Folia Microbiol. **51** (2), 121–128 (2006) **http://www.biomed.cas.cz/mbu/folia/**

Survival of Blue-Green and Green Algae under Stress Conditions

S. GUPTA, S.C. AGRAWAL

Department of Botany, University of Allahabad, Allahabad, India

Received 30 October 2005

ABSTRACT. Terrestrial blue-green algae *Scytonema millei*, *Phormidium bohneri* and *Lyngbya mesotricha* survived to 100 % at atmospheric temperatures of 5–36 °C and relative humidity 55–100 % in rainy, winter and spring seasons but the survival was 15–25 % in summer when atmospheric temperature reached 48 °C and relative humidity was ≤23 %. *Microcoleus chthonoplastes* maximum survival was ≈80 % in rainy season followed by a decrease to ≈½ and ¼ level in winter and spring, respectively; it disappeared in summer but a few cells and/or trichomes enclosed within sheath may be surviving sticking to soil, not evident microscopically, since the population reappeared at the same place with the onset of rain. Terrestrial green alga *Rhizoclonium crassipellitum* survived only in spring and died at the onset of summer without forming any dormant cell and/or reproductive structure. Only *P. bohneri* survived better and longer under submerged conditions in liquid medium than air-exposed on moist soil surface in the culture chamber, while the other algae fared almost equally or slightly better air-exposed on moist soil surface (or even on 2 % agarized medium) than when suspended in liquid medium, indicating that air exposure rather than submerged conditions was needed for most of the terrestrial algae to survive. Water stress imposed on growing algae either on high-agar-solid media or in 0.2–0.6 mol/L NaCl liquid media in the culture chamber reduced vegetative survival in all; it resulted in death without any dormant cell remaining. When stored in desiccators over fused $CaCl_2$, *M. chthonoplastes* died within ½ month, *R. crassipellitum* and *L. mesotricha* within 1 month, *P. bohneri* within 1½ month, and *S. millei* not even within 1½ month, indicating their survival pattern against atmospheric dryness to be wide; it also explained the *M. chthonoplastes* absence in summer and *S. millei* presence throughout the year. At increased atmospheric humidity the desiccation-sensitive algae (*e.g.*, *M. chthonoplastes*) survived better than a desiccation-resistant alga (here *S. millei*). All algae survived considerable darkness (*S. millei* >1½ month; *P. bohneri*, *M. chthonoplastes* and *R. crassipellitum* >1 month, and *L. mesotricha* >½ month), and low light intensity of 2 and 10 μmol m^{-2} s^{-1} which explains their prolific growth in shady places. All algae were differently sensitive to wet heat (45 °C for 5–40 min) and to UV shock (0.96–3.84 kJ/m^2).

Literature data on the survival of terrestrial algae with respect to environmental stress conditions are relatively scarce. Terrestrial forms of *Vaucheria* (Stahl 1879), *Zygnema* (Fritsch 1916) and *Protosiphon* (Moewus 1935) formed cysts and/or akinetes under drought. Bristol-Roach (1919) reported that some herbarium specimens of terrestrial blue-green algae *Schizothrix calcicola*, *Nostoc ellipsosporum* and *Microcoleus* sp. were preserved for 70 years. Terrestrial green alga *Trentepohlia aurea* was observed to withstand long periods of drying without appreciable change (Howland 1929). Cameron and Blank (1966) showed that desert algal crust, air-dried for 4 years became active and new growth started within 1 d of wetting. Trainor (1970) and Trainor and Gladych (1995) reported that 5 taxa of green soil algae, including one of *Chlorococcum*, can survive for a long time in soil and grew after being in desiccated soil for 35 years. Some terrestrial algae such as *Vaucheria geminata*, *Gloeocapsa aeruginosa*, *Aphanothece nidulans* and *Chroococcus minor* were more sensitive to water stress, heat and UV than *Scytonema hofmanni*, *Phormidium foveolarum*, *Lyngbya martensiana* and *Oscillatoria agardhii* (Agrawal and Singh 2002; Agrawal and Pal 2003). Harel *et al.* (2004) observed rapid activation of photosynthesis in dried *Microcoleus* sp. within desert sand crust when it was rehydrated.

Here we report the vegetative survival of four terrestrial blue-green algae *Scytonema millei*, *Phormidium bohneri*, *Microcoleus chthonoplastes* and *Lyngbya mesotricha*, and of one terrestrial green alga *Rhizoclonium crassipellitum* with respect to different seasons in the year under natural conditions; and under submerged and air-exposed conditions, water stress, dry storage, darkness and dim light or following heat and UV exposure in a culture chamber.

MATERIAL AND METHODS

Algal materials. All algae were collected from different and/or same locations at Allahabad (India). *S. millei* BORNET ex BORN. et FLAH, form extensive dark bluish-black cover on all and/or most of the cement

walls and/or roofs of buildings (Fig. 1A) and on trees bark surfaces (Fig. 1B). Filaments of *S. millei*, each covered with a brownish sheath, were interwoven forming a felt-like mass on the substratum (Fig. 1C, D). *P. bohneri* SCHMIDLE and *M. chthonoplastes* THURET ex GOMONT filaments, together, formed bluish-green patches sticking to soil surface (Fig. 1E). *P. bohneri* and *M. chthonoplastes* filaments were densely interwoven among themselves and with each other (Fig. 1F–H). *M. chthonoplastes* filaments, each with a number of compactly arranged trichomes within a sheath (Fig. 1G). *L. mesotricha* SKUJA was collected while growing as a blue-green mucilagenous sheet on damp soil surface. *L. mesotricha* filaments were straight, arranged in parallel and each covered with a thin hyaline sheath (Fig. 1I). *R. crassipellitum* WEST and WEST filaments, having cells covered with a thick wall (Fig. 1J), grew attached to damp soil surface underneath trees, forming a loose light green mat.

Survival of algae in nature. Different algal materials were brought to laboratory directly from nature periodically throughout the year and displayed vegetative survival (and reproduction, if any) with respect to seasonal changes in atmospheric temperature and relative humidity. Percent vegetative survival in *S. millei*, *L. mesotricha* and *R. crassipellitum* was determined by counting the number of living vegetative cells relative to dead vegetative cells (looking hyaline, empty, distorted or deformed) and in *P. bohneri* and *M. chthonoplastes* by counting living filaments (since their cells were too small to be counted) relative to dead filaments (looking pale, yellowish-brown, empty) out of ≈6000–7000 vegetative filaments cells and/or vegetative filament collected from five different locations at the same and/or different places.

Survival under submerged and air-exposed conditions. Five-d-old filaments obtained from cultures maintained in liquid BG 11 medium (Stanier *et al.* 1971; pH adjusted prior to autoclaving to 7.5) in the culture chamber were either inoculated into a fresh liquid BG 11 medium or spread air exposed on moist soil surface (sterilized dry garden soil–sterilized tap water, 1 : 1, *W*/*W*, soil pH 7.2) and kept in the culture chamber at 25 °C and light intensity of ≈40 μmol m^{-2} s^{-1} from daylight fluorescent tubes for 12 h a day. The mean relative humidity of the culture chamber during all experiments was 47–55 %. The vegetative survival in different algae was determined periodically by counting ≈6000–7000 vegetative filament cells and/or filaments till they survived under both conditions.

Survival under physical and physiological water stress. Five-d-old vegetative filaments isolated from liquid BG 11 were separately inoculated on solid media containing 2–8 % agar and into a liquid medium with 0.2–0.6 mol/L NaCl and kept in the culture chamber. The percentage survival was determined.

Survival (viability) of dried algae stored air-exposed and in desiccators. Five-d-old vegetative filaments obtained from liquid BG 11 medium were blot-dried completely and separately placed on filter papers in watch glasses and kept in the culture chamber either air-exposed as such or inside desiccators over fused $CaCl_2$. Viability of dried algae stored either way was determined by counting the number of surviving vegetative cells and/or filaments as the case may be after 3-d inoculation of dried algal materials into liquid BG 11 medium placed in the culture chamber.

Survival in darkness and in low light intensity. Five-d-old different algal materials obtained from liquid BG 11 medium maintained at 40 μmol m^{-2} s^{-1} in the culture chamber were separately exposed to light intensity of 2 and 10 μmol m^{-2} s^{-1} by adjusting the distance of inoculated culture tubes from the light source in the culture chamber. The light intensity was measured using a lux meter (*Lutron Electronics*, USA). Some of the inoculated culture tubes were wrapped in black paper and kept in the dark in the culture chamber. The percentages of vegetative survival in all algae were determined as usual.

Survival following exposure to heat and UV light. Five-d-old different algal materials were separately suspended in sterile BG 11 medium and were placed at 45 °C for 5–40 min and then kept in the culture chamber and observed how long they survive. Different algal materials separately placed in 10 mL sterile BG 11 medium, spread in open Petri dishes (diameter 90 mm) were exposed to UV light from a *Philips* germicidal lamp (main output at 254 nm and a fluence rate of 3.2 W/m^2). The energy fluence of UV light which was obtained by increasing the time of exposure from 5 to 20 min ranged from 0.96 to 3.84 kJ/m^2. After irradiation, materials were transferred directly to culture chamber and assessed periodically for vegetative survival. Materials not heated or UV-irradiated served as controls.

RESULTS AND DISCUSSION

Survival of algae in nature. S. millei, *P. bohneri* and *L. mesotricha* survived almost 100 % in rainy, winter and spring seasons when the atmospheric temperature ranged between 5 and 36 °C, relative humidity being 55–100 %, but the survival was variously lowered to ≈¼–⅙ level or more in summer when the atmospheric temperature reached 48 °C and humidity ≤23 %. However, *M. chthonoplastes* disappeared in summer but reappeared in the rainy season and survived maximally to about 80 %, and then lowered to ≈½ and

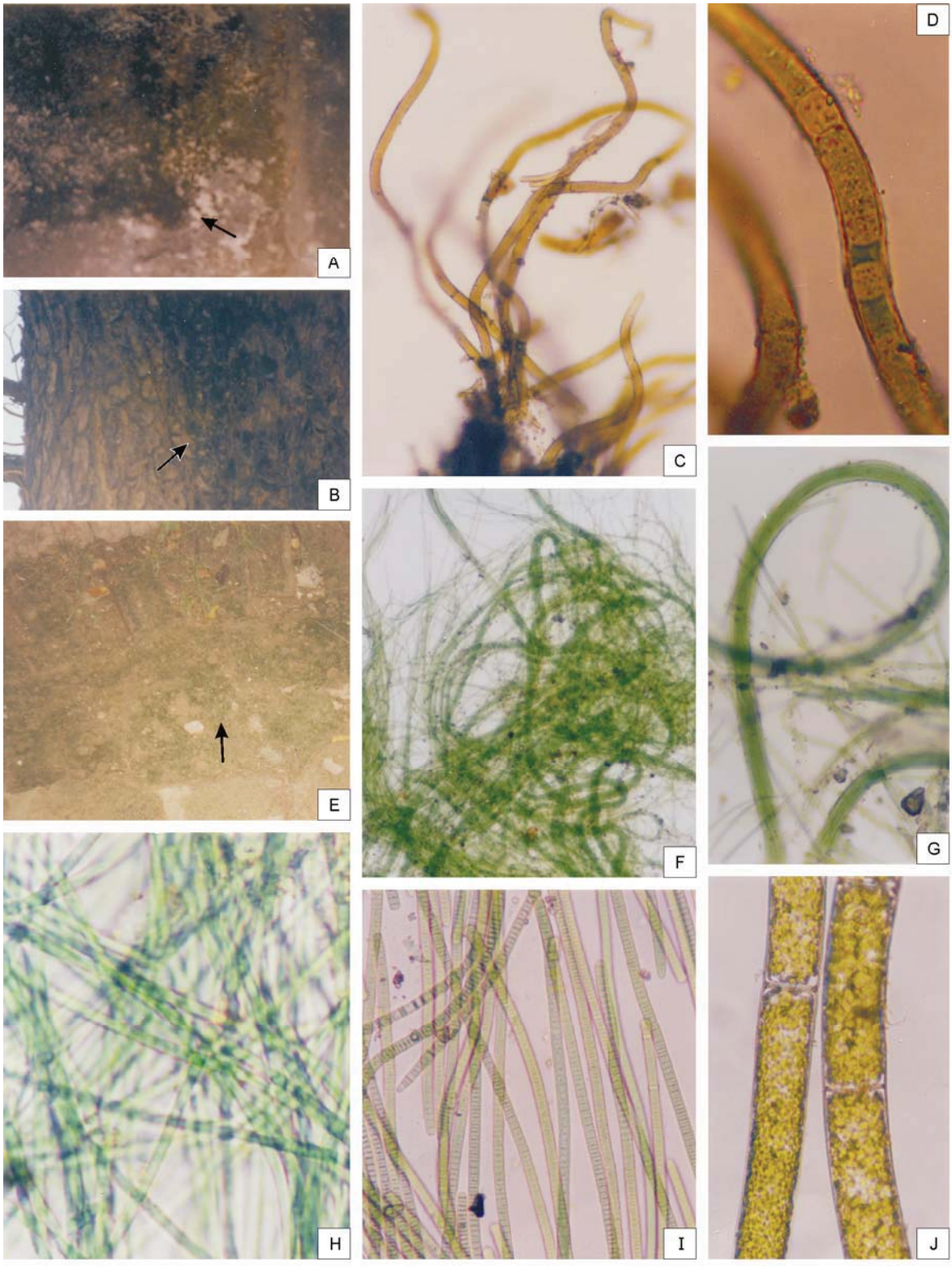

Fig. 1. **A**: Dark bluish-back patches (*arrow*) of *S. millei* on building wall; **B**: *S. millei* (*arrow*) growing on tree bark surface; **C**: *S. millei* filaments, ×109; **D**: *S. millei* filaments showing heterocysts and thick sheath, ×504; **E**: bluish-green patches of *P. bohneri* and *M. chthonoplastes* growing together (*arrow*) on the soil surface; **F**: *P. bohneri* and *M. chthonoplastes* filaments densely interwoven with each other, ×84; **G**: *M. chthonoplastes* filaments each having number of trichomes, ×185; **H**: *P. bohneri* filaments interwoven with each other, ×989; **I**: *L. mesotricha* filaments, ×420; **J**: *R. crassipellitum* filaments, ×143.

¼ level in winter and spring, respectively (Table I). It seems that few cells and/or trichomes of *M. chthonoplastes* enclosed within sheath, sticking to soil surface, not visible microscopically, still survived in summer, since the population reappeared at the same place with the onset of rain. (However, no *M. chthonoplastes* population reappeared if the dried soil in the summer containing the algal patch was brought to culture chamber and watered with tap water for many days.) Bristol-Roach (1920) demonstrated that *Nostoc muscorum* and *Nodularia harveyana* reappeared in the soil remoistened after 79 years of dryness. Fritsch (1922) found that air-dry cells of genera *Pleurococcus* and *Prasiola* possess a special power of retaining a certain amount of water and that a small amount of water may after desiccation enable them to continue their growth and other vegetative functions. Bonham and Palumbo (1951) reported that *Chlorella* species receiving nearly lethal X-ray dose was prone to have contained at least one surviving cell or more (a function of initial population size) which retained the ability finally to multiply at a normal rate under favorable conditions. Even planktonic diatoms pass unfavorable periods by maintaining a low, slowly declining stock of vegetative cells either suspended in water or lying on the sediment (Sommer 1988). *Scytonema* and *Fischerella* cells tolerate desiccation equal to or better than *Nostoc* and the physiological activities resume fairly soon after rewetting (Whitton 1987; Tomaselli and Giovannetti 1993) with liquid than atmospheric water (Lange *et al.* 1992). Harel *et al.* (2004) reported rapid activation of photosynthesis following rehydration of dried *Microcoleus* crust.

Table I. Influence of seasonal variations of atmospheric temperature and relative humidity on the percentage survival of vegetative cells and/or filaments in *S. millei* (*S.m.*), *P. bohneri* (*P.b.*), *M. chthonoplastes* (*M.c.*), *L. mesotricha* (*L.m.*) and *R. crassipellitum* (*R.c.*) in nature[a]

Season	Temperature, °C		Mean relative humidity, %	Survival, %				
	day	night		*S.m.*	*P.b.*	*M.c.*	*L.m.*	*R.c.*
Spring (mid March–mid April)	23–32	17–25	60–91	93	96	21	94	84
Summer (mid May–mid June)	38–48	32–41	23–60	25	21	0[b]	15	0
Rainy (mid July–mid August)	31–36	25–33	76–100	96	100	80	100	0
Winter (January)	15–21	5–9	55–95	93	95	39	100	0

[a]Rounded mean of ≈6000–7000 vegetative cells in all algae except *P. bohneri* and *M. chthonoplastes* where vegetative filaments, each from five different locations at the same and/or different places.
[b]Some cells, not evident microscopically, might retain alive since the population re-appear at the same place in the rainy season.

R. crassipellitum survived appreciably only in spring and died without forming any reproductive structure with the onset of summer and remained absent in rainy and winter seasons (Table I). Various species of *Spirogyra* and *Oedogonium* grew, reproduced and disappeared at different times of the year (Transeau 1916). In nature, during slow desiccation at the onset of summer, some soil algae were able to change the nature of their cells, without any apparent morphological change and resist desiccation (Petersen 1935). It was also possible that the resistant cells could remain viable with the aid of trapped pore water in sub-surface soil.

Survival under submerged and air-exposed conditions. Only *P. bohneri* survived better and longer when grown submerged in liquid medium than air-exposed on moist-soil surface in culture chamber, while *S. millei* and *R. crassipellitum* survived almost equally well, and *M. chthonoplastes* and *L. mesotricha* survived better and longer when grown air-exposed on moist-soil surface than when submerged in liquid medium (Table II). This indicates that terrestrial algae mostly prefer air-exposed moist substratum rather than submergence in the medium to survive (*cf.* Sarma *et al.* 2004). *Trentepohlia aurea*, a strict terrestrial alga, survived longer and better and formed sporangia only under air-exposed conditions (Gupta and Agrawal 2004*a*).

Survival under physical and physiological water stress. Survival in all algae was almost equivalent when grown on 2 % agarized solid media or on moist soil surface air-exposed, but was usually lowered (not in *M. chthonoplastes*, where it was almost equivalent) when grown in liquid media supplemented with 0.2 mol/L NaCl than in standard liquid media (Table II). Vegetative survival in all algae decreased progressively on 2–8 % agarized solid media and more drastically in liquid media containing NaCl beyond 0.2 mol/L level with no cell remaining at the last. However, in blue-green algae, resistance to high concentration of electrolyte may be caused by the formation of cysts or protective impervious envelopes (Hof and Fremy 1933). Increased envelope thickness was also observed in *Chroococcidiopsis* from desiccated cultures, probably contributing

Table II. Influence of submerged condition (SC; in BG 11 medium) and air-exposure (AE; on moist soil), agarized (2–8 %) solid BG 11 and NaCl-supplemented (0.2–0.6 mol/L) liquid BG 11 media, storage of dried vegetative cells and/or filaments air-exposed (SA) or in desiccators (SD; over fused calcium chloride for different time periods), different light intensity (0, 2 and 10 $\mu mol m^{-2} s^{-1}$ for 12 h) on percentage survival of *S. millei*, *L. mesotricha* and *R. crassipellitum* (vegetative cells) and *P. bohneri*, *M. chthonoplastes* (filaments)[a]

Alga	Time months	SC	AE[b]	Agar, %			NaCl, mol/L					SA[c]	SD[c]	Light, $\mu mol m^{-2} s^{-1}$		
				2	4	8	0.2	0.3	0.4	0.5	0.6			0	2	10
S. millei	¼	91	96	–	–	–	93	89	64	26	0	–	–	–	–	–
	½	78	82	95	89	68	74	57	14	0	–	57	38	59	65	74
	1	61	65	82	67	33	51	23	0	–	–	25	10	50	51	56
	1½	29	31	44	36	10	20	0	–	–	–	5	2	14	20	20
	2	7.5	9	20	0	0	0	–	–	–	–	–	–	–	–	–
P. bohneri	¼	–	–	90	81	51	95	74	36	11	0	–	–	80	90	100
	½	100	80	88	69	30	89	31	10	0	–	38	20	56	69	73
	1	81	66	58	28	15	27	0	0	–	–	15	7	12	39	52
	1½	69	30	32	11	2	0	–	–	–	–	1	0	0	10	43
	2	52	8	6	2	0	–	–	–	–	–	–	–	–	–	–
	3	21	0	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. chthonoplastes	¼	86	90	87	71	68	92	69	42	15	0	51	21	70	81	86
	½	56	68	70	51	46	50	40	0	0	–	30	0	33	46	52
	1	16	22	43	18	8	18	7	–	–	–	3	–	4	11	12
	1½	0	6	10	0	0	0	0	–	–	–	–	–	0	0	0
	2	–	0	0	–	–	–	–	–	–	–	–	–	–	–	–
L. mesotricha	¼	77	79	100	79	60	71	42	2	0	0	50	35	57	68	72
	½	42	70	75	63	51	33	12	0	–	–	36	4	20	30	36
	1	16	50	50	29	15	0	0	–	–	–	4	0	0	4	13
	1½	0	31	20	6	0	–	–	–	–	–	0	–	–	0	0
	2	–	12	0	0	–	–	–	–	–	–	–	–	–	–	–
	3	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–
R. crassipellitum	¼	93	94	95	66	59	85	79	61	40	21	46	25	66	80	88
	½	70	80	89	45	35	63	51	39	16	0	20	9	51	60	70
	1	47	59	69	10	0	31	20	8	0	–	0	0	15	23	30
	1½	23	10	36	0	–	6	0	0	–	–	–	–	0	0	8
	2	0	0	2	–	–	0	–	–	–	–	–	–	–	–	–

[a]Rounded mean of three replicates, from each of which ?6000–7000 vegetative cells or filaments were counted; algal materials maintained under a 12-h illumination (fluorescent light of 40 $\mu mol\ m^{-2} s^{-1}$) at 25 °C; mean relative humicity of culture chamber 47–55 %.

[b]Sterilized dry garden soil–sterilized tap water (1 : 1, *W/W*). [c]Survival of dried algal materials 3 d after inoculation in liquid BG 11 medium.

to prevention of water loss (Caiola *et al*. 1996). *Oscillatoria acuminata* trichomes developed a very thin sheath-like structure when grown in 0.8 mol/L NaCl-supplemented liquid media (Agrawal and Singh 1999*b*).

R. crassipellitum survived high agarized solid media less, but high-salinized liquid media more than any of the blue-green algae tested (Table II). Aquatic *R. hieroglyphicum* was twice more sensitive to desiccation (Agrawal and Singh 1999*a*; *cf*. Gupta and Agrawal 2004*b*) than terrestrial *R. crassipellitum* and this might be due to differences in their cell-sap osmotic potentials. Osmotic potential of green algae *Mesotaenium caldariorum*, *Spirogyra varians* and *Zygnema* spp. was reported to be 0.17 mol/L equivalent as NaCl, and of *Chlamydomonas eugametos* 0.11 mol/L (Lothring 1941–42), while that of blue-green algal cell 0.12 mol/L (Pernauer 1958). Terrestrial algae *C. minor*, *G. aeruginosa*, *A. nidulans* and *V. geminata* were very sensitive to water stress (Agrawal and Singh 2002; Agrawal and Pal 2003).

Survival of dried algae stored air-exposed and in desiccators. When stored in desiccators over fused $CaCl_2$, *M. chthonoplastes* lost survival by ½ month, *R. crassipellitum* and *L. mesotricha* by 1 month, *P. bohneri* by 1½ month and *S. millei* not even by >1½ month (Table II), indicating the survivability pattern of different algae against atmospheric dryness and providing a possible explanation for *M. chthonoplastes* absence in summer and *S. millei* presence round the year. It was also observed that at increased atmospheric humidity (when blot-dried algal materials were kept air-exposed than when in desiccators over fused $CaCl_2$), an alga more sensitive to atmospheric dryness (*e.g.*, *M. chthonoplastes*) survived more than the one tolerant to it (*e.g.*, *S. millei* here, Table II). No blot-dried alga survived >2 months when kept air-exposed in the culture chamber.

Chlorella cells (possessing sporopollenin in their cell wall) present frequently in air samples (Brown *et al*. 1964) were reported to be 1 % viable if stored dried for a month in the culture chamber (Agrawal and Singh 2001). However, the terrestrial green alga *Trentepohlia aurea* (possessing thick cellulosic and not sporopollenin cell wall; West and Hood 1911; Good and Chapman 1978) having a high osmotic potential of cell sap survived air-exposed conditions to some extent for >1 year (Gupta and Agrawal 2004*a*). Geitler (1923) has pointed out that *Trentepohlia* spp. vegetative cells closely resemble the resting stages of other algae in possessing a rich hematochrome content. Blue-green algae in the present study were equal to or more desiccation-tolerant than *C. vulgaris* (Agrawal and Singh 2001). All terrestrial algae are not desiccation-tolerant, since *V. geminata*, surviving only in winter, tolerated dry storage in desiccators for 1 h only (Agrawal and Singh 2002), and *C. minor*, *G. aeruginosa* and *A. nidulans* occurring only in the rainy season for >30 min (Agrawal and Pal 2003). The desiccation tolerance of an alga can depend upon its small size (*Chlorella*), cell-wall chemical composition, sporopollenin (*Chlorella*), thick cell wall and/or sheath (*Rhizoclonium*, *Trentepohlia*, *Scytonema*), hematochrome in cytoplasm (*Trentepohlia*), high osmotic potential of cell sap (*Trentepohlia*), or filaments densely interwoven and compactly arranged (*Scytonema*, *Phormidium*). Scherer and Potts (1989) observed that a field-collected *Nostoc commune* upon repeated desiccation synthesized a unique protein capable of increasing desiccation tolerance in the alga.

Survival in darkness and at low light intensity. As compared to light intensity of 40 μmol $m^{-2} s^{-1}$, all algae survived at 2 and 10 μmol $m^{-2} s^{-1}$ and at darkness (Table II). *S. millei* survived darkness to some extent for >1½ month, *P. bohneri*, *M. chthonoplastes* and *R. crassipellitum* for >1 month, and *L. mesotricha* for >½ month. *Nostoc* has been found at a depth of ≈1 meter below the surface of the soil in complete darkness (Moore and Carter 1926). *Chlorella* cells were found 100 % viable in darkness even after 45 d (Agrawal and Singh 2001). *C. minor*, *G. aeruginosa*, *A. nidulans*, *P. foveolarum* and *S. hofmanni* survived darkness variously by <½–1 month or more, and under dim light much more (Agrawal and Pal 2003). Most of the present algae were observed to grow well at shady places. *S. millei* formed a thick felt-like mass on the damp wall of a flowerpot kept in shade. *S. millei* grew equally well on shaded tree-trunk bark surface or on building walls shaded or exposed to sun. *L. mesotricha* and *R. crassipellitum* were collected growing on soil surface at shady places. It seems that low light intensity is not a critical factor for survival of these algae. Adir *et al*. (2003) observed that blue-green algal crust exposed to bright light intensity during the dry period results in severe damage to PS II. Similarly, light–dark environment affected the biochemical differentiation of cyanobacteria (Hrouzek *et al*. 2004; Prasanna *et al*. 2004).

Survival following exposure to heat and UV light. Although the temperature of 45 °C is frequently reached in summer on the open ground surface at Allahabad (India), all algae were sensitive, variously, to wet heat of 45 °C for 5–40 min. *M. chthonoplastes* and *L. mesotricha*, most sensitive to heat, died by 1 d if exposed to 45 °C for 20 min (40 d in the control), followed by *R. crassipellitum* which died by 9 d if exposed to 45 °C for 20 min (60 d in the control), *S. millei* which died by 6 d if exposed to 45 °C for 40 min (70 d in the control) and *P. bohneri* which died by 10 d if exposed to 45 °C for 40 min (than by 110 d in the control; Table III). *V. geminata* was very sensitive to 42 °C, *C. minor*, *G. aeruginosa* and *A. nidulans* to 43 °C. *P. foveolarum*, *S. hofmanni*, *L. martensiana* and *O. agardhii* can tolerate to some extent 45 °C or more (Agrawal and Singh 2002; Agrawal and Pal 2003). Glade (1914) and Buzer *et al*. (1985) reported that algae survived

high temperatures best in dry soil than in wet soil. *Nostoc sphaeroides* has been found to maintain net oxygen evolution from 5 to 45 °C but died at 50 °C (Li and Gao 2004).

Table III. Showing death day of algae following wet heat (45 °C for 5, 20, 40 min) or UV exposure (0.96, 2.88, 3.84 kJ/m^2)[a]

Alga	Control[b]	Heat shock			UV exposure		
		5	20	40	0.96	2.88	3.84
S. millei	70	18	10	6	22	18	15
P. bohneri	110	38	20	10	35	19	15
M. chthonoplastes	40	9	1	-	20	12	9
L. mesotricha	40	10	1	-	40	20	15
R. crassipellitum	60	20	9	-	20	17	15

[a]All algae maintained in culture chamber following wet heat or UV exposure.
[b]No heat or UV treatment.

UV sensitivity of different algae did not vary as much as high temperature sensitivity. Irrespective of their death at 40–110 d in the controls, they all died between 12 and 20 d after exposure to 2.88 kJ m^{-2} s^{-1} of UV, and between 9 and 15 d after 3.84 kJ m^{-2} s^{-1} of UV (Table III). *M. chthonoplastes* minimize UV-induced damage by vertical migration induced by radiation (Bebout and Garcia-Pichel 1995). It was observed that mucilage covering over *C. minor*, *G. aeruginosa* and *A. nidulans*, hyaline and/or colored sheath over *L. martensiana* and/or *S. hofmanni* did not protect them much against UV damage (Agrawal and Singh 2002; Agrawal and Pal 2003). In contrast, alleviation of an oxidative damage caused by UV-B irrradiation was observed in the green alga *Chlorella pyrenoidosa* (Chen *et al*. 2003). In the present study, *S. millei* covered with a thick, colored sheath was found to be more UV-sensitive than *L. mesotricha* covered with a thin, hyaline sheath (Table III). The presence of the extracellular pigment, scytonemin in the blue-green alga *Chlorogloeopsis* sp. (Garcia-Pichel *et al*. 1992) and mycosporine-like compounds among blue-green algal isolates (Garcia-Pichel and Castenholz 1993; Dembitsky and Řezanka 2005) have been found to be important in screening UV light.

The authors thank the *University Grants Commission* (New Delhi) for financial assistance in the form of a research project.

REFERENCES

ADIR N., ZER H., SHOCHAT S., OHAD I.: Photoinhibition: a historical perspective. *Photosynth.Res*. **76**, 343–370 (2003).

AGRAWAL S.C., PAL U.: Viability of dried cells or filaments, survivability and/or reproduction under water and light stress, and following heat and UV exposure in some blue-green and green algae. *Folia Microbiol*. **48**, 501–509 (2003).

AGRAWAL S.C., SINGH V.: Viability of dried vegetative cells and the formation and germination of reproductive structures in *Pithophora oedogonia*, *Cladophora glomerata* and *Rhizoclonium hieroglyphicum* under water stress. *Folia Microbiol*. **44**, 63–70 (1999*a*).

AGRAWAL S.C., SINGH V.: Viability of dried vegetative trichomes, formation of akinetes and heterocysts and akinete germination in some blue-green algae under water stress. *Folia Microbiol*. **44**, 411–418 (1999*b*).

AGRAWAL S.C., SINGH V.: Viability of dried cells, and survivability and reproduction under water stress, low light, heat and UV exposure in *Chlorella vulgaris*. *Israel J.Plant Sci*. **49**, 27–32 (2001).

AGRAWAL S.C., SINGH V.: Viability of dried filaments, survivability and reproduction under water stress and survivability following heat and UV exposure in *Lyngbya martensiana*, *Oscillatoria agardhii*, *Nostoc calcicola*, *Hormidium fluitans*, *Spirogyra* sp. and *Vaucheria germinata*. *Folia Microbiol*. **47**, 61–67 (2002).

BEBOUT B.M., GARCIA-PICHEL F.: UV-B induced vertical migrations of cyanobacteria in a microbial mat. *Appl.Environ.Microbiol*. **61**, 4215–4222 (1995).

BONHAM K., PALUMBO R.: Effects of X-rays on snails, crustacea, and algae. *Growth* **15**, 155–188 (1951).

BRISTOL-ROACH B.M.: On the retention of vitality by algae from old stored soils. *New Phytol*. **18**, 92–107 (1919).

BRISTOL-ROACH B.M.: On the alga-flora of some desiccated English soils: an important factor in soil biology. *Ann.Bot*. **34**, 35–80 (1920).

BROWN R.M. Jr., LARSON D.A., BOLD H.C.: Airborne algae: their abundance and heterogeneity. *Science* **143**, 583–585 (1964).

BUZER J.S., DOHMEIER R.A., DU TOIL D.R.: The survival of algae in dry soils exposed to high temperatures for extended time periods. *Phycologia* **24**, 249–251 (1985).

CAIOLA M.G., BILLI D., FRIEDMANN E.I.: Effect of desiccation on envelopes of the cyanobacterium *Chroococcidiopsis* sp. (*Chroococcales*). *Eur.J.Phycol*. **31**, 97–105 (1996).

CAMERON R.E., BLANK G.R.: Desert algae: soil crusts and diaphanous substrata as algal habitats. *Jet Propulsion Laboratory Pasadena Tech.Rep.No. 32-971*, pp. 1–45. Pasadena (USA) 1966.

CHEN K., FENG H., ZHANG M., WANG X.: Nitric oxide alleviates oxidative damage in the green alga *Chlorella pyrenoidosa* caused by UV-B radiation. *Folia Microbiol*. **48**, 389–393 (2003).

DEMBITSKY V.M., ŘEZANKA T.: Metabolites produced by nitrogen-fixing *Nostoc* species. *Folia Microbiol.* **50**, 363–392 (2005).

FRITSCH F.E.: The morphology and ecology of an extreme terrestrial form of *Zygnema ericetorum* (KUTZ.) HASS. *Ann.Bot.* **30**, 135–149 (1916).

FRITSCH F.E.: The moisture relations of terrestrial algae. I. Some general observations and experiments. *Ann.Bot.* **36**, 1–20 (1922).

GARCIA-PICHEL F., CASTENHOLZ R.W.: Occurrence of UV-absorbing, mycosporine-like compounds among cyanobacterial isolates and an estimate of their screening capacity. *Appl.Environ.Microbiol.* **59**, 163–169 (1993).

GARCIA-PICHEL F., SHERRY N.D., CASTENHOLZ R.W.: Evidence for an ultraviolet sunscreen role of the extracellular pigment scytonemin in the terrestrial cyanobacterium *Chlorogloeopsis* sp. *Photochem.Photobiol.* **56**, 17–23 (1992).

GEITLER L.: Studien über das Haematochrom und die Chromatophoren von *Trentepohlia*. *Oesterr.Bot.Z.* **73**, 76–83 (1923).

GLADE E.: Zur Kenntnis der Gattung *Cylindrospermum* COHNS. *Beitr.Biol.Pflanz.* **12**, 295–343 (1914).

GOOD B.H., CHAPMAN R.L.: The ultrastructure of *Phycopeltis* (*Chroolepidaceae*; *Chlorophyta*). I. Sporopollenin in the cell walls. *Am.J.Bot.* **65**, 27–33 (1978).

GUPTA S., AGRAWAL S.C.: Vegetative survival and reproduction under submerged and air-exposed conditions and vegetative survival as affected by salts, pesticides, and metals in aerial green alga *Trentepohlia aurea*. *Folia Microbiol.* **49**, 37–40 (2004*a*).

GUPTA S., AGRAWAL S.C.: Zoosporangia survival, dehiscence and zoospore formation, and motility in the green alga *Rhizoclonium hieroglyphicum* as affected by different factors. *Folia Microbiol.* **49**, 549–556 (2004*b*).

HAREL Y., OHAD I., KAPLAN A.: Activation of photosynthesis and respiration to photoinhibition in cyanobacteria within biological desert crust. *Plant Physiol.* **136**, 3070–3079 (2004).

HOF T., FREMY P.: On *Myxophyceae* living in strong brines. *Rec.Trav.Bot.Neerland.* **30**, 140–162 (1933).

HOWLAND L.J.: Periodic observations of *Trentepohlia aurea* MARTIUS. *Ann.Bot.* **43**, 173–202 (1929).

HROUZEK P., LUKEŠOVÁ A., ŠIMEK M.: Comparison of light and dark nitrogenase activity in selected soil cyanobacteria. *Folia Microbiol.* **49**, 435–440 (2004).

LANGE O.L., KIDRON G.J., BÜDEL B., MEYER A., KILIAN E., ABELIOVICH A.: Taxonomic composition and photosynthetic characteristics of the "biological soil crusts" covering sand dunes in the Western Neger desert. *Funct.Ecol.* **6**, 519–527 (1992).

LI Y., GAO K.: Photosynthetic physiology and growth as a function of colony size in the cyanobacterium *Nostoc sphaeroides*. *Eur. J.Phycol.* **39**, 9–15 (2004).

LOTHRING H.: Beitrage zur Biologie der Plasmolyse. *Planta* **32**, 600–629 (1941–42).

MOEWUS F.: Die Vererbung des Geschlechts bei Verschiedenen Rassen von *Protosiphon botryoides*. *Arch.Protistenkd.* **86**, 1–57 (1935).

MOORE G.T., CARTER N.: Further studies on the subterranean algal flora of the Missouri Botanical Garden. *Ann.Missouri Bot.Garden* **13**, 101–140 (1926).

PERNAUER S.: Das Verhalten einiger Cyanophyceen bei osmotischen Impulsen. *Protoplasma* **49**, 262–295 (1958).

PETERSEN J.B.: Studies on the biology and taxonomy of soil algae, pp. 1–180 in *Dansk Botanisk Arkiv.Bd.* **8** (no. 9). Dansk Botanisk Forening, Copenhagen (Denmark) 1935.

PRASANNA R., PABBY A., SINGH P.K.: Effect of glucose and light–dark environment on pigmentation profiles in the cyanobacterium *Calothrix elenkenii*. *Folia Microbiol.* **49**, 26–30 (2004).

SARMA T.A., GURPREET AHUJA, KHATTAR J.I.S.: Nutrient stress causes akinete differentiation in cyanobacterium *Anabaena torulosa* with concomitant increase in nitrogen reserve substances. *Folia Microbiol.* **49**, 557–562 (2004).

SCHERER S., POTTS M.: Novel water stress protein from a desiccation-tolerant cyanobacterium. *J.Biol.Chem.* **264**, 12546–12553 (1989).

SOMMER U.: Growth and survival strategies of planktonic diatoms, pp. 227–260 in *Growth and Reproductive Strategies of Freshwater Phytoplankton* (C.D. Sandgren, Ed.). Cambridge University Press, Cambridge (UK) 1988.

STAHL E.: Ueber die Ruhezustände der *Vaucheria geminata*. *Bot.Z.* **37**, 129–137 (1879).

STANIER R.Y., KUNISAWA R., MANDEL M., COHEN B.: Purification and properties of a unicellular blue-green alga (order *Chroococcales*). *Bacteriol.Rev.* **35**, 171–205 (1971).

TOMASELLI L., GIOVANNETTI L.: Survival of diazotrophic cyanobacteria in soil. *World J.Microbiol.Biotechnol.* **9**, 113–116 (1993).

TRAINOR F.R.: Survival of algae in a desiccated soil. *Phycologia* **9**, 111–113 (1970).

TRAINOR F.R., GLADYCH R.: Survival of algae in a desiccated soil: a 35-year study. *Phycologia* **34**, 191–192 (1995).

TRANSEAU E.N.: The periodicity of freshwater algae. *Am.J.Bot.* **3**, 121–133 (1916).

WEST G.S., HOOD O.E.: The structure of the cell wall and the apical growth in the genus *Trentepohlia*. *New Phytol.* **10**, 241–248 (1911).

WHITTON B.A.: Survival and dormancy of blue-green algae, pp. 109–167 in *Survival and Dormancy of Microorganisms* (Y. Henis, Ed.). John Wiley & Sons, New York 1987.