Patterns of CO₂ exchange in biological soil crusts of successional age

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Abstract

The objective of this paper was to determine whether CO₂ exchange rates could be used as an indicator for determining the state of development and species or functional composition of biological soil crusts in different successional stages. We quantified the CO₂ exchange rates, i.e., CO₂ assimilation and respiration, in samples from different microhabitats at two different sites in the Negev desert. In the successional pathway of the crust communities, the pioneers in colonising the soil surface are the cyanobacteria; green algae, mosses and lichens then follow. Physical influences such as soil structure and types, radiation intensity, and topographic traits such as slope directions that affect water availability and soil moisture, influence the successional pathways and the soil crust community. When physical conditions are the same, disturbances are key factors for a specific successional stage. We found a substantial gradient of CO₂ exchange at the Nizzana site for both respiration and photosynthesis. Samples from the sand dunes at the Nizzana site showed a pronounced activity gradient with high rates for assimilation (around 70 μmol CO₂ m⁻² min⁻¹) as well as respiration (60–70 μmol CO₂ m⁻² min⁻¹) at the base of dunes, decreasing towards the top. The soil crust samples of the Negev desert show comparable values. Hence, as ecotypes containing such biological soil crusts with dominant photosynthetically active organisms are a widespread phenomenon in desert, boreal and arctic systems, their contribution to the global cycling of trace gases and elements can be significant for global budgets. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Studies on the biological crusts have been based on surveys of communities, morphology and species composition, geographical distribution, nutrient cycling, soil stabilisation, and changes after disturbances such as grazing, fires and desert storms (Johansen and St. Clair, 1986; West, 1990).

Well-developed microphytic crusts are relatively

hydrophobic because microphytes such as cyanobacteria and soil green algae secrete polysaccharides (Mehta and Vaidya, 1978; De-Philipis et al., 1993), creating mucilaginous sheaths on the soil surface that bind the soil surface particles (Baily et al., 1973; Anantani and Marathe, 1974). This reduces rainfall infiltration and generates runoff (Yair, 1990; Zaady and Shachak, 1994). By binding soil particles, the crusts play an important role in soil stabilization by preventing wind and soil erosion (Belnap, 1995). Some individual groups in the soil crust communities such as cyanobacteria, free living bacteria, lichens, and microbial associations with moss species can fix nitrogen (Friedman and Galun, 1974; Reddy and Giddens,

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1975; Eskew and Ting, 1978; Skujins, 1984; Terry and Burns, 1988; Jefferies et al., 1992; Zaady et al., 1998; Evans and Belnap, 1999). Soil crust communities, as well, have considerable photosynthetic potential, although this is limited by the hydration status (Lange et al., 1992, 1998; Jefferies et al., 1993) and is thus highly dependent on precipitation, i.e., rain, fog, dew and atmospheric water vapour. The extensive cover of even a thin layer of photosynthetically active organisms can be an important basis for carbon fixation in an environment like the Negev desert where primary production is low (Lange et al., 1992).

The landscape of the Negev desert in Israel is described by two different types of vegetation: (i) perennial vegetation and (ii) microphytic soil crust communities (Friedman and Galun, 1974; Evenari, 1985; West, 1990; Johansen, 1993; Shachak et al., 1998). Crust origin can either be biotic (West, 1990) or abiotic (Eldridge et al., 1995). Microphytic soil crust cover is characterised by a tightly structured surface (Fletcher and Martin, 1948) with a complex community of mosses, lichens, soil algae, fungi, cyanobacteria and soil bacteria (Friedman and Galun, 1974; Skujins, 1984; West, 1990). The crust communities vary along the rainfall gradient in the Negev, from a 2–3 mm thick and relatively homogeneous cyanobacterial crusts at 75–125 mm of average annual rainfall in the central Negev, to crusts of 15 mm thickness with complex communities at 200–300 mm year⁻¹ in the northern Negev (Zaady et al., 1997).

In the successional pathway of the crust communities, the pioneers in colonising the soil surface are the cyanobacteria; green algae, mosses and lichens then follow. The latter represent a well-developed crust because of their slow growth rate. Lange et al. (1992) reported that filamentous cyanobacteria initialize the first step of colonization in sand dunes of the eastern Negev desert as in other part of the world (Starks et al., 1981; West, 1990; Belnap, 1993; Johansen, 1993), while green algae and mosses appear later. The ability of the filamentous cyanobacteria (e.g., *Microcoleus* sp.) to colonize new areas is due to their ability to withstand high temperatures, radiation, low water potential, and their capability to move 2 mm up and down the soil surface (Friedman and Galun, 1974; Brock, 1975; Danin, 1978; Buzer et al., 1985; Levy and Steinberger, 1986; Yair, 1990; Belnap, 1993). Physical influences such as soil structure and types, radiation intensity, and topographic traits such as slope directions that affect water availability and soil moisture, influence the successional pathways and the soil crust community. Microphytic soil crust succession studies have been characterized by measuring percentage of crust cover (Johansen et al., 1982; Kleiner, 1983; West, 1990), chlorophyll quantification and phytomass of algae and lichens (West, 1990). Crusts cannot maintain

an imbalance in water potential between their tissue and the surrounding atmosphere for long periods of time. Under dry conditions they lose water and enter a state of latent life. Due to this poikilohydric character, the biological crusts are finely tuned in their physiology to the colonized habitat, i.e., predominantly adapted to the nature and the timing of their water supply. Different factors can modify successional pathways from the same initial state of the system. When physical conditions are the same, disturbances are key factors for a specific successional stage (Connell and Slatyer, 1977; Starks and Shubert, 1982; Pickett et al., 1987; Facelli and Pickett, 1990).

The objective of this paper was to determine whether CO₂ exchange rates could be used as an indicator for determining the state of development and species or functional composition of biological soil crusts in different successional stages. In order to do so, we quantified the CO₂ exchange rates, i.e., CO₂ assimilation and respiration, in samples from different microhabitats at two different sites in the Negev desert.

2. Methods and materials

2.1. Study areas

One research site was the Sayeret Shaked Ecological Park near Beer-Sheva in the northern Negev of Israel (31°17'N, 34°37'E). The site is a watershed that has been closed of livestock grazing since 1987, 9 years prior to this study. The landscape is covered with scattered patches of shrubs: *Noeae mucronata* (Forssk.) Asch. et Schw. (Chenopodiaceae) and *Atractylis serratuloides* Sieb. (Compositae) (Feinbrun-Dothan and Danin, 1991; Zaady et al., 1996). The soil surface between the shrubs is covered by a microphytic soil crust composed of cyanobacteria with scattered mosses on the south-facing slopes (about 8–10 mm thick), and a crust consisting of cyanobacteria, algae, and dense moss cover and lichens on the north-facing slopes (about 10–15 mm thick) (Zaady et al., 1996, 1998).

Rainfall in the study site has a long-term annual average of 200 mm and occurs only in the winter season. The 200-mm isohyet forms the transition zone between arid and semiarid deserts in Israel. The soil is loessial, 1.10 m thick with 14% clay, 27% silt and 59% sand (US classification: loess soil with sandy loam texture — Calcixerollic, Xerochrepts).

A second site was chosen at the Nizzana sand field, that is located in the central-western Negev (30°75'N, 34°22'E) and represents the eastern extension of the Sinai continental sandy area (Tsoar and Moller, 1986). Average annual rainfall in the area is about 90 mm. The rainy season is limited to the

winter months. The general landscape comprises linear west–east trending sand dunes superimposed on a broad sand ridge (Tsoar and Moller, 1986). The upper part of the linear dunes is composed of unconsolidated sand and is almost devoid of vegetation. The lower flanks of the dunes are stabilized with perennials and the surface is covered by a smooth and relatively continuous biological soil crust (Lange et al., 1992). The upper part of the dunes is composed of mostly sand particles (more than 95%), and the crust in the lower parts has a particle size distribution of about 21% sand, 55% silt and 24% clay (Yair, 1990) (US classification: sandy texture — Typic Torripsamment).

The soils on the dunes are sparsely vegetated by *Retama raetam* (Forssk.) Webb (Papilionaceae), *Anabasis articulata* (Forssk.) Moq. (Chenopodiaceae), *Artemisia herba-alba* Asso (Compositae) and *Thymelaea hirsuta* (L.) Endl. (Thymelaeaceae) on the lower slopes and the grass *Stipagrostis* sp. (Gramineae) on the crests (Yair, 1990; Danin, 1996). The lower flanks of the dunes are well vegetated and contain a contiguous, flexible biological crust (Yair, 1990).

The crust material was collected in Sayeret Shaked Eco-Park from six stations (each with three sampling plots), which were located along a cross section of the watershed perpendicular to the water flow (wadi). The north-facing slope of the watershed with an angle of ca. 7–10% and the south facing slope with an angle of ca. 15%. Three stations (up, middle, and down) were set up on the near-top, middle, and base of the north-facing slope (35–40 m in between) and the corresponding three, on the south-facing slope (15–20 m in between).

In Nizzana site, average slope angle of the dunes is 22% with an average height of 15 m (Yair, 1990), samples were collected from five stations set by their height from the dune base about 10–12 m between them: north down — 1–2 m high from the dune base; north down-middle (i.e., between middle and down) — 4–5 m high; north-middle — 7–8 m high; north-up — 12–13 m high; and the top on the north-facing slope — about 15 m high. One sample was collected from the top of the south-facing slope (about 15 m southern to the last one, at the same height). We also collected loose sand samples as controls.

Sufficient crust samples, with underlying soil of 5 mm thickness, to allow for statistical analysis (2 cm × 5 cm) were extracted randomly in each of the plots and carefully placed into plastic dishes, arranged in their natural position and density. Samples were collected at the end of the summer season, transported to the Max Planck Institute for Chemistry, Germany air-dried and stored at room temperature in a desiccator over silica-gel until used for experimentation.

2.2. Enclosures

For the CO₂ exchange studies of the crusts, we applied two slightly different open, dynamic (flow-through) cuvette systems (Kuhn, 1997; Kuhn and Kesselmeier, 1997; Wilske and Kesselmeier, 1999). The enclosures were constantly flushed with ambient air, which was artificially moistened to a relative humidity of 70–90%. The airflow was regulated and monitored using mass-flow controllers. All inner surfaces in contact with the sample gas were made of Teflon. Previous studies demonstrated that Teflon does not interfere with trace gases and that the applied Teflon film is fully light permeable in the spectral range of 300–900 nm (Schaefer et al., 1992; Kesselmeier et al., 1996; Kuhn, 1997). Cylindrical chambers of 9 or 11 cm in height and 14.5 cm in diameter, consisting of Teflon film supported by an external PVC frame, were installed. The lower side of the cylindrical enclosure was closed with a Teflon covered, transparent PVC-lid. The air inside the chamber was well mixed by Teflon propeller driven by a magnetically coupled motor attached outside. The internal volumes of the chambers were 1.5 and 1.7 l. With a constant flow rate of 1 or 2 l min⁻¹, a complete turnover of the air within the cuvette was achieved approximately once every 1–1.5 min. Air- and thallus-surface temperatures within the cuvette were continuously monitored with teflonized thermocouples. Photosynthetically active radiation (PAR) was measured with a LICOR quantum sensor (LI-190SZ, LICOR, Lincoln, NE, USA) outside the chamber, the relative humidity was measured with a temperature/relative humidity probe model 133Y (VAISALA, Finland). The data were recorded on a data logger (model 21X, CSI Ltd. UK). Quantification of CO₂ and water vapour exchange was achieved by a standard infrared gas analyzer (Model 6262, LICOR, Lincoln, NE, USA) in the differential mode, measuring the difference between the outlets of the cuvette containing the crust and an empty reference cuvette. It was maintained in a temperature-insulated box to prevent signal fluctuations due to temperature effects as well as water condensation.

Three days prior to the gas exchange measurements, the crusts were routinely reactivated by regularly moistening them in a greenhouse. The light-dark cycle was 9 h light and 15 h dark; PAR was 365 μmol m⁻² s⁻¹; temperatures were 22°C (light) and 16°C (dark); humidities were 50% (light) and 70% (dark). In accordance with Lange et al. (1992) we detected an enhanced emission rate directly after the first moistening (data not shown). The CO₂ exchange rates were found to be constant after the first day. Directly before insertion into the cuvettes for final measurements (day 4), the samples were brought to field capacity (22%

wt/wt) with double distilled water. Cuvette temperatures increased slightly (1–2°C) under light conditions.

Microphyte performance — moss identification and number of caulidia (the stem with leaf-like structures) were measured. The moss density is an indicator of crust development, therefore, their density may indicate the stage of succession. Using 2-mm pore net, moss identification and their density were measured using a binocular ($\times 40$).

2.3. Long cuvette adaptation

After insertion of the crusts into the cuvettes, respiration rates were monitored under dark conditions for at least 1.5 h. Then the light was turned on ($\approx 500 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a series of another five to six measurements, each integrating over a period of 5 min were carried out. For the data evaluation only the last two–three data periods were taken into account because they revealed steady state rates.

2.4. Short cuvette adaptation

All samples were kept moist under light for at least 1 h before incubation and moistened again 15 min before insertion into the cuvettes under light conditions. For short adaptation gas-exchange measurements, the samples were enclosed for less than 15 min. For data evaluation, the last five steady state values (1-min averaging periods) were taken for further consideration.

2.5. Porometer measurements under field conditions

At the Nizzana site we also measured the CO_2 exchange of some crust samples using a porometer system (LCA-4, Analytical Development, Hertfordshire, UK) using a Parkinson leaf chamber PLC-3 (same manufacturer).

2.6. Statistical analysis

One-way analysis of variance (ANOVA) with the Scheffe F-test (Sokal and Rohlf, 1981) was used to test differences in CO_2 exchange rates of respiration and photosynthesis determined for samples from the different sampling plots in each station at the two sites. The same analysis was used to test differences in the moss density of caulidia (the stem with leaf-like structures) from the stations of each of the two research sites.

3. Results

3.1. Structure and the biological crust composition

The south-facing slope of the watershed at the Sayeret Shaked Eco-Park is exposed to high radiation and is covered with cyanobacteria with a low-density moss cover (Table 1). The group of cyanobacteria includes two dominant species: *Microcoleus vaginatus* (Chroococcales) a filamentous cyanobacterium that grows 1–2 mm under the soil surface and *Nostoc punctiforme* (Oscillatoriales) that grows above the soil surface. These two species also predominate on the north-facing slope. Other species present in low numbers are *Chroococcus turgidus*, *Calothrix* sp. (Oscillatoriales) (Metting, 1981) and the green algae *Palmella* sp. (Tetrasporales) (Metting, 1981). The most common moss in the area is *Aloina bifrons* (Pottiaceae), while the second most common species is *Crossidium crossinerve* var. *laevipillum* (Pottiaceae), both are species adapted to arid climates (Scott, 1982). Other moss species appearing in low numbers are *Ephemerum* sp. (Ephemera-ceae) on both slopes of the watershed. The *Bryum* sp. (Bryaceae) appeared in the lower shady parts of the watershed where soil moisture may accumulate below the surface.

At the Nizzana site, well described by Lange et al. (1992), cyanobacterial crusts are composed of *Microcoleus sociatus* (Chroococcales), the dominant alga *Nos-*

Table 1

Moss density (in number of caulidia cm^{-2}) patterns found in cross sections of the watershed at the Sayeret Shaked Eco-Park and of the sand dune at Nizzana

Plot location		Moss density
Sayeret Shaked Eco-Park		
Watershed	North up ^a	129 $\pm$ 10 ^b
	North middle	91 $\pm$ 8
	North down	260 $\pm$ 10
	South down	48 $\pm$ 4
	South middle	19 $\pm$ 2
	South up	26 $\pm$ 2
	Loess soil (control)	ND
Nizzana		
Dune	North down	430 $\pm$ 26
	North down-middle	133 $\pm$ 15
	North middle	ND
	North up	ND
	North top	ND
	South top	ND
	Sand dune (control)	ND

^a Three stations (up, middle, and down) were set up on the near-top, middle, and base of the north-facing slope (35–40 m in between) and the corresponding three, on the south-facing slope (15–20 m in between).

^b Values are mean $\pm$ SE of moss number of caulidia. No determination = ND.

toc sp. (Oscillatoriales), *Calothrix parietina* (Oscillatoriales). The chlorophytes are represented by *Chlorococcum* sp. (Chroococcales) and *Stichococcus* sp. (Ulotrichales). Dense communities of cyanobacteria were found in the two plots at the base. Although we detected filamentous cyanobacteria in all the plots, they were rarely found on the upper parts of the north- and the south-facing slope. Only the lowest plots: north down and north middle-down, of the dune were covered with mosses (Table 1). Species common in this area were *Bryum bicolor* (Bryaceae), *Pterygoneurum subsessile* (Pottiaceae), *Aloina* sp. and *Crossidium* sp. (Lange et al., 1992; Danin, 1996).

3.2. CO₂ exchange

Rates of net photosynthesis and respiration obtained using the two different enclosures as well as two different experimental approaches (long- and short-cuvette adaptation) were found to be comparable. For the Sayeret Shaked Eco-Park, we found neither a clear gradient in respiration rates between the stations nor in assimilation activity (Fig. 1), however, we noted that the net photosynthesis rates of the soil crusts are lowest at the middle of the north- as well as the south-facing slope, a result which might reflect the water availability on the middle of the slope integrated over

Fig. 1. CO₂ assimilation in the light and respiration in the dark of crust samples from a Negev-loess (Eco-Park site). Data shown are means $\pm$ SD of three independent experiments (crust samples) with 3–10 replicates (1- or 5-min averages) each under controlled laboratory conditions. Light ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (PAR) = 365 (short adaptation) and 500 (long adaptation); $T = 22^\circ\text{C}$.

time. The investigations showed no significant activity gradients, neither on the north- nor on the south-facing slope and showed net assimilation rates in light (PAR = 365–500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) between 30 and 100 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ min}^{-1}$. Respiration under dark conditions showed fluctuations between 20 and 70 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ min}^{-1}$.

In contrast to the Eco-Park crust, we found a substantial gradient of CO₂ exchange for respiration as well as for photosynthesis at the Nizzana site dunes (Fig. 2). The largest activities were observed at the base of the dunes, which is in accordance with the high density of moss coverage (Table 1). The net assimilation at the base of dunes in light ranged between 40 and 70 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ min}^{-1}$, and respiration between 20 and 70 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ min}^{-1}$, both rates decreasing towards the top of the dune. Samples from the upper part of the dunes still showed substantial respiration and light-driven CO₂ assimilation, which we interpreted as an activity of a non-moss containing crust.

The pronounced gradient of the CO₂ exchange on the slope of a Nizzana sand dune was confirmed by spot measurements under field conditions at the site. Here we found a high assimilation rate in light (Fig. 3) at the base of the dune. Samples taken in the middle of the slope and at the top showed no net uptake, but emission of CO₂. Artificial darkening under these conditions revealed a pronounced respiration activity, especially at the moss-containing base of the dune.

Fig. 2. CO₂ assimilation in the light and respiration in the dark of crust samples from a Negev-dune (Nizzana site), under controlled laboratory conditions. Light = 500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (PAR); $T = 22^\circ\text{C}$. Data shown are means $\pm$ SD of three replicates of 5-min measurements of a crust sample.

Fig. 3. CO₂ assimilation in the light and respiration in the dark of crust samples from a Negev-dune (Nizzana site), under field conditions. Light = 2400 μmol photons m⁻² s⁻¹ (PAR); *T* = 20–23°C. Data shown are means ± SD of 5–12 replicates of 1-min measurements of a crust sample.

4. Discussion

Successional growth of biological soil crusts can be affected by physical components such as soil structure and types, radiation intensity, topographic attributes such as slope directions affecting water availability and soil moisture (West, 1990; Belnap, 1995; Belnap and Gillette, 1997; Lange et al., 1997). The data sets obtained in the course of this study show substantial net CO₂ assimilation rates, which are in a range similar to dark respiration rates.

Vegetated dune sand as in Nizzana site, is very vulnerable to anthropogenic activities and can be degraded quickly as a result of trampling or grazing (Danin, 1996). Sand is still arriving to the area from two sources — namely, Egypt which lies to the west (about 1 km), where heavy grazing still occurs and the local dunes themselves (Karnieli and Tsoar, 1995; Danin, 1996). The growth of the filamentous cyanobacteria is relatively rapid and is followed by other crust associates. Mosses need stabilized soil for their

growth, because their life cycle begins with a germinating spore developing to a branched network of filaments (protonema) (Scott, 1982). This protonema is fragile and movement of the soil surface will destroy it. The southern sides of the local dunes because of their angle and exposure to high radiation have very low stability because of minor amounts of vegetation (Tsoar and Moller, 1986; Tsoar, 1990) and biological crust, formed on the soil surface. Grains of fine dune sand are transported easily by wind (Tsoar, 1990) and do not allow crust colonization cores to develop (Danin, 1996). For these reasons, the colonization and development of the crust community in, north down plots, with low radiation intensity, is much faster than at the top or in the south-facing slope of the dune. In the Nizzana site, sand movement by wind erosion clearly influenced the development processes of the biological soil crusts, as seen by its CO₂ exchange rate. We found a gradient of CO₂ exchange at the Nizzana site for both respiration and photosynthesis (Figs. 2 and 3).

Sayeret Shaked Eco-Park has been fenced and enclosed from grazing, since 1987, the slopes showed the same pattern as in Nizzana site, although the angles are less steep. Slopes investigated at this site (Fig. 1) showed that the pattern described in Nizzana site, of differentiation between the CO₂ exchange rates, is limited to the early successional stages, until the thick crust was produced. This may suggest that exposure to high radiation, might affect the distribution of species composition of the crust components. Although mosses substantially contribute to CO₂ exchange rates, well-developed cyanobacterial crusts with low density of moss at the south facing slope of the watershed (Table 1), can produce similar results. Hence, no significant statistical differences were found for CO₂ exchange rates, in poor or rich moss crusts (Fig. 1). The measured CO₂ exchange of samples from the two different Negev sites and different locations

Table 2

Rates of net photosynthesis (NP, in μmol CO₂ m⁻² s⁻¹) of crust samples from the watershed at the Sayeret Shaked Eco-Park and from the sand dune at Nizzana in comparison with some related literature data. PAR is given in μM photons m⁻² s⁻¹

Plot location	NP	Remarks	Reference
Biological crust			
Sayeret Shaked Eco-Park	0.35–1.6	PAR 365–500	This work
Nizzana sand dunes, north-facing slope			
Moss base (laboratory)	1.1–1.2	PAR 365–500	This work
Middle (laboratory)	0.5–0.9	PAR 365–500	This work
Moss base (field)	0.9–2.1	PAR 2400; 20°C	This work
Nizzana sand dunes, north-facing slope	0.7–1.2	PAR 200–600	Lange et al. (1992)
Crust related lichens			
Endolithic lichens	1.1	Negev desert	Lange et al. (1992)
Soil crust lichens	4–11.3	Namib desert	Lange et al. (1992)
Other lichen species	1–20	Negev desert	Lange et al. (1992)

therein show quite significant amounts. The net photosynthesis rates are in close accordance with data reported by Lange et al. (1992) for crust samples from a northern slope from the Nizzana dune site (Table 2).

In order to discuss biological crusts in terms of a net sink for carbon, we need careful measurements of diurnal cycles of such soil crusts under natural conditions, including studies of seasonal variation. Biotic soil crusts are a worldwide phenomenon in arid and semi-arid landscapes (Lange et al., 1992, 1997, 1998). According to Lange et al. (1990), for short times of a day, *Teloschistes capensis*, a lichen species in the Namib desert, photosynthesize, at rates of $0.28\text{--}1.5\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ (ground area), similar to that of a closed layer of beech leaves in a forest in Germany. The soil crust samples of the Negev desert show comparable values. Biological soil crusts with dominant photosynthetically active organisms are a widespread phenomenon in desert, boreal and arctic systems, their contribution to the global cycling of trace gases and elements can be significant for global budgets and should be investigated more intensively.

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