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Short communication

Litterfall and decomposition rates in Biosphere 2 terrestrial biomes

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Abstract

Litterfall and decomposition rates were examined in four terrestrial biome areas within Biosphere 2, Oracle, AZ during 1992–1993, the second year of closure. Mean $\pm$ S.E. of 14 areas studied was 539 ± 105 g (dry wt.) m^{-2} $year^{-1}$. Litterfall was greatest in the lowland rainforest (1317 ± 283 g m^{-2} $year^{-1}$) and least in the sand dune desert (141 ± 88 g m^{-2} $year^{-1}$). Decomposition bags were measured for 15 leaf types or mixes with a mean loss rate of 90% per year. Decomposition rates were lowest in the desert region. Litterfall and subsequent decomposition were a small percentage ($\sim 7\%$) of Biosphere 2 respiration.

Keywords: Litterfall; Decomposition; Biosphere 2; Closed ecological systems; Biospherics; Self-organization; Biomes; Rainforest; Savannah; Desert; Thornscrub

1. Introduction

After planting with a high diversity of plant species, Biosphere 2 began a self-organization process with closure in September 1991. After 1 year of closure, the present study of patterns of leaf fall and decomposition was started as one measure of the ecosystem processes developing in the new closed ecological system and to assist in determination of the facility's carbon budget.

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2. Study areas

Biosphere 2, as originally designed and built, featured seven areas based on biomes. Three areas were modeled on natural terrestrial biomes: rainforest, savannah and desert. In addition, the thornscrub was an ecotonal area transitional between savannah and desert. Each terrestrial biome had differing annual patterns of temperature and artificial rain.

The rainforest area received year-round rain. Litterfall was collected from five habitats:

1. The gingerbelt formed a several meter deep perimeter planting around three sides of the rainforest. This area received more sidelighting and was dominated by light-tolerant species, such as *Musa* spp., ginger and *Heliconia* spp.
2. Terrace rainforest, a raised area in from the west and north gingerbelts.
3. Lowland rainforest occupied the central basin of the biome. Both lowland and terrace ecosystems included a number of pioneer, fast-growing trees (such as *Cecropia peltata* and *Leuceana leucocephela*) which were intended to shade and thus protect the plants envisioned as the mature rainforest community.
4. Varzea, modeled on a riverine Amazonian ecology, and dominated by a winding stream which traversed the area, and heavily shaded by *Phytolaca* spp. trees.
5. Bamboo belt—a 3–4 m wide perimeter area dominated by about a dozen bamboo species, intended to shield the rainforest from salt aerosols from the adjacent ocean area.

The savannah was designed to be predominantly spring and summer active, with a dormant (dry) season during the winter. Litterfall in the savannah was collected from sites underneath the *Acacia* spp. trees of the upper savannah.

Two small thornscrub areas had similar climate management to the savannah, with dry and wet seasons alternating. The upper thornscrub mostly had plants from northern Sonora, Mexico, and the lower thornscrub had many species from Malagasy.

The Biosphere 2 desert was managed with its rainy season in fall and winter, and a spring/summer dormant period like that in Baja California, which was the source of most of the plant species. Humidity was high, as it was throughout the terrestrial wilderness areas. Litterfall was collected from six habitats in the desert:

1. Playa area which included a number of *Atriplex* (saltbush) species.
2. West arroyo area, which included desert species with tolerance for higher moisture.
3. Bajada area, with succulents and cacti.
4. Ramp area, a sloping habitat on the western side of the desert which led up to the upper thornscrub.
5. East desert, up from the playa basin, which included *Larrea tridentata* (creosote bush) as well as a range of other desert species.
6. Sand dune, with a sandier soil, and planted with desert shrubs and grasses.

3. Methods

3.1. Litterfall

Ten litterfall traps each were located in lowland rainforest, terrace rainforest, gingerbelt rainforest and under upper savannah acacia trees. There were five each in the varzea rainforest, bamboo belt rainforest, upper thornscrub, lower thornscrub, sand dune desert, west arroyo desert, playa desert, east desert, west ramp desert and bajada desert areas.

Litterfall traps were 0.25 m^2, made of 1 mm fiber-glass screening, supported 0.3–0.6 m above the soil surface. Litter was collected near the end of the month from October 1992 through September 1993. Litter was exported through the Biosphere 2 airlock to outside labs where they were dried for 24 h at 70°C and weighed to within 0.1 g. Statistical significance of differences in litterfall was calculated using t-tests.

3.2. Decomposition bags

Decomposition studies were done using 1 mm plastic mesh bags. Each were filled with 7.0 ± 0.1 g of air dry leaf material collected from the ecosystems. A total of 12 or 36 bags were placed on the soil surface of the different locations. Decomposition bags were collected each month from October 1992 to September 1993. After export from Biosphere 2, decomposition bags were oven dried at 70°C for 24 h and weighed to 0.1 g. Graphs of decomposition over time were analyzed using Excel 7.0 software, the exponential decrease regression equation having the form, $y = \text{constant} * e^{-kt(x)}$, and r^2 (coefficient of determination) representing the goodness of fit.

Series with 12 decomposition bags included the following materials and locations: *Acacia* spp. leaves in upper savannah; *Pereskia* spp. leaves in lower thornscrub; *Zingerberale* spp. in gingerbelt; *Bambusa vulgaris* in bamboo belt; mix of leaves in the upper thornscrub; mix of leaves in the sand dune; mix of leaves in the desert bajada; mix of leaves in the east desert; mix of leaves in west desert ramp; mix of grasses in the lower savannah; and mix of grasses in the upper savannah area. The decomposition bags with a mix of leaves were collected from plants growing in that habitat. A total of 36 bags, allowing three replicates per month, were used for *Phytolaca* spp. in the varzea rainforest; *Musa* spp. in gingerbelt rainforest; *Leuceana leucocephela* in lowland rainforest; and *Cecropia peltata* in lowland rainforest.

4. Results

4.1. Litterfall

Highest yearly litterfall was from the lowland rainforest with 1317 ± 283 g m^{-2} $year^{-1}$, followed by lower thornscrub (905 ± 188 g m^{-2} $year^{-1}$) (Table 1). Lowest yearly litterfalls were in the desert, with the least occurring in the sand dune desert area with 141 ± 88 g m^{-2} year^{-1}. Large and statistically significant differences in litterfall were found between biomes (e.g. rainfall and desert, $p < 0.01$) and between some habitats within the same biome area. For example, the lowland rainforest annual litterfall was twice that of the varzea habitat (641 ± 89 g m^{-2} year^{-1}) ($p < 0.01$). The seasonal patterns for gingerbelt and varzea litterfall were also distinctly different ($p < 0.03$). The 320 ± 111 g m^{-2} year^{-1} litterfall in the east desert was significantly higher ($p < 0.03$) than the sand dune habitat of the desert.

Averaged by biome type, the thornscrub (795 ± 139 g m^{-2} year^{-1}) and rainforest (723 ± 158 g m^{-2} year^{-1}) are not statistically significantly different ($p < 0.29$), but the rainforest and thornscrub are both significantly different (both $p < 0.01$) than savannah *Acacia* (656 ± 134 g m^{-2} year^{-1}). The desert litterfall average (300 ± 38 g m^{-2} year^{-1}) was significantly less ($p < 0.01$) when compared with rainforest, thornscrub or savannah. The mean of all litterfall from the 14 areas studied was 539 ± 105 g m^{-2} year^{-1}.

Monthly litterfall totals had considerable variability. For example, the three highest monthly totals (434, 195 and 125 g m^{-2}) for a single litterfall trap were all in the lowland rainforest, resulting from branch breakage or treefall events. Within individual ecosystem types, litterfall could vary widely over individual months and the course of the year. For example, in the lowland rainforest, highest individual litterfall trap locations reached 3138, 2607 and 1545 g m^{-2} year^{-1}, while the three lowest were 425, 628 and 669 g m^{-2} year^{-1}.

Table 1
Annual litterfall in Biosphere 2 from October 1992 to September 1993

Name of area	Number of replicates	Litterfall (av. ± S.E.) (g m^{-2} year^{-1})
Rainforest areas		
Bamboo belt	5	578 ± 81
Terrace rainforest	10	466 ± 70
Lowland rainforest	10	1317 ± 283
West Gingerbelt st	10	491 ± 46
Varzea rainforest	5	641 ± 89
Savannah		
Savannah acacia	10	656 ± 134
Thornscrub areas		
Upper thornscrub	5	686 ± 91
Lower thornscrub	5	905 ± 188
Desert areas		
East desert	5	320 ± 111
Sand dune desert	5	141 ± 88
W. Arroyo desert	5	408 ± 59
W. Ramp desert	5	372 ± 76
Bajada desert	5	265 ± 72
Playa desert	5	294 ± 79
Average for 90 areas		539 ± 105

Selected series are plotted on the same scale in Fig. 1. Fig. 1a shows average rainforest and desert litterfall, Fig. 1b presents savannah and average thornscrub litterfall and Fig. 1c compares litterfall from two of the rainforest habitats.

4.2. Leaf decomposition rates

Thornscrub and savannah both had rapid initial loss followed by slower decomposition, with an overall loss of 97% of initial material by the end of the year (Fig. 2a). The rainforest decomposition began slower but also reached nearly complete decomposition. Desert bags lost 2/3 of their weight during the wet period from September to March but had little loss thereafter during the dry period from April to September. Ginger and *Leuceana* decomposed more rapidly than the heavy-leafed *Cecropia*, but 90% of the ginger leaves and all of the *Leuceana* and *Cecropia* leaves was decomposed by the end of the year (Fig. 2b). Decomposition rates were less in the desert region with over 35% of the original biomass remaining at the end of the year.

5. Discussion

The large variation among litterfall stations in 1992–1993, the second year after planting, occurred during a period of transition and self-organization when some of the initial species died and were displaced by vigorous growth of others. Where the climate was managed uniformly, as in the rainforest, there was little seasonal difference even though there was greater light reaching plants in summer compared to winter. Litter accumulation often exceeds decomposition rates in aggrading ecosystems, in agreement with the theory that as standing biomass accumulates, net primary productivity of an ecosystem increases during early succession (Swift et al., 1979).

Unique environmental conditions inside Biosphere 2 included elevated CO_2 levels (from 400 to 4500 ppm during the 2 year closure, 1991–1993), decline in atmospheric oxygen (Severinghaus et al., 1994), decreased insolation from loss of light through the spaceframe coupled with exposure of some tropical species to a more temperate seasonality of day length and little or no wind. These factors helped produce extremely rapid growth accompanied by marked etiolation in a number of species and lack of stress-wood (Nelson et al., 1993, 1994; Nelson and Dempster, 1996).

5.1. Seasonal differences

Marked seasonal differences were found in those biomes types where the artificial rain was managed with dry and wet seasons. In the desert, litterfall was greater in the dry summer season. However, in the savannah and thornscrub there were several months with high litterfall in their summer wet season. Rates of litterfall and decomposition were of similar order of magnitude in the wet areas, but in the

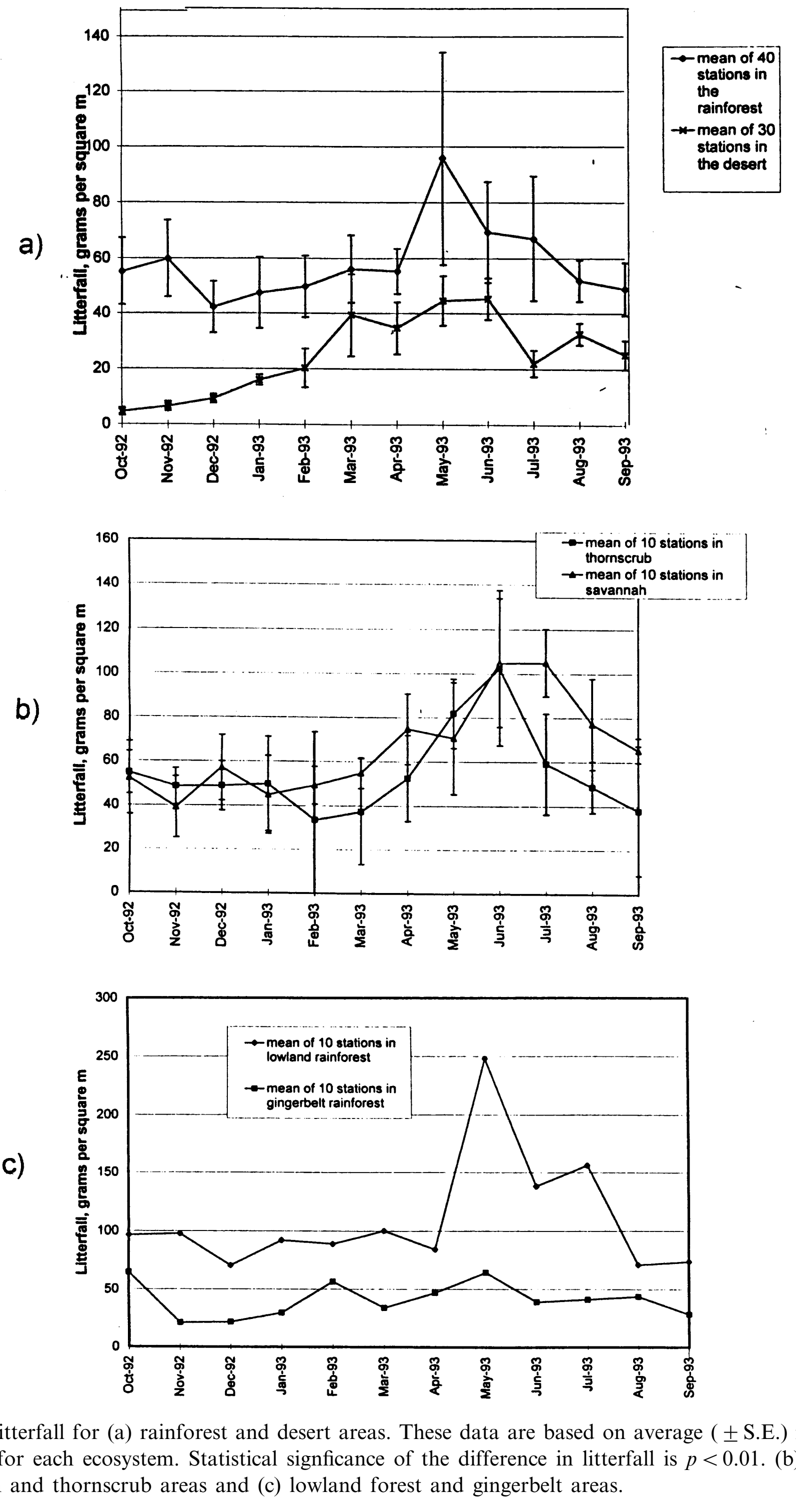

Fig. 1. Litterfall for (a) rainforest and desert areas. These data are based on average (± S.E.) monthly litterfall for each ecosystem. Statistical signficance of the difference in litterfall is $p < 0.01$. (b) Acacia savannah and thornscrub areas and (c) lowland forest and gingerbelt areas.

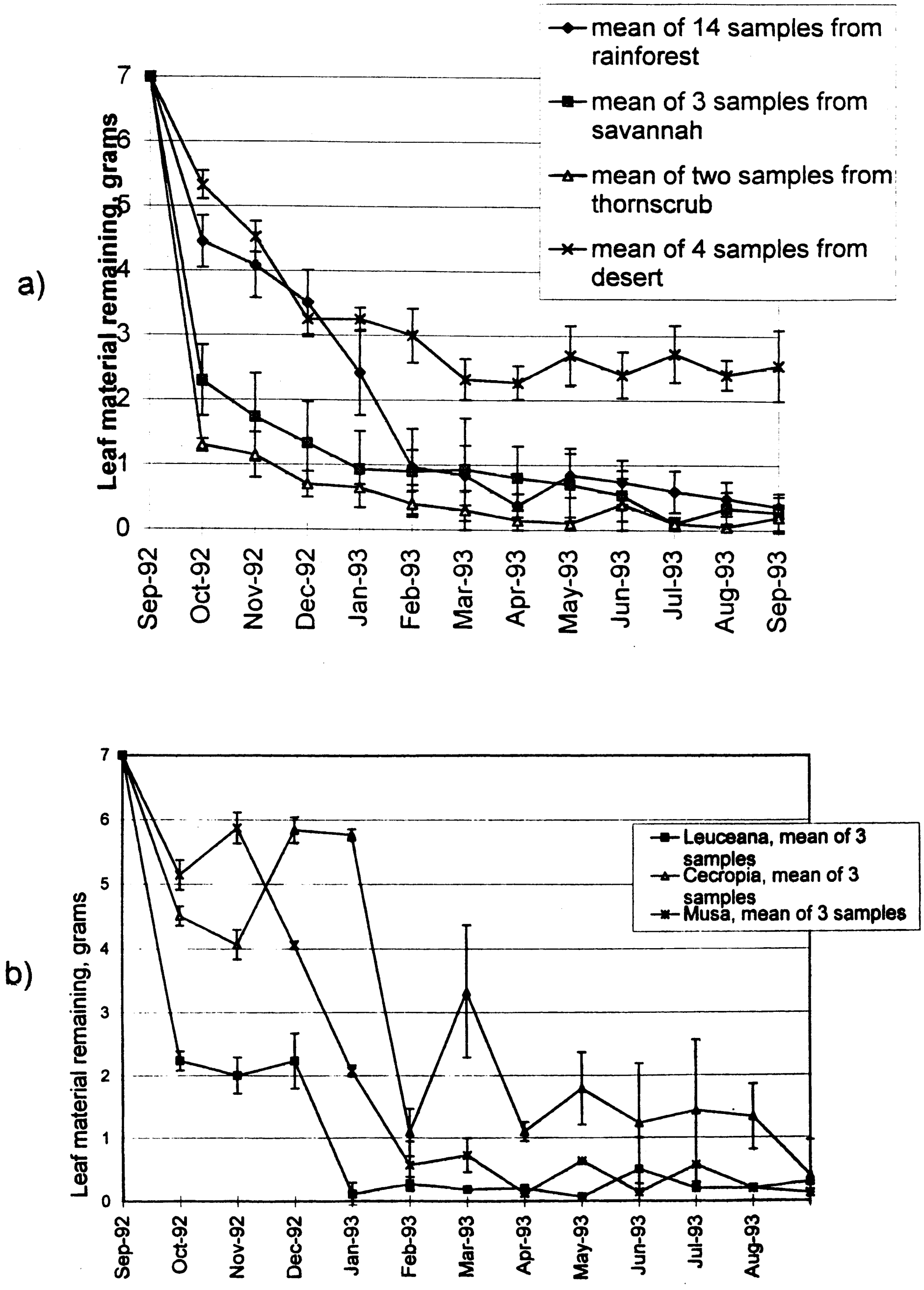

Fig. 2. (*Continued*)

drier biome areas, decomposition rates were slower, and considerable litterfall material organic matter remained at the end of the year.

5.2. Comparison with natural ecosystems

5.2.1. Litterfall

Rainforest litterfall has been reported as ranging from 1350 to 2700 g m^{-2} $year^{-1}$ (Swift et al., 1979) and 400–1100 g m^{-2} $year^{-1}$ with a mean of 830 g m^{-2} $year^{-1}$ for a Puerto Rican rainforest (Odum, 1970). The somewhat lower annual litterfall from the Biosphere 2 rainforest (723 ± 158 g m^{-2} $year^{-1}$) during its third year after planting is what we might expect, given the data from Puerto Rican forests which show that litterfall from newly planted forests (1–2 years old) were about only 25% of those from a mature forest (Lugo and Murphy, 1986).

The Biosphere 2 *Acacia* litterfall (655 ± 134 g m^{-2} $year^{-1}$) was about 76% of the 863 g m^{-2} $year^{-1}$ reported for natural savannahs (Swift et al., 1979).

The Biosphere 2 desert litterfall (300 ± 38 g m^{-2} $year^{-1}$) was comparable to those in natural deserts. Litterfall in the Sonoran desert is 220–440 g m^{-2} $year^{-1}$ (O'Brien, 1978, cited in McMahon and Wagner, 1985), and 310 ± 92 g m^{-2} $year^{-1}$ in wet years and ~ 200 g m^{-2} $year^{-1}$ under perennial shrubs in the Negev desert (Whitford, 1986).

5.2.2. Decomposition rates

Studies in rainforest decomposition have reported higher rates of disappearance for leaf material from primary climax species compared to secondary successional species, and for high N leaf material (La Caro and Rudd, 1985). This type of pattern was not upheld in our leaf decomposition results. *Leuceana leucocephela*, a legume, one of Biosphere 2's intentional successional species, had a faster decline ($k = 0.25$, $r^2 = 0.49$) than *Cecropia peltata* ($k = 0.18$, $r^2 = 0.73$), though Biosphere 2's 8 month decomposition loss of 75% far exceeded the 22% reported by La Caro and Rudd (1985) for *Cecropia* spp.

This study's observed rates of loss of desert materials (av. $k = 0.07$, $r^2 = 0.69$) are comparable with those reported in the literature, where from 40 to 90% loss of creosote bush litter, for example, occurs in the first year (Whitford, 1986). The decomposition exceeded the 15–24% for the first year reported for two chaparral species growing in coastal mountains of southern California in the same winter-active climate (Schlesinger, 1985). However, Biosphere 2's desert experienced an

Fig. 2. (a) The overall seasonal patterns of decomposition loss of leaf material in the Biosphere 2 for (a) rainforest ($k = 0.24$, $r^2 = 0.81$), savannah ($k = 0.24$, $r^2 = 0.81$), thornscrub ($k = 0.244$, $r^2 = 0.86$) and desert ($k = 0.07$, $r^2 = 0.69$) and (b) three different leaf materials. The rainforest average is based on the collection of 14 monthly samples, the savannah represents three monthly samples (one *Acacia* spp. and the other two grass mixtures), the thornscrub represents two monthly samples from mixed leaves, and the desert represents four monthly samples of mixtures of desert leaf materials. Graph (b) is based on data from three decomposition bags collected monthly for each species. *Leuceana* had $k = 0.25$, $r^2 = 0.49$, *Cecropia* had $k = 0.18$, $r^2 = 0.73$, and *Musa* had $k = 0.36$, $r^2 = 0.80$.

Table 2
Estimates of litterfall and decomposition over entire planted area of Biosphere 2 terrestrial biomes[a]

Biome area	Size, planted (m^2)	Average annual litterfall ($g\ m^{-2}\ year^{-1}$)	Total biome litterfall (kg)	Average annual decomposition (%)	Total biome decomposition (kg organic matter)
Rainforest	1540	700	1078	95	1024
Savannah/thornscrub	1060	730	774	97	751
Desert	1280	300	384	64	246
Total	3880		2236		2021
Average		576		90	

[a] The areas of the terrestrial biomes include only planted areas.

unusual amount of dry season moisture from condensation from the spaceframe, and high humidity levels. This led to a strengthening of the shrub/grass/annual dominance as the biome self-organized after closure, producing an ecosystem shift to more chaparral and less succulent-dominance (Alling et al., 1993; Nelson et al., 1993; Nelson and Dempster, 1996).

5.3. Comparison with Biosphere 2 metabolism

Total litterfall in the terrestrial biomes was ~2200 kg $year^{-1}$ and average annual decomposition consumed ~2020 kg (Table 2). If carbon constituted 45% of the litter biomass, ~910 kg (or 75.8 kmol) of C was oxidized during the year of this study.

Biosphere 2's terrestrial biome litterfall averaged 539 g m^{-2} $year^{-1}$ (1.48 g m^{-2} day^{-1}) and an annual decomposition loss of ~90%. Thus, litterfall decomposition averaged ~1.33 g m^{-2} day^{-1}. This is ~7% of the 19 g m^{-2} day^{-1} total respiratory consumption calculated by Engel and Odum (1999) in simulating the total gas metabolism of Biosphere 2.

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