Ecophysiological responses of desiccation-tolerant cryptobiotic crusts

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Abstract: In our present studies, the recovery of photosynthetic activity after rehydration was demonstrated. We measured chlorophyll fluorescence, CO$_2$ gas exchange and the pigment composition in the previously long-term air-dried cryptogamic inselberg crusts collected from two tropical areas. The cryptobiotic crusts were collected from different localities on similar ecological and climatic conditions from extreme habitats of inselbergs (outcrops). These inselbergs are characterized by a dry microclimate and are covered by scarce soil. We found that the ecophysiological responses of both cryptogamic inselberg crusts showed an extremely high degree of desiccation-tolerance due to the fast and full recovery during rehydration. The photosynthetic activity of the cryptobiotic crusts were restored and regained within 15 and 40 min, respectively, after rehydration. Photosynthetic activity of the crusts was retained at all applied light intensities when enough water was available, however the degree of the recovery was different between the crusts. Photosynthetic pigment contents were strongly and positively correlated with water content. Our results indicated that tropical desiccation-tolerant cryptogamic crusts found on inselberg rock surfaces have CO$_2$ fixation ability in the range of cyanobacteria and lichens, suggesting that at a global scale they can assimilate CO$_2$ in a significant amount.

Keywords: Chlorophyll fluorescence • Chlorophyll content • CO$_2$ assimilation • Cryptogamic crust • Rehydration • Tropics

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1. Introduction

The global importance of inselbergs for several aspects of biodiversity research has been recognized in recent years. Inselbergs occur in a broad range of sizes, vary significantly in their degrees of isolation throughout the Earth and they are characterized by low soil development and unique vascular plant cover [1]. At global scale, the cyanobacterial biomass forms a significant part of the whole vegetation of inselbergs in the semi-arid and arid regions [2] and nearly cover up two-thirds of the dry-land areas [3,4]. The cryptogamic crusts (biological soil crusts, cryptobiotic crusts, BSCs, CBCs) are dominant constituents of many ecosystems of the Earth from the arctic and alpine through the temperate and mediterranean to the tropical/subtropical climate region [5,6]. These cryptogamic crusts exist under very harsh environments such as the seemingly naked rock surfaces of inselbergs (isolated rock outcrops), which are fully exposed to sunlight and high intensity UV-B radiation, extreme temperature and water stress [7]. The limits of tolerance, the suites of physiological, anatomical, and molecular changes that accompany desiccation and the effects of desiccation on metabolism and ecological processes have been documented in a variety of species [8]. The cryptogamic crusts of inselberg rock surface in
tropical/subtropical areas revealed a surprisingly high variety of cyanobacteria, algae, fungi and lichens [9,10] which are the main primary producers in these regions [11]. Organisms that can grow on limestone, chalk, dolomite, sandstone and granite as well as on any type of soils [12] sometimes exist bound tightly to the surface and are hard to remove (at least without any hurt or damage to the crust). The most important common feature of cryptogamic crust is that organisms composing the crusts are mostly desiccation-tolerant. These life forms are able to tolerate the loss of their total limited free water content and acclimatize to frequent hydration/dehydration cycles. Therefore, the physiology of these cryptogamic crusts fully depends on the amount of available water or dew [13-15]. However, the biological activity of CBCs is based on the time and frequency of dehydration and on the amount of precipitation and light exposure [16,17]. In addition, these crusts composed of mainly cyanobacteria, which have chlorophyll a and also phycobilin pigments, generally have the ability to fix atmospheric nitrogen and improve the nutrient content of the soil in the tropical regions [11,18]. Due to these features cryptogamic organisms can occupy the extreme environmental areas and have the ability to survive the unfavourable periods (limit of water) for which the vascular plants are incapable.

Similarly to other low productivity ecosystems, such as rock surfaces, where the domination of higher plants is restricted [8], the cryptogamic organisms form a considerable part of the whole biomass, and thereby they contribute essentially to the carbon budget of arid and semi-arid areas. However, the cryptobiotic crusts of tropical and subtropical inselberg rock surfaces dominate a significant amount of area in a global scale [1]. Due to the large extension of rocks they probably constitute a huge biomass in the tropics [19]. Therefore, the role of this cryptogamic crust in carbon turnover must have a global importance [2,20]. Even though the number of studies concerning inselbergs has increased over the past years, large gaps still exist in regard to our understanding of basic attributes of this ecosystem, e.g. how can they activate the photosynthetic system upon rehydration and develop protection against high light intensities during growth as well as dehydration periods [19,21]. Most of the studies [22-25] have focused mainly on structure, distribution, nitrogen fixation or work with isolated cultures. Despite their importance only a few studies are interested in the ecophysiology of cyanobacterial crust communities of the tropical and subtropical inselberg rock surfaces [7,9,19,21,26-28] and seasonally inundated system of plans and dunes [29,30]. Most studies deal with the photosynthesis of the cryptogamic crusts under laboratory conditions [29] while only few characterize the photosynthesis of free-living cyanobacteria under natural conditions in the tropical field [7,21,28,31] and desert [11,13,30]. In addition, as BSCs dry out more slowly due to their embedment to the rock or soil surfaces (under their natural habitats) and therefore may retain water longer than lichens and mosses. Nevertheless, there are no reports about some very important properties of the cryptobiotic crusts namely their structural adaptations, how long they can tolerate the desiccation state and what are the dynamics and the time scale of their recovery, especially on the inselberg rock surfaces.

The goal of this study was to investigate the recovery of photosynthetic activity after rehydration by measuring chlorophyll fluorescence, CO₂ gas exchange and photosynthetic pigment composition in the previously long time air-dried cyanobacteria dominated cryptogamic inselberg crusts. Our observations were based on the different structural adaptations and recovery dynamics of photosynthetic parameters in response to rehydration following a continuous unhydrated state of the crusts.

2. Experimental Procedures

2.1 Collection and structural investigation of the cryptobiotic samples

The cryptogamic crusts with their original rock surfaces were collected in an air-dried state from the granite rock surface of inselberg in a more seasonal climate with about five dry months in Tanzania (2004) and from gneiss inselberg rock surface, with a much shorter dry season and higher amount of rainfall, from French Guiana (2000), during the dry seasons. Inselbergs appear black coloured due to a dense cover of consolidated cryptobiotic crusts which are tightly bound to the rock surfaces. The rock surfaces were covered by approximately 1 to 1.5 mm of thick microbial crust layer with a dense crumbly structure, mainly composed by cyanobacteria providing greater water infiltration. The crust samples, intact on their original rock surface, were stored in dry state at room temperature in the dark and were used in the rehydration experiments. Their structure and species composition was investigated in a rehydrated state. Although the species composition of different African and Neotropical crusts was studied at many places, no one has tried to investigate their structure, which connects closely with the function of different crust elements. The first impression about the layering of the crusts and its structure could be obtained by dissecting microscope by fracturing the crust covered rock substrate. The finer structure and species composition with dominance relations could be established using a higher (40-1250 x) magnification of...
light microscopy, and finally by using scanning electron microscope. Evaluation of the dominance of different crust components has been founded on the basic works of Jaag [32] and of Golubić [33] by applying the Braun-Blanquet’s AD values in possibly 5 light fields of the microscope at low magnification. During his cryptobiotic crust studies Pócs [34] distinguished 22 strategy types according to their structure, of which at least 10 occur on inselberg rock surfaces.

2.2 Rehydration procedure
Rehydration of the air-dried cryptogamic crust samples was carried out by the addition of distilled water. The water was spread as a thin, continuous water layer on their surfaces using a home-made rehydration chamber in which the water was circulated by a water pump trying to simulate the natural infiltration process. Pieces of crusts with their original substrata which were dried for various times were rehydrated for 10 min and 3 h, respectively and exposed to 250-300 μmol photon m⁻² s⁻¹ at room temperature. During the measurements the water supply of the samples was continuously provided through a thin water layer. The structural investigations were carried out after five hours of rehydration.

2.3 Chlorophyll-α fluorescence and CO₂ assimilation measurements
Quantum efficiency of PSII was determined by chlorophyll fluorescence measurements using a Hansatech (King’ Lynn, UK) MFMS1 modulated fluorometer. The previously wetted samples (10 min and 3 h, respectively) were dark adapted for 15 min before measuring the fluorescence kinetics on intact crusts together with their basic substrate. The light intensity of the modulated measuring beam (1.6 kHz) was 100-150 nmol photons m⁻² s⁻¹, actinic light (650 nm, 370 μmol photons m⁻² s⁻¹) was used to assess steady state fluorescence and the maximum fluorescence level was measured with saturating white light pulses of 3000 μmol photons m⁻² s⁻¹. The effective PSII quantum yield (ΦPSII/ΦPSII), the potential quantum yield of PSII (FV/FM), the photochemical fluorescence quenching (qP) and non-photochemical quenching (NPQ) was observed from dark-adapted samples using the chlorophyll fluorometry method described by Genty et al. [35] and Schreiber and Bilger [36]. The protocol of analysis of chlorophyll fluorescence quenching, the calculation of fluorescence parameters and the standards are based on: Fv/Fm = (Fm-Fo)/Fm, ΦPSII = (Fm’-Fs)/Fm’, qP = (Fm’-Fs’)/ (Fm’-Fo’), NPQ = Fm/Fm’-1.

Measurements of net CO₂ assimilation rate were carried out by a portable IRGA system (CIRAS-2, PP Systems, UK) operated in differential mode under controlled conditions of temperature and light intensities that were used in closed system mode. To examine the kinetics of the CO₂ gas exchange rate, we constructed a special 5x7 cm sized chamber to attain the continuous measurements of samples that were illuminated by different light intensities. Measurements were carried out at 500, 1000, 1500, 2000 μmol m⁻² s⁻¹ photosynthetically active radiation and a CO₂ flow rate of 200 μmol s⁻¹. Photon flux densities were calibrated by LiCor quantum sensor. Illumination was supplied by a cold light (FLQ 150, Hund Wetzlar) source. Experiments were carried out under ambient CO₂ concentration (approx. 370 μmol mol⁻¹) at room temperature (22-25°C). The net CO₂ assimilation rate was referred to as surface area (μmol CO₂ m⁻² s⁻¹). The surface of the samples was 3-5 cm² in case of CO₂ exchange measurements and 6-10 cm² in the event of fluorescence measurements. At least five replicates were done in all experiments.

2.4 Water content, cryptobiotic crust biomass and photosynthetic pigments and element content
The water content (WC, %) of the crusts were measured and calculated by a direct thermogravimetric method using the fresh (FW) and dry (DW) weight of the samples after 5 hours of rehydration by removing the crusts from rock surfaces and drying out at 80°C to a constant mass, respectively: WC= [(FW-DW)/FW] ×100 [37]. After 5 hours of rehydration, we took samples from the crusts within 3 hours to determine the water content – pigment compositions during deprivation of water supply (dehydrated period).

The photosynthetic pigments such as chlorophylls as well as total carotenoids were quantitatively determined in 100 % acetone extract solution by spectrophotometer after scratching off the rehydrated cyanobacterial crust from the rock surface [38]. Photosynthetic pigment contents of the crust samples related to total dry weight were quantified as mg g⁻¹. The measurements were repeated at least five times.

The total content of carbon and nitrogen of the crusts were determined by flash combustion using a Carlo-Erba (Fisons) NA 1500 elemental analyzer following careful separation of the air-dried crusts from the rock surfaces.

2.5 Statistical analyses
The data were analyzed by the Student’s t-test. Differences are considered to be significant at a level of P<0.05 or below. Linear and second order exponential equations corresponded to the data for the relationship of the photosynthetic pigment content and water content.
3. Results

3.1 Structure and species composition of the investigated samples

3.1.1 Cryptobiotic crust from French Guiana, South America (collected by Schultz, Porembski and Büdel in April 2000)

This CBC is composed of cyanobacteria (up to 40%) in an alternating mosaic with lichens (60%) on the surface of bare gneiss inselbergs, surrounded by seasonal rain forests. By naked eye it is hard to distinguish the two, being similar in color and thickness. Where the cyanobacterial component dominates, it is present in the form of a purplish black, 0.1-0.5 mm thick crust divided into three-stories (Figure 1A). The uppermost layer is 200-500 μm high and made up of treelike branching *Stigonema ocellatum* (Dillwyn) Thuret (AD value 4). Below the “canopy” of *Stigonema* a much lower (up to 100 μm high), horizontally branching “shrub” layer is found follows by *Scytonema ocellatum* Lyngbye (AD value 2). The lowermost, discontinuous ground layer, direct on the rock substrate, is formed by the shade tolerant *Chroococcidiopsis* sp., with globose cells of 10-30 μm diameter (AD value 2). This structure was described first by Pócs [34], as the “siliciferous subtype of the Compound (fruticose-coccoid) Type” from the south-west Australian inselbergs.

3.1.2 Cryptobiotic crust from Tanzania, East Africa (collected by Pócs and Tuba in July 2004)

The CBC sample (No. 04102/XII) was taken from granite outcrops of Mindu Hill, South of Morogoro town, at 560 m altitude, with strongly seasonal rainfall of 850 mm per year. It developed in a silted, shallow depression of 1 m² on a gently sloping rock surface, which during rainy season becomes a typical temporary “pool”. The surrounding area is dominated by dry deciduous forest and its fire derivate, a “miombo” woodland with loose canopy of *Brachystegia* and *Julbernardia* (Caesalpiniaeae) trees.

The macrovegetation of sample itself consists of scattered, annual grasses. The thin quartz sand layer in the pool is covered by a 1 mm thick, lilac-brownish black, two layered crust (Figure 1B), with upstanding fur of *Scytonema millei* Born. ex Born. et Flah. (Figure 2A, AD value 4). Below the *Scytonema* fur a weft of *Schizothrix purpurascens* (Kütz.) Gomont spreads (Figure 2B, AD value 3), intermixed with the filaments of scattered annual grasses.

![Figure 1](image1.png)

**Figure 1.** Schematic profile of the cryptobiotic crust from French Guiana (A) and Tanzania (B). St: *Stigonema ocellatum*, So: *Scytonema ocellatum*, C: *Chroococcidiopsis* sp., L: Lichen thallus, Sm: *Scytonema millei*, SP: Mixed weft of *Schizothrix purpurascens* and of *Porphyrosiphon notarisii*.

![Figure 2](image2.png)

**Figure 2.** *Scytonema millei* Born. ex Born. et Flah. (A) and *Schizothrix purpurascens* (Kütz.) Gomont. (B) from the Tanzanian crust sample. Scale bars represent 50 μm.
Porphyrosiphon notarisii (Menegh.) Kütz. (Figure 3B, AD value 2). This type of sample should be classified into the “vertical subtype of the Filamentous Type” first described by Pócs [34].

The lichen parts of the collected cryptogamic crust from both French Guiana and Tanzania contain mostly cyanobacteria as photobiont (cyanolichens) but a few parts of the crusts may be composed of green algae (not identified). Nevertheless we suppose that the assimilation rate of the whole crust can be assigned mainly to different cyanobacteria associations.

### 3.2 Photosynthetic pigments, water content and biomass, and element content

Chlorophyll, carotenoid, carbon and nitrogen content, as well as C/N ratios can be found in Table 1. The chlorophyll content showed large differences between the two samples (Table 1). The cryptobiotal crust collected from Tanzania had almost twice as much chlorophyll contents as in samples collected from French Guiana. The carotenoids were also found in higher amount in samples from Tanzania but there were no significant difference between the two crusts (Table 1). However, chlorophyll and carotenoid contents showed strong relation with the water content ($r^2$=0.9469 for chlorophylls and 0.8333 for carotenoids, Figure 4). The correlations between chlorophyll or carotenoid content and water content include all measuring points of the crusts independently from the habitat type. The photosynthetic pigment concentrations of the crusts continuously increased following rehydration and actually dropped when WC decreased below 40 %. The C/N ratio was significantly higher in French Guiana crust caused by the lower N content (lower more than 57%) compared to Tanzania crust. The C content was also higher in Tanzanian crust but it did not show significant differences (Table 1).

![Figure 3. Mixed Schizothrix purpurascens (Kütz.) Gomont (the paler filaments) and Porphyrosiphon notarisii (Menegh.) Kütz. (the darker filaments) (A) and Porphyrosiphon notarisii (Menegh.) Kütz. (B) from the Tanzanian crust sample. Scale bars represent 50 μm.](image)

![Figure 4. Relationship between the water content (WC) and the photosynthetic pigment concentration (○ indicated the chlorophylls (●) carotenoids) of the cyanobacterial crusts from the rock surface of the inselberg under different water conditions. Data is derived from both crusts independently from the habitat type.](image)

<table>
<thead>
<tr>
<th>Content per dry weight</th>
<th>Tanzania</th>
<th>French Guiana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophylls (mg g⁻¹)</td>
<td>1.07±0.13*</td>
<td>0.68±0.08</td>
</tr>
<tr>
<td>Carotenoid x+c (mg g⁻¹)</td>
<td>1.32±0.14</td>
<td>1.10±0.13</td>
</tr>
<tr>
<td>C (g kg⁻¹)</td>
<td>351.39±9.99</td>
<td>239.99±38.63</td>
</tr>
<tr>
<td>N (mg kg⁻¹)</td>
<td>42.74±1.064</td>
<td>18.58±1.94</td>
</tr>
<tr>
<td>C/N</td>
<td>8.23*</td>
<td>12.86</td>
</tr>
</tbody>
</table>

* indicates significant difference at $P<0.005$; ± indicated the standard deviation. Comparisons were made between the Tanzanian and French Guiana samples.
3.3 Chlorophyll fluorescence responses

All measured fluorescence parameters increased rapidly in both crusts previously wetted for 10 min however samples from French Guiana showed lower values than Tanzania's (Figure 5, 6). The Fv/Fm values had changed between 0.25 and 0.85 and were found to continuously increase in both measured samples after a short-term of rehydration but there was no significant difference between the two samples except after 15 and 30 min of rehydration (P<0.05, Figure 5). The effective quantum yield of PSII (ΦPSII) reached its maximum parallel with Fv/Fm values (Figure 5). Fv/Fm and ΦPSII remained almost constant following previous long-term rehydration (3 h) (Figure 6) but the values were lower compared to short-terms of rehydration, 0.6 to 0.8 and 0.4 to 0.55, respectively for the two crusts. The photochemical fluorescence quenching parameter (qP) was not detected in samples derived from French Guiana after a 10 min short term of rehydration. After 3 h of rehydration qP had similar values in both samples. In the case of Fv/Fm and ΦPSII curves, after 270 min of rehydration a significant difference was observed between the two samples, because the samples collected from French Guiana showed a rapid decrease in the mentioned two parameters (Figure 6). However, the non-photochemical fluorescence quenching parameter (NPQ) values of the two samples were very low; they did

![Figure 5](image_url)

**Figure 5.** Chlorophyll-α fluorescence parameters in previously air-dried cryptobiotical crust derived from Tanzania and French Guiana after 10 min of rehydration. Error bars represent standard deviation (n = 5).

![Figure 6](image_url)

**Figure 6.** Chlorophyll-α fluorescence parameters in previously air-dried cryptobiotical crust collected from Tanzania and French Guiana after 3 h of rehydration. Error bars represent standard deviation (n = 5).
not really change and had not even reached the value of zero (data not shown).

3.4 Net CO$_2$ assimilation responses
Net CO$_2$ assimilation rates of cryptobiotic crusts were measured at different light intensities from 500 to 2000 $\mu$mol m$^{-2}$ s$^{-1}$ after 10 min of rehydration (Figure 7). The maximal net CO$_2$ assimilation rate of the cryptobiotic crusts from Tanzania was observed after 15-20 min of rehydration while the samples collected from French Guiana attained it after 40-50 min of rewetting at all applied light intensities (Figure 7). The maximum values were higher in the case of samples collected from Tanzania at almost all light intensities (except at 1000 PPFD). Interestingly, the maximum net CO$_2$ assimilation rate of cyanobacterial crusts collected from Tanzania approached the value of 1.7 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ after 15 min of illumination while the samples collected from French Guiana had not reached the 1.0 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ value at 2000 PPFD even after 40 min of illumination (Figure 7 and 8). The differences in the maximal net CO$_2$ assimilation rates at different light intensities between the two samples rose with increasing light intensity (Figure 8).

4. Discussion

4.1 Cryptobiotic crust types
We suppose from the comparison of the two investigated (and from the analysis of many other) crust types, that among tropical inselberg conditions, the multilayered “siliciferous subtype of the Compound (fruticose-coccoid) Type” characterizes the naked rock surfaces which are temporarily wetted, only during rainfall while the weftlike “vertical subtype of the Filamentous Type” occurs in temporarily waterlogged, small depressions called “oriçangas” according to the terminology of Porembski and Barthlott [1]. Most known species of Chroococcidiopsis are named as sciophilic, living in rock crevices, in caves or even under the disintegrating surface of rocks (chasmooendolithic) as their cells do not have protective pigment in their mucilaginous sheath. In the lowermost layer they are relatively protected from strong UV radiation, even on the exposed rock surface. This genus is often mentioned as the first colonizers of rock surfaces. Similarly, Porphyrosiphon notarisii was reported to be an efficient colonizing strain. In contrast to lowermost layers in upper regions of the crusts, dominated...
by dark-coloured cyanobacteria (e.g. Scytonema sp.), species have UV-protective pigments such as scytonemin and gloecapsin [39-41] which protect them against high solar UV radiation [42]. The upper layer of the crusts is colonized later than the lower ones and the taxa found in the upper layer usually possess less gelatinous sheaths and are more filamentous in form. Stigonema is one of the most frequently mentioned genera which can survive for very long dry periods and are widely distributed in dried areas [43] and similarly to Scytonema species compose black films and crusts over desert and semi-desert soils and on exposed rock faces. Schizothrix purpurascens may form dense and tough mats, can be found in the lower, shaded layer of samples from Tanzania (Figure 1A), prefers low illumination and was collected from temporally wet inselberg surfaces as was described in Schizothrix perforans [44]. Porphyrosiphon species are important and conspicuous components of the surfaces of arid and semiarid soils worldwide such as the volcanic soils [45]. Porphyrosiphon, Schizothrix and Scytonema species possess gelatinous sheaths to provide a strong bind for basic substrate, such as water particles, by their intertwined rope-like growth forms. Covering surfaces by algae can maintain about eight times the moisture than pure soil areas. Occurrence of different cyanobacteria species in crusts reflects the high degree of adaptation to extreme environments such as periodic and short rehydration periods. Stratification and consecutive appearance of species builds a well organized and hieratic construction such as the existence of specialized structures [46]. Stronger pigmented and thicker sheathed species occur at drier sites, while pools and streams are characterized by thin-sheathed species e.g. Schizothrix sp.

### 4.2 Analysis of the photosynthetic pigments, water content and biomass

A recent study showed that the ecophysiological responses of the cyanobacterial crusts can vary mainly depending on the microclimatical adaptation. Their photosynthetic apparatus showed fast regeneration following rehydration. However the ability and degree of their ecological adaptations changed with microenvironmental circumstances (living in an exposed or pool site). This is reflected by lower chlorophyll content in samples collected from French Guiana which had a more opened and sun exposed microhabitat and an absence of standing water (Table 1). The higher chlorophyll content of the Tanzania crust corresponded to shaded pool site conditions, which are necessary for optimal and effective photosynthetic activity. In the daytime when the radiation and the crust temperature are very high, the wetness is insufficient for the activity of CBCs organisms which showed high chlorophyll degradation. Based on C and N contents it also supported that the productivity of the Tanzanian sample is higher due to microclimatical conditions of extreme pool habitat (Table 1). Decreased chlorophyll content in the French Guiana crust could contribute to lower photosynthetic activity which could appear in lower C storage.

A significant correlation was observed between water content and photosynthetic pigment contents independently from the crust types (Figure 4). This also showed that the recovery of chloroplasts is very fast following rehydration and showed immediate responses to water availability. The differences between the two crusts were revealed in the response of cyanobacteria to rehydration. Differences were observed in CO₂ assimilation rate and also in the fluorescence parameters as described below. The strength and sensitivity of the relationship between the photosynthetic properties and the amount of available water may be influenced by the different species compositions which are determined by the ecological factors and circumstances.

### 4.3 Chlorophyll-α fluorescence responses

Our results might indicate that the length of the desiccation and rehydration period have very important roles in the values of fluorescence parameters. In the case of both long term desiccated samples, progressive increases were found in all fluorescence parameters following 10 min of rehydration. Figure 5 and 6 showed that all measured fluorescence parameters after different times of...
rehydration were lower in samples from French Guiana than in samples from Tanzania. Cryptobiotic crusts derived from Tanzania showed an unusually high Fv/Fm fluorescence value, approximately 0.8, after 80 min of rehydration. This value corresponded to the observation in healthy leaves of higher plants that is about 0.8 [47] and higher than the highest value observed in cyanobacterial lichens, 0.62 [48]. However, the crusts did not contain just cyanobacteria but green algae also, which might explain the values of variable fluorescence. Potential quantum yield of PSII after dark adaptation, Fv/Fm, was mostly between 0.2 and 0.4 in free living cyanobacteria from tropical inselbergs [21] they only observed cyanobacterial mats in the field to reach values of Fv/Fm near 0.6. Samples collected from French Guiana reached the value 0.6 after 80 min of rehydration. The different responses of the two samples might be attributed to the length and frequency of desiccation-rehydration cycles as well as to the diversity of species adapted to special microclimatical conditions. For example, Stigonema dominated crusts are characterized by straggling and a less dense structure (Figure 1A) which is explained by exposition of strong solar radiation while the 1 mm thick crust is rather compact and complex. This is due to more protected and shaded pools which temporarily cover the microhabitat with water (Figure 1B). Long-term rehydration (3 hours) resulted in lower and steady-state values of Fv/Fm, between 0.4 and 0.6 compared with 10 min of rehydration due to the complete recovery of photosynthetic system (Figure 6). Many studies observed similar results for cyanobacteria that reflect a steady-state condition of photochemistry [21,48]. The relatively high qP, even at high light intensities, is related to the ability of cyanobacteria to remove electrons from PSII and maintain the centres open [21,49]. This provides an expressive index of the balance between excitation of PSII and the electron transport chain and reflects a complex and flexible electron transport system, as well as a generally high PSI/PSII ratio [50]. Presumably, following a desiccation period the disassembled photosynthetic apparatus undergo a fast recovery upon rehydration [16,51] due to the immediate reactivation of the PSII, PSI complexes and phycobilisomes which do not require de novo protein and pigment synthesis [52,53]. The protection mechanism of PSII against desiccation as well as photodamage significantly depends upon the species as well as on the environmental conditions [54]. The NPQ values of the measured cryptobiotical crusts were very low (data not shown) and, similarly to cyanobacteria, NPQ is often lacking as reported by earlier studies on cyanolichens [55].

4.4 Net CO₂ assimilation responses
Recovery from desiccation depends on the duration of the dormant state of desiccation [21] and the degree of microclimatical adaptation. This finding was reflected in our results as the maximal CO₂ assimilation rate was observed earlier (following 15-20 min rehydration) in samples collected from inselberg pools (Tanzania) periodically covered by standing-water compared with the responses of French Guiana samples exposed to opened and fast flowing water surfaces (Figure 7). The relatively fast recovery of net CO₂ assimilation ability in both samples (15 and 40 min, respectively) would seem to indicate special adaptation of cryptobiotical crusts to the extreme environment on inselbergs. Lichens, mosses and desiccation tolerant plants need more time (several hours) to reach the compensation point of respiration to photosynthesis while our crusts attain it within less than half an hour following rehydration. However, differences in the CO₂ assimilation rates between Tanzanian and French Guiana samples are most probably related to the complex ecological relationship which contains extreme microhabitats, varied microclimatical adaptations and different species composition. All of these result in various ecophysiological responses which could derive directly from the different adaptation strategy of the two crusts. Previous studies [29,30] reported a similar tendency of the CO₂ assimilation rate of different ecological characteristics of cryptogamic crusts although the authors did not investigate the ability of the layers to tolerate the desiccation and these samples were collected from completely different climatic conditions compared to our samples. Various crusts species have typical responses to environmental factors resulting in different C gain under the same environmental conditions that were also reflected in our results. The photosynthetic responses of cyanobacteria to high light intensities depend on the irradiance during growth [19]. Crusts did not showed light saturation curves at any applied light intensities while light-saturated rate as high as of 2.5 μmol·m⁻²·s⁻¹ was recorded at light intensities of 200–400 μmol·m⁻²·s⁻¹ reported by Schleshinger et al. [56] from crust Majove Desert and others reported at least twice higher photosynthetic rates at 1500-2000 μmol·m⁻²·s⁻¹ [29]. These also reflect that considering only the diversity of species, microhabitat, and microclimatical conditions is not enough but one should also take the differences into account not of just level of community but rather their association. The success of the two studied tropical inselberg cryptogamic crusts on exposed rock surfaces is due to their special ecophysiological abilities, such as the possibility to adapt to the high light intensities, to
desiccation tolerance and especially to the intercellular \( \text{CO}_2 \) (\( \text{Ci} \)) concentrating mechanism of cyanobacteria and to their \( \text{N}_2 \) fixation (neither investigated in this paper).

Inselbergs are characterized by short, infrequent and variable hydration periods (in many cases hydration occurs just in the early morning hours originating from high vapour from the air) and by extremely high radiation. The two cryptobiotic crusts were collected from different localities (Tanzania and French Guiana) with similar ecological and climatic conditions. We examined the effect of high light intensities on the photosynthetic properties of the samples when water supply is not a limiting factor and we measured the response of the crusts to different length of drying-wetting cycles. As we expected, the optimal photosynthetic activities of the cyanobacterial crusts exist at rather low light intensities and show an adaptation to their natural microclimatical conditions where the most suitable time for activation is early morning when the water is available and the radiation is not too high [14]. The characteristic and above described multilayered structure of the investigated crusts surely contributes a lot to their solar and desiccation tolerance. The strongly pigmented upper “canopy” layer acts as an UV filter for the lower strata [7,40,41] where they can utilise better both strong and weak radiation periods. We supposed there would also be an important role in our investigated crusts in similarly protecting pigment content in both crusts. Concerning desiccation tolerance, the described structure enables the lower strata to assimilate for a much longer period under the protection of upper strata, preventing quick desiccation.

We can conclude that both investigated cryptobiotic crusts become physiologically active with relatively high rates of photosynthesis under wet conditions.

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