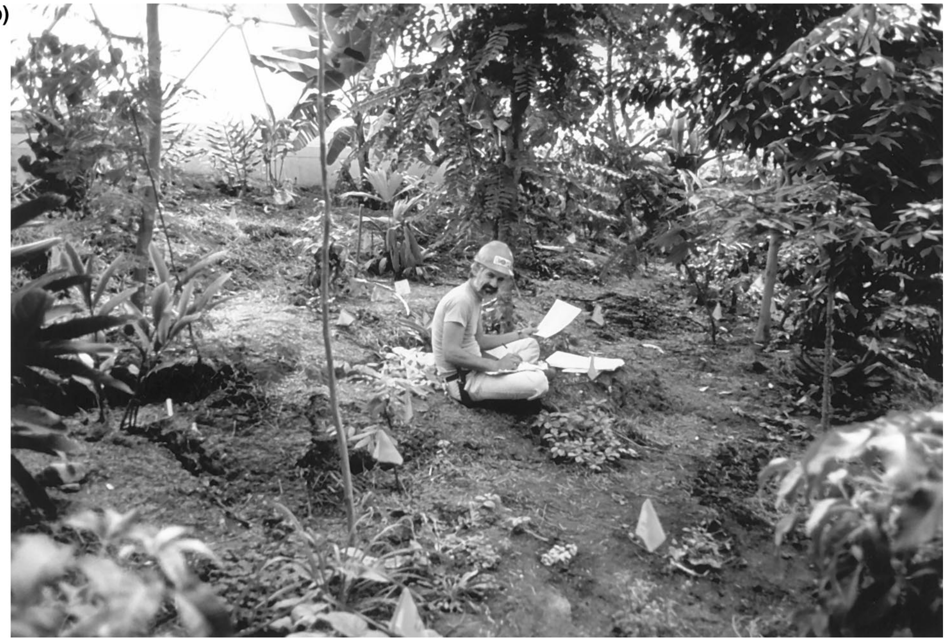

Fig. 8. (*Continued*)

Estimates of aboveground plant biomass in the rainforest were made using plant measurements before and during closure. The biomass in November, 1990, was estimated to be 2000 kg dry weight (1.0 kg m^{-2}). A subset of measurements made of rainforest trees in July 1993 showed an increase of ≈400% in aboveground biomass. After 32 months of growth, the rainforest aboveground plant biomass was ≈8000 kg dry weight (4.2 kg m^{-2}) (Bierner, report on file).

5. Discussion

The temperatures in the rainforest biomes were within daily and seasonal ranges appropriate for the marginal tropics but not for humid equatorial or montane forests. The usual daily range of the Biosphere 2 rainforest temperatures was about 6°C, and the lowest monthly average around 21°C. In equatorial rainforest areas, the mean temperature of the coldest month is never below 24°C; in the marginal tropics the coolest month may have an average as low as 18°C (Lauer, 1989). The relative humidity in the Biosphere 2 rainforest was kept within limits published for tropical rainforests (Lauer, 1989).

Plant biomass density in the Biosphere 2 rainforest in 1993 was ≈4.2 kg m^{-2}. This is an order of magnitude lower than an average of estimates made for mature pantropical rainforests, 45 kg m^{-2} (Brunig, 1983). The biomass within the Biosphere 2 rainforest will continue to increase as the system matures, though the size

(c)


Fig. 8. (*Continued*)

of the structure and the thermocline will constrain the maximum height of the tall trees and thus the maximum total biomass of the biome. The reason for the increased growth of *Cecropia* is not known but could be related to the high levels of atmospheric CO_2, which were as high as 4500 ppm per volume (ppmv) during the closure, and to high levels of nutrients in the rainwater (e.g. Marino et al., 1999).

On the short term, human intervention in the rainforest biome forced community assemblages more rapidly towards a later successional stage than would have developed had no intervention taken place. Prioritization of species that were to persist on the long term, particularly the large trees, drove some of the management decisions. Thus human as well as environmental and biological factors influenced the ecology of the rainforest biome.

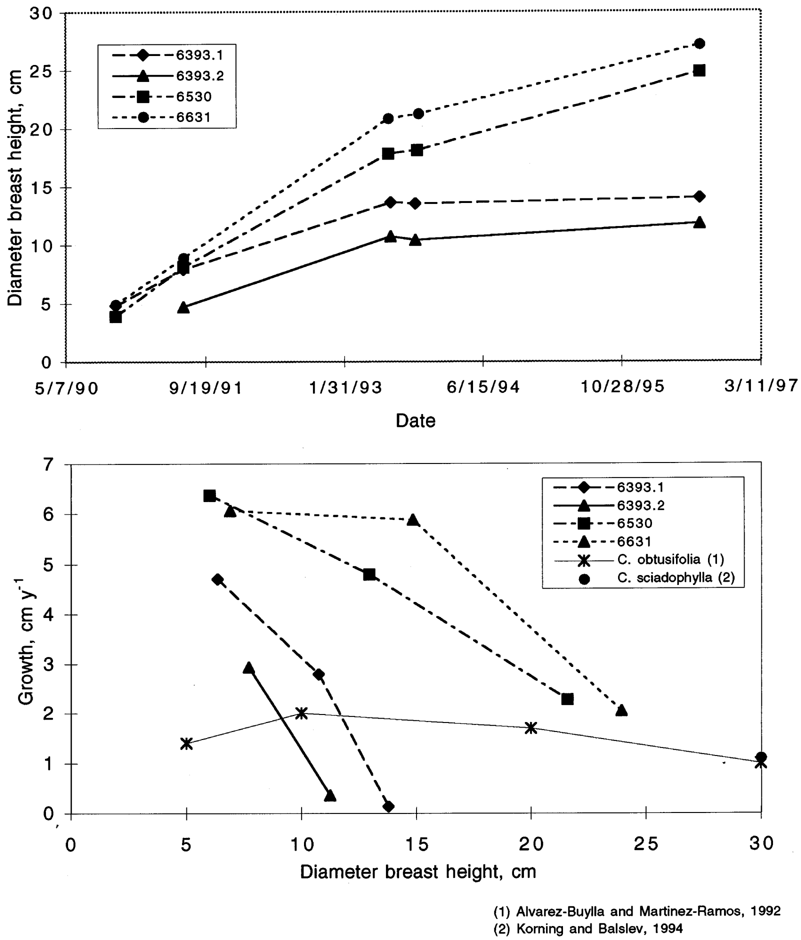

Fig. 9. (a) *Cecropia schreberiana* diameter at breast height as a function of time in the rainforest biome. (b) Growth rate as a function of dbh with comparative data for a related species in the wild.

Initial dynamics seem to approach those in other tropical rainforests. Decades will be required to converge on mature canopy structure. Space constraints will inhibit formation of a canopy identical to mature equatorial lowland rainforests. The different light and CO_2 regimes may alter biogeochemical cycling; hence the Biosphere 2 rainforest is a suitable platform for innovative research.

Acknowledgements

The plant survey data used for this paper are the result of the efforts of Mission 1 Biospherians and the Mission Control Team; inventory and survey teams of Space Biospheres Ventures; the rainforest design team which included staff of the

Royal Botanic Garden at Kew and the Institute of Economic Botany of the New York Botanical Garden. Jessica Bolson assisted with the 1996 plant survey. We acknowledge John Adams, Hewitt Stewart and Adrian Southern for assistance with figures and Jeff Chamberlain for providing the database containing plant inventory data. K. Dyhr created the original graphic for Fig. 5. Photographs were provided by Biosphere 2 Center. Photo credits are D.P. Snyder (Fig. 8a and b) and L. Leigh (Fig. 8c).

References

Alvarez-Buylla, E.R., Martinez-Ramos, M., 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree-an evaluation of the climax-pioneer paradigm for tropical rain forests. J. Ecol. 80, 275–290.

Atkinson, M.J., Barnett, H., Anderson, H., Langdon, C., Carpenter, S.J., McConnaughey, T., Smith, M., Marino, B.D.V., 1999. The Biosphere 2 coral reef biome. Ecol. Eng. 13, 147–172.

Bierregaard, R.O Jr., Lovejoy, T.E., Kapos, V., Augusto dos Santos, A., Hutchings, R.W., 1992. The biological dynamics of tropical rainforest fragments. BioScience 42, 859–866.

Brunig, E.F., 1983. Vegetation structure and growth. In: Golley, F.B. (Ed.), Tropical Rain Forest Ecosystems: Structure and Function. Elsevier Scientific Publishing, Amsterdam, pp. 49–73.

Dempster, W.F., 1993. Biosphere 2: System dynamics and observations during the initial two-year closure trial. 23rd International Conference on Environmental Systems, Colorado Springs, Colorado. SAE Technical Paper Series 932290.

Engel, V.C., Odum, H.T., 1999. Simulation of community metabolism and atmospheric carbon dioxide concentrations in Biosphere 2. Ecol. Eng. 13, 107–134.

Finn, M., 1996. The mangrove mesocosm of Biosphere 2: design, establishment and preliminary results. Ecol. Eng. 6, 21–56.

Korning, J., Balslev, H., 1994. Growth rates and mortality of tropical lowland tree species and the relation to forest structure in Amazonian Ecuador. J. Trop. Ecol. 10, 151–166.

Lauer, W., 1989. Climate and weather. In: Lieth, H., Werger, M.J.A. (Eds.), Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies. Elsevier, Amsterdam, pp. 7–53.

Marino, B.D.V., Mahato, T.R., Druitt, J.W., Leigh, L., Lin, G., Russell, R., Tubiello, F.N., 1999. The Agricultural biome of Biosphere 2: Structure, composition, and function. Ecol. Eng. 13, 199–234.

Petersen, J., Haberstock, A., Siccama, T., Vogt, K., Vogt, D., Tusting, B., 1992. The making of Biosphere 2. Restor. Manag. Notes 10 (2), 158–168.

Prance, G.T., 1991. Building a Rainforest: The Biosphere 2 Project. Longwood Grad. Program Semin. 20, 35–40.

Scarborough, R., 1994 Soil. In: T. Burgess and L. Ratener (Eds.), The Biosphere 2 rainforest: A net assessment, a report for Space Biospheres Ventures, Inc., Oracle, AZ, pp. 50–112.

Scott, H. J., 1994. Soil chemical and physical properties of the tropical rain forest of Biosphere 2: A comparison with other humid tropical forests. School of Forestry, Yale University, New Haven, CT, 29 pp.

Silverstone, S.E., Nelson, M., 1996. Food production and nutrition in Biosphere 2: Results from the first mission in September 1991 to September 1993. Adv. Space Res. 18 (4/5), 49–61.

Thompson, J., 1992. Biosphere 2. Prof. Surv. 12, 4–10.