Cyanobacteria in biological soil crusts of India

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Species of filamentous, sheath-forming cyanobacteria were the major component in the blackish-brown crusts on the upper millimetre of soils in different regions of India. Chlorophyll *a* density of these biological crusts on lateritic soils of Bhubaneswar, Orissa, brown forest soils of Salbani, West Bengal, arid soils of Tiruchirappalli, Tamil Nadu and sandy soils of old Goa ranged between 248 and 282 mg m^{-2}, which is of the same order as in the leaves of higher plants. The species composition of cyanobacterial community in these soil crusts of India has been documented. Organisms in the crust absorbed water rapidly, regained photosynthesis and nitrogenase activity, which were stabilized within 48 to 72 h of wetting. The dominant cyanobacteria in the crust were rich in carotenoid pigment, absorbing at 507 nm and mycosporine amino acid-like substances absorbing in UV only when desiccated and simultaneously exposed to bright sunlight. It is concluded that the highly active upper layers of arid soils contain certain sheathed cyanobacteria that bind with soil particles forming a matrix protecting them from wind erosion. In addition, they are finely tuned in their physiology to the natural environmental conditions contributing organic matter and nitrogen through carbon and nitrogen fixation, thus increasing soil fertility.

Keywords: Algae, biological soil crust, cyanobacteria, nitrogen fixation, photosynthesis.

THE upper millimetre of dry soil often appears crusty in nature due to growth of microorganisms comprising cyanobacteria, algae and/or lichens. Soil particles form an intimate association among these organisms, resulting in a biological crust that covers the surface of the soil as a coherent layer[1]. Biological soil crusts often occur in hostile environmental regimes that include extremes in temperature and light, and scarcity of water[2]. Many microorganisms withstand such adverse ecological conditions and respond to the onset of dry conditions by entering into a dormant resistant state, and thus have been distinguished as pioneers of succession on soil. As a component of the soil crust, the microflora acts as a reservoir of plant nutrients, as organisms influencing the soil structure and activity of other microorganisms, and as agents for the incorporation of organic carbon and nitrogen through photosynthesis and nitrogen fixation[3–5].

Occurrence of biological soil crust has been reported from almost all arid and semi-arid ecoregions world wide[6]. Despite their widespread occurrence, the global picture of distribution of soil crust biota and communities is not available in many regions, especially from Asia and almost nothing from the Indian subcontinent[7,8]. Recently, it has been stated that biodiversity of biological crusts on the top soil surfaces is the most poorly researched habitats on earth[9,10]. In India, there are few reports of soil cyanobacteria and algae, however, are independent of their relationship to biological soil crusts[11,13]. Occurrence of blackish-brown crusts in the upper millimetre of dry soils of barren lands was observed in almost all regions of India showing tropical climatic conditions. Nothing is known yet about the composition of soil crust organisms and their physiological responses to wetting. A study was therefore carried out to evaluate the occurrence and distribution of algae and cyanobacteria in the biological crusts at four different locations in India differing in soil characteristics, and the photosynthesis, nitrogen fixation and spectral characteristics of the organisms inhabiting therein.

Materials and methods

Sampling and identification

Crust samples were collected from the upper surface of dry soils from varied locations at four different regions of India during the summer season (March–May, 2003 and 2004). These were from: (i) laterite soils in and around Bhubaneswar (N 20°16′28″, E 85°50′37″) in the east coast; (ii) brown soils in the forest of Salbani (N 22°38′24″, E 87°20′19″) under the ancient Gondwanaland in the central regions; (iii) arid soils in and around Tiruchirappalli (N 10°48′33″, E 78°41′36″) in the southern region and (iv) sandy soils of old Goa (N 15°28′03″, E 73°56′14″) in the west coast of India. Scraping of surface soil in open ground devoid of vegetation (in the immediate area) was collected, stored in presterilized screw cap Tarson bottles and transported to the laboratory for analysis.

Soil crust samples were wetted with sterile water and examined under light microscope. Within 12 to 24 h of wetting cyanobacterial filaments could be visualized; however, isolation and culturing under defined conditions was required for their identification. A pinch of each crust was transferred to agarized BG 11 medium[14] with or without combined nitrogen and incubated at 25 ± 1°C under continuous light from fluorescent tubes at an intensity of 7.5 Wm^2. Cyanobacterial filaments that grew in the culture plates were isolated and subsequently transferred to nutrient media in cotton-stoppered conical flasks. Morphometric analysis of each

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species was made and identified following Desikachary[15], Komerak and Anagnostidis[16,17] and Anagnostidis and Komerak[18,19]. The dominant organism in each crust was purified following standard methods[20] and axenic culture of the organisms was used in certain experiments. Bright field-illuminated photomicrographs of the cyanobacterial forms were taken with a Meiji ML-TH-05 trinocular research microscope using a F-108 Nikon camera.

Extraction of pigment

Equal amounts of crust and/or organism from the experimental cultures (air-dried weight = 100 mg) were extracted with 5 ml of 90% (v/v) methanol for 3 h followed by incubation for approximately 2 min at 60°C in a waterbath. The supernatant was taken in a quartz cuvette and absorption spectra was measured in a Hitachi U-2000 UV-visible spectrophotometer in the wavelength range of 250 to 700 nm. The amount of chlorophyll *a* was determined following Mackinney[21].

Acetylene reduction assay

Approximately 1 g of soil crust or air-dried organism from culture was dispensed into 25 ml glass vials. Sterilized distilled water was added to give a total volume of 7.5 ml (except one tube containing dried crust material collected from nature). The vials were sealed with screw caps fitted with silicon rubber septa. Acetylene generated from calcium carbide was injected into the vials, giving a gas atmosphere in the vials of air plus 10% acetylene. All samples were set up in duplicate sets of three each for light and dark incubations; the latter for assessing dark nitrogen fixation. After incubation for specific duration in light or dark according to the requirement of the experiment, 100 µl of gas phase was withdrawn using a gas-tight Hamilton syringe and analysed for ethylene on AIMIL–Nucon 5765 model gas chromatograph with FID detector fitted with Porapak-T SS column (80–100 mesh; carrier gas nitrogen, 30 ml min^{-1}; column temperature, 100°C; injector temperature, 100°C; detector temperature, 120°C). Acetylene reduction activity was expressed as n mol ethylene g^{-1} air-dried material h^{-1}.

Measurement of photosynthesis

Photosynthetic oxygen evolution was measured using a Clark-type oxygen electrode (Hansatech, UK). Homogenized suspension of a known quantity of crust was transferred to a reaction vessel fitted with an outer jacket for water circulation and temperature maintenance (25°C). The suspension was stirred on a magnetic stirrer. Light was provided by a Xenophot 100 W halogen lamp. Signal from the cathode was fed through a preamplifier to increase the efficiency of recording. Photosynthetic oxygen evolution was expressed as µmol O_2 g^{-1} dried material h^{-1}.

Table 1. Chlorophyll *a* content of soil crusts from different regions of India

Soil crust from location	Chlorophyll *a* (µg/g crust)	Chlorophyll *a* (mg/m^2)
Bhubaneswar (Orissa)	180 ± 17	256 ± 21
Salbani (West Bengal)	196 ± 22	282 ± 14
Tiruchirappalli (Tamil Nadu)	284 ± 29	264 ± 29
Old Goa (Goa)	121 ± 11	248 ± 33

Values represent mean of ten determinations ± SD.
Freshly collected, air-dried crusts were used in the experiment.

Results

Blackish-brown soil crusts tightly adhering to the upper surface of soil were observed in all the study sites (Figures 1 *a*, *b* and 2 *a*, *b*). Chlorophyll *a* content of the dried crust varied from 122 to 181 µg. However, when chlorophyll *a* content of each crust spread over 1 m^2 area was calculated, it appeared to be almost similar quantitatively (248 to 282 mg m^2), irrespective of the region of occurrence, with minor variation (Table 1).

Biological composition of the soil crusts was studied in laboratory culture. Microscopic examination of each wetted soil crust for up to 72 h revealed brownish coloured filaments of a particular cyanobacterium; however, the morphological features of these organisms at this state were insufficient for identification (Figures 1 *c*, *d* and 2 *c*, *d*). Upon culture in BG 11 medium, different cyanobacterial species were found as major components of the soil crusts (Figures 1 *e*, *f* and 2 *e*, *f*). The crust on lateritic soils of Bhubaneswar harboured non-heterocystous cyanobacterium *Lyngbya arboricola*, whereas the dominant organism in the brown soil in the forest floor of Salbani was *Scytonema ocellatum*. In the arid soil of Tiruchirappalli, heterocystous *Scytonema chiastum* was dominant, and in the sandy soils of old Goa, non-heterocystous *Plectonema notatum* dominated. Several other cyanobacterial species appeared on prolonged incubation and made a minor component in the soil crusts. However, all of them belonged to cyanobacteria, but the association of organisms differed in various crusts (Table 2). In general, dominant forms belonged to *Lyngbya*, *Plectonema* or *Scytonema*, all covered by a distinct coloured sheath layer. The associated components were represented by genera *Oscillatoria*, *Phormidium Microcoleus*, *Nostoc*, *Calothrix*, *Aulosira*, *Fischerella*, *Westiellopsis* and *Hapalosiphon*; other species of *Lyngbya*, *Plectonema* or *Scytonema* different from those dominant, were also encountered. During monsoon, however, green algal forms of the genera *Fritschiella*, *Vaucheria*, *Chlorella*, *Chlorococcum*, few diatoms, liverworts and mosses were found intermingled with cyanobacteria in the crusts.

All the soil crusts absorbed water rapidly and became saturated within 15 min of wetting. Photosynthetic oxygen evolution increased steadily and within 12 to 24 h of wetting, it was nearly stabilized. Early stabilization of the rate of photosynthesis within 12 h of wetting was observed in the crust from Tiruchirappalli; this also showed maximum oxy-

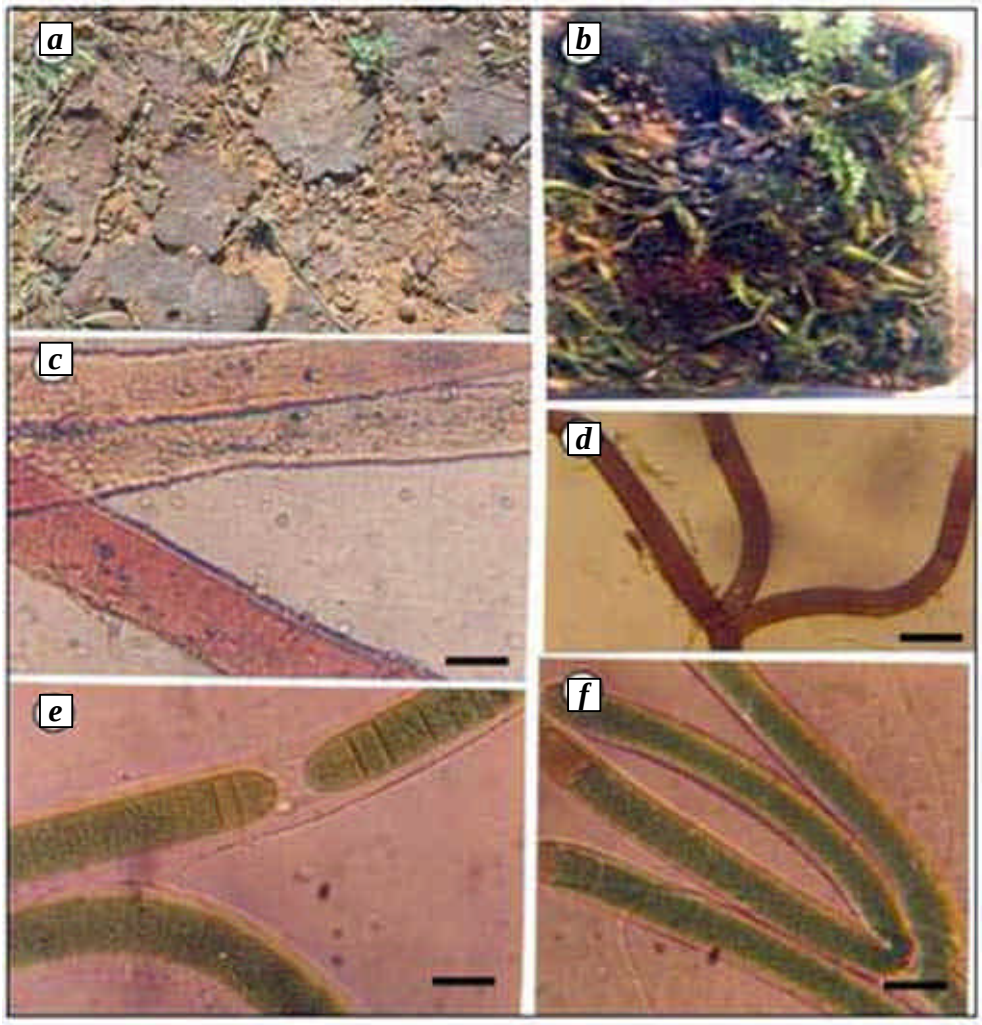

Figure 1 ***a–f.*** ***a***, ***b***, Photograph of (***a***) crust on lateritic soils of Bhubaneswar, Orissa, and (***b***) brown forest soils of Salbani, West Bengal. ***c***, ***d***, Light microscopic photograph of cyanobacteria filaments after 24 h wetting of crusts from (***c***) lateritic soils and (***d***) brown forest soils. ***e***, ***f***, Light microscopic photograph of cyanobacteria (***e***) *Lyngbya arboricola* isolated from lateritic soil crusts of Bhubaneswar and (***f***) *Scytonema ocellatum* isolated from brown soil crust of Salbani. Bar for photographs ***c***–***f*** = 10 μm.

gen evolution per gram of crust (Figure 3). Photosynthesis of the wetted crusts from sandy soils of Goa and lateritic soils of Bhubaneswar took longer time for saturation. Nitrogenase activity (acetylene reduction assay; ARA) of soil crusts from all the four regions increased with time of wetting, and maximum activity was obtained after 72 h. This was comparable with the values obtained taking the same quantity of air-dried cells of the corresponding cyanobacterium from the culture (Table 3). The crust from lateritic soils of Bhubaneswar and sandy soils of old Goa contained non-heterocystous forms of cyanobacteria; hence it did not show ARA in light up to 72 h of incubation. However, the brown forest soils of Salbani and arid soil of Tiruchirappalli showed nitrogenase activity in light as well as dark due to presence of heterocystous cyanobacteria, *S. ocellatum* and *S. chiastum*; ARA value in dark was much lower corresponding to incubation in light (Table 3).

Dominant cyanobacterial forms recovered from the four crusts showed brownish-coloured sheath layer around their trichomes (Figures 1 *c*, *d* and 2 *c*, *d*); this imparts specific colouration to the soil crust. Absorption spectra of the 90% (v/v) methanolic extracts of soil crusts showed a prominent absorption at 671 nm due to chlorophyll *a*, at 507 and 480 nm due to carotenoids, and in the UV (344 and 266 nm) due to mycosporine amino acid-like substances (MAAs). In addition, the crust from sandy soils of Goa showed absorption at 298 and 282 nm due to presence of additional MAAs (Figure 4). Presence of MAAs in all these soil crusts was also confirmed from the absorption maxima of their 20% (v/v) methanolic extracts in the UV-region of the spectrum (Figure 4; dotted line). However, when the dominant organisms from each of the crusts were isolated and grown in culture, they showed bluish-green colouration and lost the coloured pigment from their sheath layer (Figures 1 *e*, *f* and

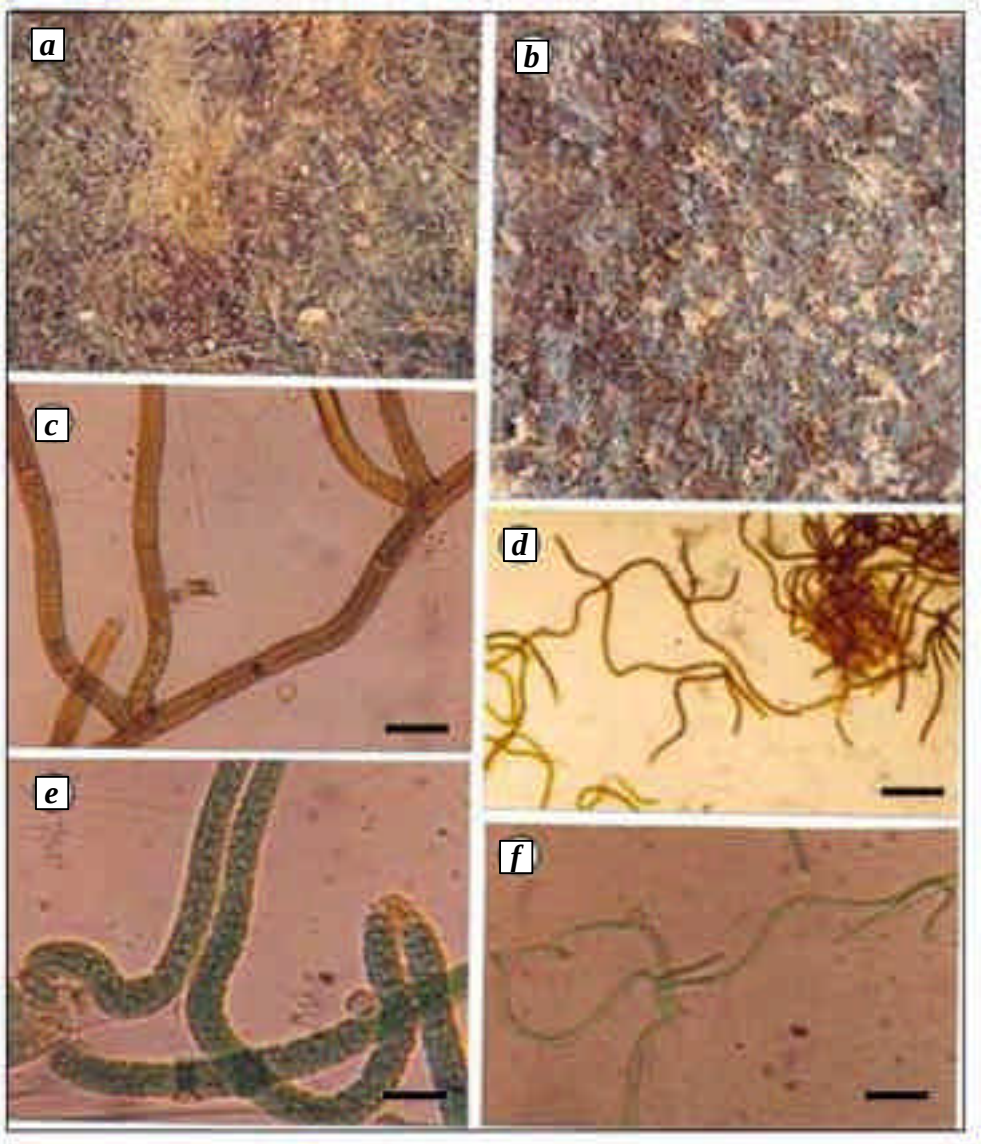

Figure 2 ***a–f.*** ***a***, ***b***, Photograph of (***a***) crust on arid soils of Tiruchirappalli, Tamil Nadu and (***c***) sandy soils of old Goa. ***c***, ***d***, Light microscopic photograph of cyanobacteria filaments after 24 h wetting of crusts from (***c***) arid soils and (***d***) sandy soils. ***e***, ***f***, Light microscopic photograph of cyanobacteria (***e***) *Scytonema chiastum* isolated from arid soil crusts of Tiruchirapalli and (***f***) *Plectonema notatum* isolated from sandy soil crust of old Goa. Bar for photographs ***c***–*f* = 10 μm.

2 *e*, *f*). Absorption spectra of the 90% methanol extract of these organisms from culture did not show absorption at 507 nm and also in the UV region of the spectrum (Figure 4).

Discussion

Soil is a dynamic system comprising physical, chemical and biological components. While physical and chemical status of the soil has a bearing on fertility level of the soil, productivity of soil largely depends on the microbial population. In countries like India having tropical climatic conditions, even though the soil surface is exposed to direct sunlight and is virtually dry during most part of the year, it showed visible growth of blackish-brown soil crusts inhabited by several cyanobacterial forms. Early reports on soil algae from India did not distinguish between the typical aquatic and edapic cyanobacterial forms, as many have been reported to occupy the border line. Forms like *Microcystis*, *Anabaena* and *Oscillatoria* were reported as strict hydrophytes, while *Scytonema* and many species of *Calothrix*, *Nostoc*, *Tolypothrix* and *Westiellopsis* were reported only on moist shaded soil surfaces[13] or on dry exposed substratum[22,23]. On the contrary, forms like *Plectonema*, *Phormidium*, *Nostoc*, *Calothrix* and *Cylindrospermum* have been reported to occupy intermediate positions, as they were capable of growing

both in water as well as soil[11,24]. In the present work, however, it has been reported that certain species of *Scytonema*, *Plectonema* or *Lyngbya* were the dominant component of soil crusts in different regions of India. These organisms occur in the upper millimetre of dry soil along with other cyanobacterial species belonging to genera *Oscillatoria*, *Phormidium*, *Microcoleus*, *Nostoc*, *Calothrix*, *Aulosira*, *Fischerella*, *Westiellopsis* and *Hapalosiphon*. All these organisms produce copious mucilage and/or enveloped with coloured sheath layer and occurred binding with finely textured soil particles that form their matrix.

Table 2. Dominant cyanobacteria in soil crust from different regions of India and associated species appearing in culture

Cyanobacteria	Soil crust from different sites			
	Bhubaneswar	Salbani	Tiruchirappalli	Old Goa
Oscillatoria formusa	+	–	+	–
O. ornate	+	+	–	–
Lyngbya arboricola	++	–	+	–
L. ceylanica	–	+	+	–
L. major	+	–	+	–
L. palmarum	–	–	+	+
Phormidium ambiguum	–	+	+	+
Plectonema notatum	–	–	–	++
P. putuale	–	–	+	+
Microcoleus lacustria	+	–	+	+
M. sociatus	+	–	+	+
M. subtorulosus	+	–	–	–
Cylindrospermum indicum	+	–	–	–
Nostoc calcicola	+	–	+	–
N. carneum	–	+	–	–
N. coeruleum	+	–	–	–
N. ellipsosporum	+	+	–	–
N. linckia	+	–	–	–
N. microscopicum	+	+	+	–
N. piscinale	+	+	+	–
N. punctiforme	+	–	+	+
Anabaena torulosa	+	–	–	–
Calothrix brevissima	+	–	–	–
C. bharadwajae	–	+	+	–
C. castellii	+	+	–	+
C. clavatoides	+	+	+	–
C. fusa var. *crassa*	+	–	–	–
C. javanica	+	–	–	–
C. marchica	+	+	+	–
C. parietina	+	+	–	–
C. scytonemicola	+	+	–	–
Aulosira prolifica	+	+	–	–
A. pseudormamusa	–	+	–	–
Scytonema chiastum	–	–	++	–
S. ocellatum	+	++	–	–
S. rivulare	+	–	–	–
S. schimidtii	–	–	+	–
S. varium	+	–	+	–
Tolypothrix bouteillei	+	–	–	–
T. nodusa	–	–	+	+
Westiellopsis prolifica	+	+	+	–
Fischerella ambigua	+	–	–	–
F. muscicola	+	+	+	–
Hapalosiphon welwitschii	–	+	+	+
Stigonema tomentosum	+	–	–	–

++, Dominant organism in the crust; +, Associated species appearing in culture.

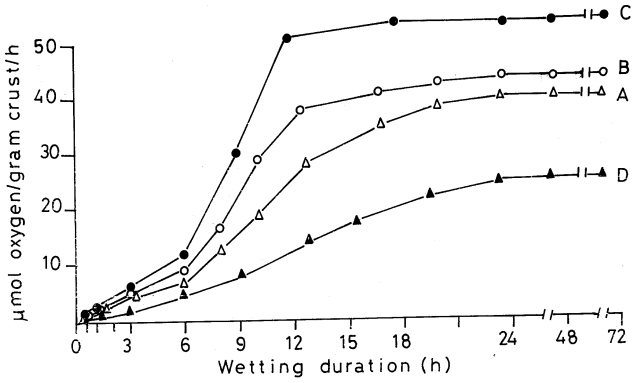

Figure 3. Photosynthetic activity of soil crusts from different locations after wetting for different durations. A, Lateritic soil crusts of Bhubaneswar; B, Brown forest soil crust of Salbani; C, Arid soil crust of Tiruchirappalli and D, Sandy soil crust of old Goa.

All these cyanobacterial species gained their photosynthetic activity within 12 to 24 h of wetting and also were capable of recovering their nitrogenase activity within 72 h of water saturation. Even the non-heterocystous cyanobacteria occurring as dominant component in certain crusts showed ARA in darkness, demonstrating their nitrogen-fixing capability. Thus nutritional independence for carbon in general and for both carbon and nitrogen in the nitrogen-fixing forms, makes these organisms the predominant component of soil microflora. In addition, the cyanobacteria, while occurring in the crust, are enveloped by brownish-coloured sheath layers and are known to contain extracellular sunscreen pigments and MAAs. This has been suggested as an adaptive strategy of terrestrial cyanobacteria for photo-protection against short wavelength irradiance[25,26].

Cyanobacteria occupy just the upper few millimetres of the soil crust because many of them need light for their photosynthetic activities and also because less water is available in these superficial layers derived from dew, fog and showers. Presence of free-living, nitrogen-fixing cyanobacteria in the upper layer of soil suggests their contribution of fixed nitrogen to the arid soil ecosystems. Further, the thin cover of photosynthetic microorganisms as soil crust is an important source of carbon fixation. The chlorophyll density in the soil crust varied from 248 to 282 mg m^{-2} in four different regions of India. Almost similar rates of chlorophyll density of microbial mats from Namib desert of South Africa varying between 200 and 500 mg m^{-2} has been reported[27], which is of the same order as in the leaves of higher plants.

Conclusion

These results showed that the soil crusts have considerable photosynthetic potential, although this is limited by the need for hydration before it becomes functional.

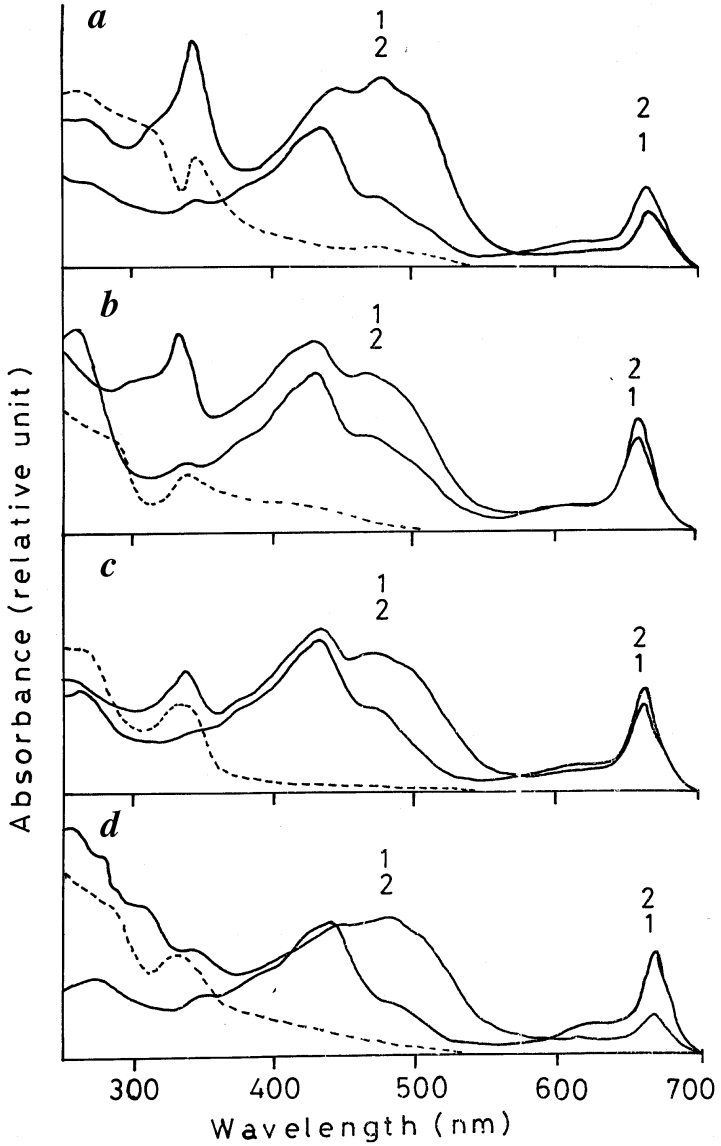

Figure 4. Absorption spectra of methanolic extract (90%, v/v) of (1) soil crust from different locations and (2) corresponding dominant cyanobacterium from culture. Absorption spectra of 20% (v/v) methanolic extract of soil crust are shown as dotted lines. Equal amounts of crust and air-dried organisms from culture (100 mg) were used for pigment extraction. ***a–d***, Soil crust and corresponding cyanobacterium of (***a***) lateritic soils of Bhubaneswar, (***b***) brown forest soil of Salbani, (***c***) arid soils of Tiruchirappalli and (***d***) sandy soils of old Goa.

Table 3. Acetylene reduction activity (nmol ethylene g^{-1} air dried material h^{-1}) of soil crusts from different regions of India after wetting for different durations, and also from corresponding cyanobacterium from culture

Soil crust from location	Dominant species	Condition of incubation	Time of wetting of crust			Corresponding cyanobacterium from culture
			0 (without wetting)	24 h	72 h	
Bhubaneswar (Orissa)	*L. arboricola*	Light	0	0	0	0
		Dark	12 ± 3	44 ± 8	49 ± 6	64 ± 5
Salbani (West Bengal)	*S. ocellatum*	Light	16 ± 5	87 ± 12	242 ± 28	394 ± 33
		Dark	12 ± 4	29 ± 4	36 ± 7	58 ± 12
Tiruchirappalli (Tamil Nadu)	*S. chiastum*	Light	21 ± 8	119 ± 14	387 ± 41	542 ± 43
		Dark	13 ± 6	31 ± 7	39 ± 6	54 ± 15
Old Goa (Goa)	*P. notatum*	Light	0	0	0	0
		Dark	6 ± 2	58 ± 11	63 ± 9	92 ± 14

Values represent mean of five determinations ± SD.

Under hydrated condition, they add substantial quantities of organic matter through primary production, narrow the C : N ratio making the soil more fertile and also increase humus content of soil. The ecological value of biological crusts is important as it protects soils from wind erosion, and also act as an absorptive organ for moisture/water, which in turn provides germination grounds for seeds of flowering plants.

1. Belnap, J., Büdel, B. and Lange, O. L., Biological soil crust: Characteristics and distribution, In *Biological Soil Crusts: Structure, Function and Management* (eds Belnap, J. and Lange, O. L.), Springer, Berlin, 2001, pp. 3–30.
2. Ullmann, I. and Büdel, B., Ecological determinants of species composition of biological soil crusts on landscape scale. In *Biological Soil Crusts: Structure, Function and Management* (eds Belnap, J. and Lange, O. L.), Springer, Berlin, 2001, pp. 203–213.
3. Smith, G. D., Lynch, R. M., Jacobson, G. and Barnes, C. J., Cyanobacterial nitrogen fixation in arid soils of central Australia. *FEMS Microbiol. Ecol*., 1990, **74**, 79–90.
4. Adhikary, S. P. and Sahu, J. K., Survival strategies of cyanobacteria occurring as crust in the rice fields under drought conditions. *Indian J. Microbiol.*, 2000, **40**, 53–56.
5. Johansen, J. R., Cryptogamic crusts of semiarid and arid lands of North America. *J. Phycol*., 1993, **29**, 140–147.
6. Büdel, B., Diversity and ecology of biological crusts. *Prog. Bot*., 2002, **63**, 386–404.
7. Büdel, B., Biological soil crust of Asia including the Don and Volga region. In *Biological Soil Crusts: Structure, Function and Management* (eds Belnap, J. and Lange, O. L.), Springer, Berlin, 2001, pp. 87–94.
8. Büdel, B., Synopsis: Comparative biography and ecology of soil crust biota and communities. In *Biological Soil Crusts: Structure, Function and Management* (eds Belnap, J. and Lange, O. L.), Springer, Berlin, 2001, pp. 141–152.
9. Moore, P. D., Life in the upper crust. *Nature*, 1998, **393**, 419–420.
10. Copley, J., Ecology goes underground. *Nature*, 2000, **406**, 452–454.
11. Marathe, K. and Kushaldas, C., Observations on the algal crusts of Nagpur soils. *J. Univ. Bombay*, 1997, **44**, 66–76.
12. Awasthi, D. D., A key to the microlichens of India, Nepal and Sri Lanka. *Bibl. Lichenol*., 1991, **40**, 1–337.
13. Venkataraman, G. S., Goyal, S. K., Kaushik, B. D. and Roychoudahury, P., *Algae: Form and Function*, Today and Tomorrows, New Delhi, 1974, pp. 183–186.
14. Rippka, R., Deruelles, J., Waterbury, J. B., Herdman, M. and Stanier, R. Y., Generic assignments, strain histories and properties of pure cultures of cyanobacteria. *J. Gen. Microbiol*., 1979, **111**, 1–61.
15. Desikachary, T. V., *Cyanophyta*, ICAR Monograph on Algae, ICAR, New Delhi, 1959, p. 686.
16. Komerak, J. and Anagnostidis, K., Modern approach to the classification system of cyanophytes. 2. Chlorococcales. *Arch. Hydrobiol. Algolog. Stud*., 1986, **43**, 157–226.
17. Komerak, J. and Anagnostidis, K., Modern approach to the classification system of cyanophytes. 4. Nostocales. *Arch. Hydrobiol. Algolog. Stud*., 1989, **56**, 247–345.
18. Anagnostidis, K. and Komerak, J., Modern approach to the classification system of cyanophytes. 3. Oscillatoriales. *Arch. Hydrobiol. Algolog. Stud*., 1988, **50–53**, 327–472.
19. Anagnostidis, K. and Komerak, J., Modern approach to the classification system of cyanophytes. 5. Stigonematales. *Arch. Hydrobiol. Algolog. Stud*., 1990, **59**, 1–73.
20. Venkataraman, G. S., *The Cultivation of Algae*, ICAR, New Delhi, 1969, p. 319.
21. Mackinney, G., Absorption of light by chlorophyll solutions. *J. Biol. Chem*., 1941, **140**, 315–322.
22. Tripathy, P., Roy, A., Anand, N. and Adhikary, S. P., Blue-green algal flora on the rock surface of temples and monuments of India. *Feddes Repert*., 1999, **110**, 133–144.
23. Pattanaik, B. and Adhikary, S. P., Blue-green flora on archeological monuments of India. *Bull. Bot. Surv. India*, 2002, **44**, 61–74.
24. Sahu, J. K., Nayak, H. and Adhikary, S. P., Blue-green algae of rice fields of Orissa state. I. Distributional pattern in different agroclimatic zones. *Phykos*, 1996, **35**, 93–110.
25. Garcia-Pichel, F. and Castenholz, R. W., Occurrence of UV-absorbing mycosporine amino acid-like compounds among cyanobacterial isolates and an estimate of their screening capacity. *Appl. Environ. Microbiol*., 1993, **59**, 163–169.
26. Potts, M., Mechanism of desiccation tolerance in cyanobacteria. *Eur. J. Phycol*., 1999, **34**, 319–328.
27. Lange, O. L., Meyer, A., Zellner, H. and Heber, U., Photosynthesis and water relations of lichen soil crusts: Field measurements in the coastal fog zone of the Namib desert. *Funct. Ecol*., 1994, **8**, 253–264.

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