REVIEW

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Factors Affecting Spore Germination in Algae — *review*

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ABSTRACT. This review surveys whatever little is known on the influence of different environmental factors like light, temperature, nutrients, chemicals (such as plant hormones, vitamins, *etc*.), pH of the medium, biotic factors (such as algal extracellular substances, algal concentration, bacterial extracellular products, animal grazing and animal extracellular products), water movement, water stress, antibiotics, UV light, X-rays, γ-rays, and pollution on the spore germination in algae. The work done on the dormancy of algal spores and on the role of vegetative cells in tolerating environmental stress is also incorporated.

Abbreviations

GRM germination
SG spore germination

CONTENTS

1 INTRODUCTION

Algal spores are cells that can independently reproduce an individual of the given species. They may either be asexual (zoospores, akinetes, cysts, *etc*.) or sexual (zygospores, oospores, zygotic cysts, *etc*.). SG is initiated either by (*i*) lack of motility of motile spores, (*ii*) rejuvenation, (*iii*) change in color, or (*iv*) cracking of the thick cell wall of the dormant spore, and is completed with the emergence of a germling from the spore. SG is supposed to be influenced by a range of environmental factors, but much less is known on the GRM of algal spores than on bacterial or fungal spores. The goal of this review paper is to incorporate all the available and relevant information on the influence of different environmental factors such as light, temperature, inorganic nutrients, chemicals (plants hormones, vitamins, *etc*.), pH of the medium, biotic factors (algal extracellular products, algal density, bacterial extracellular substances, animal grazing and extracelluar products), pH of the medium, water movement, water stress, antibiotics, UV light, X-rays, γ-rays and pollution on the SG. This review also deals with the dormancy of algal spores, and the role of vegetative cells of algae in the tolerance to environmental stress. By knowing the influence of different environmental factors on the SG, one can better understand the life cycle and ecology of algae. The spores and/or germlings represent critical stages in the life cycles and mass-development of algae. The SG (and not the growth) appeared to be the eco-physiological bottleneck for initiating mass-development of algae.

2 LIGHT

Most of algal spores need light to germinate, but some spores can germinate even in darkness (Table I; p. 284), but SG percentage was always higher in light than in darkness). In *Anabaena cylindrica* and *A. variabilis*, akinete GRM was impaired when photosynthetic electron transport was blocked by DCMU (Yamamoto 1976; Braune 1979). Blue-green algal akinetes usually contain a high amount of phycocyanin and glycogen (Sutherland *et al.* 1979) serving respectively as N- and C-source during akinete GRM (Suther-

land *et al.* 1985). Akinetes of *Nostoc punctiforme* (Harder 1917*a*,*b*) and *Anabaena circinalis* (Van Dok and Hart 1997) can germinate in the dark in the presence of suitable organic carbon acting as a source of energy. Akinetes of *Pithophora oedogonia* stored in the dark (than in the light) for 1½ year exhibited a complete failure of GRM (Chaudhary and Singh 1987). Spores of *Enteromorpha flexuosa* incubated in the dark displayed a linear decrease in the GRM rate coupled with a linear increase in the effective period of GRM (Kolwalkar *et al.* 2007). GRM of resting spores of *Aulacoseira skvortzowii* occurred when they were placed in the new medium, with stored reserves sufficient to complete 2–3 divisions even in the dark (Jewson *et al.* 2008). The largest recruitment of *Ceratium hirundinella* cysts occurred in profundal zone of water body (Rengefors and Anderson 1998; Rengefors *et al.* 2004).

In most of the members of *Nostocaceae* a definite relationship exists between the time period that elapses before akinete GRM start and the quantity of light that was available (Harder 1917*a*,*b*). A minimum light intensity of 0.5 μmol m^{-2} s^{-1} was required to initiate akinete GRM in *Nodularia spumigena* (Hüber 1985), 6 μmol m^{-2} s^{-1} for akinete GRM in *Anabaena iyengarii*, *Westiellopsis prolifica*, and *Nostochopsis lobatus* (Agrawal and Singh 2000), and 12 μmol m^{-2} s^{-1} for SG in *Aulacoseira skvortzowii* (Jewson *et al.* 2008). An increase in light intensity shortens the lag period of SG and increases the percentage GRM of spores, *e.g.*, akinete GRM in *Anabaena cylindrica* was favored by an increase in light intensity of 2–60 μmol m^{-2} s^{-1} (Yamamoto 1976), that in *Stigeoclonium pascheri* by 5–70 μmol m^{-2} s^{-1} (Agrawal 1984), that in *Pithophora oedogonia* by 10–30 μmol m^{-2} s^{-1} (Agrawal 1986*a*), and zygospore GRM in *Spirogyra hyalina* by 60–80 μmol m^{-2} s^{-1} (Agrawal and Chaudhary 1994).

The presence of silt and sediments in the water reduces light penetration and prevents SG and colonization of *Himanthalia elongata* (Moss *et al.* 1973). Kelp canopies typically reduced the light level reaching the substratum by ≈95–99 % and decreased the SG (Reed and Foster 1984). GRM of spores in *Macrocystis* and other kelps was greatest after the canopy had been thinned (Dayton *et al.* 1984).

Roelofs and Oglesby (1970) concluded that light was probably the triggering factor for recruitment of blue-green alga *Gloeotrichia echinulata*, while temperature influenced the metabolic activity and thus the length of the lag phase between triggering and GRM. GRM of *Anabaena* sp. akinetes occurred in water column, presumably after certain minimum light intensity and/or temperature requirements had been satisfied (Reynolds 1972). Laboratory incubation of akinetes under continuous illumination at 40 μmol m^{-2} s^{-1} light intensity and at 18 °C induced GRM (Livingstone and Jaworski 1980). GRM of akinetes of *Anabaena circinalis* and *A. flos-aquae* occurred more likely in shallow lagoons than in the main river, principally because of frequent resuspension of sediments containing akinetes to the euphotic zone or because of direct penetration of light to the sediment (Baker 1999). Light availability in shallow sediments (of <3 m depth) appears to be important for recruitment of *Gloeotrichia echinulata* (Karlsson-Elfgren 2003).

In algae, white light was found to be most favorable for SG, but in some algae it was red light (Table I). The red light promoted or induced akinete GRM in *Anabaena fertilissima*, *Anabaenopsis arnoldii* (Reddy *et al.* 1975) and *Nostoc ellipsosporum* (Ahluwalia and Kumar 1980); zygospore GRM in *Spirogyra hyalina* (Agrawal and Chaudhary 1994) was prevented by subsequent irradiation with far-red light and a further exposure to red light again induced the GRM. Thus, photoreversible phenomena mediated by pigment functionally similar to phytochrome of higher plants seems to operate in algae. However, red light-promoted akinete GRM in *Nodularia spumigena* was reversed not by far-red light but by subsequent irradiation with green light, and a second red exposure induced GRM again (Pandey and Talpasayi 1981).

In *Anabaena doliolum* and *Fischerella muscicola*, akinete GRM was equally favored by green, blue, yellow, red, and white light (Kaushik and Kumar 1970). In green alga *Pithophora*, green and blue light were most favorable for akinete GRM, while red light had a poor effect, and no photoreversible effect occurred between green or blue and red light (Patel 1971; Agrawal 1986*a*). Akinetes of *Pithophora oedogonia* germinated quickly and showed a higher percentage of GRM when formed under green or blue light than under red one (Agrawal 1986*a*).

3 TEMPERATURE

It is one of the significant environmental factors regulating survival and reproduction of algae and producing a shift in algal number and composition in a period of time. Every alga has its own temperature optima (and temperature tolerance limit) for vegetative survival, spore formation and SG. Depending upon its temperature tolerance, an alga may survive either a certain time period of the year or all the year. The optimum temperature for SG of different algae is given in Table II (p. 286).

Timing of SG has been suggested to play an important role in seasonal succession of different algae. Water temperature is one of the main factors controlling initiation of blue-green algal bloom. Most blue-

green algae are known to grow poorly at low water temperature (Fogg 1963) and their growth is favored by high water temperature. Akinetes of *Aphanizomenon flos-aquae*, *Anabaena circinalis* and *Gloeotrichia echinulata* undergo a wintering phase and their apparent GRM occurred in spring or in early summer (Jones 1979; Baker 1999; Karlsson-Elfgren 2003). Species-specific differences in optimum GRM temperature corresponding to differences in optimum growth temperature have been found in *Anabaena* species (Baker and Bellifemine 2000). *Anabaena solitaria* akinetes germinated immediately when exposed to 17 °C, light, and sediment mixing (Rengefors *et al.* 2004). Akinetes in most of blue-green algae germinate at an optimum at ≥22 °C (Table II). GRM of *Cylindrospermopsis raciborskii* akinetes occurred more or less synchronously in response to water temperature rising to 22–24 °C in temperate regions (Gorzo 1987; Padisak 2003; Hong *et al.* 2006). In Baltic ocean, the GRM of *Nodularia* akinetes was inhibited in 1998 due to low water temperature (Kanoshina *et al.* 2003). The formation of *Aphanizomenon flos-aquae* and *Nodularia spumigena* blooms was favored by warm and calm weather (Kanoshina *et al.* 2003). Blue-green algae dominate the phytoplankton community at its greatest when high water temperature is combined with high nutrient load (Elliott *et al.* 2006).

In green algae, most of the spores germinated optimally at ≈20 °C or more, but microzoospores of *Ulothrix* sp. germinated best at ≈10 °C or less (Klebs 1896) and akinetes of *Cladophora* sp. at 11.5–13.8 °C (Mason 1965). Oospores of *Chara zeylanica* germinated better at 28 than at 24 °C, while those of *C. contraria* yielded higher GRM percentage at 18 °C than at 24 or 28 °C (Proctor 1967). Probably the oospores collected from the warmer regions germinated at higher temperature than those collected from colder regions (temperate regions). Temperature extremes (of ≥35 °C or ≤10 °C) decreased or altogether inhibited akinete and zoospore GRM in *Stigeoclonium pascheri* and akinete GRM in *Pithophora oedogonia* (Agrawal 1984, 1985*a*, 1986*a*).

Pithophora oedogonia survived annual diurnal water temperature variations of 10–28 °C. The alga formed akinetes at 10–24 °C and most of the akinetes germinated at 19–24 °C (Gupta and Agrawal 2007). *Rhizoclonium hieroglyphicum* survived throughout the year in the water. The alga exhibited zoosporangial stages when water temperature was 20–25 °C, and no zoosporangial stage at 30–31 °C (Gupta and Agrawal 2004). *Vaucheria geminata* is a seasonal terrestrial alga; its vegetative patches appeared on the soil surface when atmospheric diurnal temperature was 9–16 °C in January. The alga started sexual reproduction when temperature increased to 20–23 °C in April, and died thereafter with further increase of temperature (Gupta and Agrawal 2007). In culture, oospores of *Vaucheria sessilis* germinated optimum at 15 °C but not at 21–27 °C (League and Greulach 1955).

In dinoflagellates, GRM rate of *Peridinium cinctum* cysts remained maximal at 20 °C (Pfiester 1975), that of *Scrippsiella trochoidea* cysts at 22–25 °C (Binder and Anderson 1987), and of *Ceratium hirundinella* cysts at 17 °C (Rengefors and Anderson 1998). The dramatic reduction in GRM rate of *Scrippsiella* cysts at low temperature permits them to serve as over-wintering cells, and once the dormancy period of 25 d was completed the cysts germinated optimally in nutrient-replete medium at 22–25 °C (Binder and Anderson 1987).

In Chesapeake Bay, the climax of reproductive capacity for most of the seaweeds is in summer and early autumn. During that period, *Chlorophyta* produced swarmers, the *Phaeophyte Punctaria plantaginea* had plurilocular reproductive organs, and all *Florideophyceae* developed either carposporangia or spermatangia or both. Most *Florideophyceae* pass the winter in tetrasporophytic stage (Zaneveld and Barnes 1965). Zygotes and zoospores of some brown algae germinated in a wide range of temperatures, *e.g.*, zygotes of *Halidrys siliquosa* germinated equally well both at 3 and 10 °C (Moss and Sheader 1973), of *Ascophyllum nodosum* at 4–23 °C (Sheader and Moss 1975), and of *Spermatochnus paradoxus* equally well both at 9 and 20 °C (Müller 1981), and zoospores of *Ecklonia stolonifera* within 10–30 °C (Notoya and Asuke 1983) and of *Pilayella littoralis* at 5 °C (Lotze *et al.* 1999). Brown alga *Macrocystis integrifolia* sporophyte growth responded better at the lowest temperature tested (8 °C), but the population showed higher spore release and GRM at 15 and 18 °C, respectively (Buschmann *et al.* 2004).

4 INORGANIC NUTRIENTS IN THE CULTURE MEDIUM

Lack of nitrogen or phosphorus or both decreased spore and/or cyst GRM in some algae (Table III; p. 287) indicating the synthesis of fresh nucleic acids and proteins during GRM. Need of magnesium during zygospore GRM in *Blastocladiella emersonii* (Soll and Sonneborn 1972) and akinete GRM in *Stigeoclonium pascheri* and *Westiellopsis prolifica* (Agrawal and Sarma 1982*a*; Agrawal and Sharma 1994*a*) indicates that fresh chlorophylls are synthesized during their GRM. Stored nitrogen and glycogen have been found to decrease during akinete GRM of *Aphanizomenon flos-aquae* (Wildman *et al.* 1975). Akinetes of *Anabaena cylin-*

drica had phaeophytin in place of chlorophyll (Fay 1969*a*). The GRM of non-photosynthetic akinetes of *Anabaena doliolum* commenced in the light with new protein synthesis followed by simultaneous development of oxygenic photosynthesis and nitrate reductase activity (Rai *et al.* 1988).

The SG was decreased not only by the lack of nitrogen, phosphorus or magnesium but also when their (and of calcium) concentration exceed certain levels; *e.g.*, nitrate or phosphate at ≥5-fold level, or magnesium at 10-fold level of that present in the basal medium inhibited akinete GRM in *Westiellopsis prolifica* (Agrawal and Sharma 1994*a*). Magnesium at ≥5-fold level or calcium at ≥2-fold level also inhibited akinete GRM in *Stigeoclonium pascheri* (Agrawal and Sarma 1982*a*). This indicates that SG in algae is sensitive to high levels of inorganic nutrients. Omission of microelements ($ZnSO_4$, $MnCl_2$, MoO_3, $CuSO_4$, $Co(NO_3)_2$, H_3BO_3) from the basal medium increased SG in *Stigeoclonium pascheri*, and by increasing their concentration to ≥2-fold levels, the condition was reversed (Agrawal and Sarma 1982*a*). The presence of microelements in the basal medium therefore serves as a check in reaching maximum level of SG under control conditions. More study is needed to clear the role of micro- and macronutrients in SG.

5 CHEMICALS STIMULATORY TO SPORE GERMINATION

Plant hormones such as indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), naphthalene-2-acetic acid (NAA), gibberellic acid (GA_3), kinetin, and tryptophan (a precusor of IAA) at certain levels (either individually or in combination) stimulated SG in some algae (Table IV; p. 288). They probably promote cell enlargement, cell division or have some other cellular and molecular effects. IAA at 0.4 ppm, and kinetin at 0.8 ppm promoted the growth of *Porphyra* conchocelis stage (Lin and Stekoll 2007).

Moewus (1940) described a type of soil solution prepared without heat (containing some natural substance) inducing zygospore GRM of *Chlamydomonas eugametos*. In *Botrytis cinerea*, the GRM ability was lost in old spores, but it was restored by the addition of glucose, maltose or malt extract (Bernard 1973), which probably act as energy source.

Vitamins are required to stimulate growth in many algae (Machlis 1962; Ellis and Machlis 1968; Saito 1972; Dawson and Denny 1983). Ascorbic acid (vitamin C) and serine at certain levels increased akinete GRM in *Stigeoclonium pascheri* (Agrawal 1988*a*). Akinetes of *Pithophora oedogonia* formed in the presence of vitamin B_2 (2 ‰) and vitamin C (10 ‰) showed quicker and higher GRM (Agrawal 1988*b*). A wide range of intracellular amino acids, characteristic of proteins, was utilized to sustain the new protein synthesis in *Cyanospira* spp. (Sili *et al.* 1994). In *Stigeoclonium pascheri*, pretreatment of akinetes with caffeine (500–1000 ppm) or with the dyes crystal violet (2–5 ppm) or methylene blue (20–50 ppm) for certain time periods induced quick and abundant GRM (Agrawal 1985*c*; 1992*a*). Dyes produced changes in membrane permeability and active transport processes (Spikes 1968).

6 THE pH OF THE MEDIUM

Akinetes of *Cladophora* sp., *Anabaena* spp., *Anabaenopsis arnoldii*, *Stigeoclonium pascheri*, *Pithophora oedogonia*, *Westiellopsis prolifica* and *Nostochopsis lobatus*, zoospores of *S. pascheri*, *Cladophora glomerata* and *Rhizoclonium hieroglyphicum*, and zygospores of *Spirogyra hyalina*, all, germinated optimally at neutral or slightly alkaline pH (Table V; p. 288). Not only zoospores of *S. pascheri* germinated optimally at pH 8, but zoospore germlings also grew optimally at the same pH (Agrawal 1985*a*). It seems that SG usually occurred at the same pH at which the alga grew. Although the percentage akinete GRM in *Pithophora oedogonia* was optimal at pH 7 and 8, akinetes started to germinate earlier at acidic pH and this was probably due to dissolution of thick akinete cell wall at acidic pH (Agrawal 1986*a*). High pH tolerance of *Nodularia spumigena* in natural environments might be important in the competition with other phytoplankton species (Mogelhoj *et al.* 2006).

7 BIOTIC FACTORS

SG is sensitive to (*i*) algal extracellular products and algal density, (*ii*) bacterial extracellular products, and (*iii*) animal grazing and extracellular products.

(*i*) *Algal extracellular products and algal density*. Algae secrete many organic substances, such as saccharides, lipids, amino acids, peptides, proteins, organic acids, phenolic substances, enzymes, vitamins, *etc*.

in the culture medium, and their quality and quantity increase with culture age (Fogg 1971; Nalewajko and Marin 1969; Jones 1988; Agrawal 1994; Agrawal and Sharma 1994*b*, 1996). The culture filtrate of an alga, depending upon its age (or on the concentration of the extracellular products it had) may be ineffective or inhibitory at different levels to SG of the same or other alga. The akinetes, zygospores, oospores, or cysts are formed usually in old-age cultures, which already have accumulated a lot of algal extracellular products that proved to be inhibitory to their GRM; thus they require fresh culture media to germinate (Table VI; p. 289). However, zoospores of most algae are formed usually in young-age cultures, which have released little of any extracellular products that are not inhibitory to their GRM; thus zoospores germinate in the same medium in which they are formed.

In nature, diatoms attached to substratum prevent spores of *Monostroma* from reaching the substratum and GRM (Segi and Kida 1961). Some brown algal crusts inhibited the ability of the spores of red algae to settle and germinate (Fletcher 1975). Benthic diatoms inhibited the growth of zygotes and germlings of *Fucus spiralis* (Schonbeck and Norton 1979). In the Baltic ocean, a mixture of algal species and their slime prevents *Fucus* zygotes from settling and attaching (Kangas *et al.* 1982). The main barrier to colonization by *Sargassum* is the presence of an algal cover (Deysher and Norton 1982). Reed (1990) demonstrated intra-specific interactions between spores, gametophytes and young sporophytes in kelps. The per capita sporophyte production was negatively density-dependent at spore concentration $\geq 10/mm^2$.

(*ii*) *Bacterial extracellular products*. Bacteria *Pseudoalteromonas*, *Alteromonas* or *Pseudomonas* form biofilms in various marine eco-niches. They produce an array of low and high-molar-mass compounds including toxic proteins, poly-anionic polymers, substituted alkaloids, cyclic peptides, and a range of bromine-substituted compounds. These compounds have anti-fouling and various pharmaceutically relevant activities. They showed excellent inhibitory activity on the settlement and GRM of various algal spores including *Ulva lactuca* and *Polysiphonia* species (Holmström *et al.* 1998; Egan *et al.* 2000, 2001; Burgess *et al.* 2003; Browman 2007; Silva-Aciares and Riquelme 2008).

(*iii*) *Animal grazing and extracellular products*. Paucity or absence of visible green algae on many shores can often be reversed with the removal of herbivores; this suggests that early stages of algal life cycle were prevented from settling or else quickly grazed (Lubchenco 1980; Hawkins 1981, 1983). Grazing by animals was one of several factors thought to cause high mortality of *Cystoseira* and *Halidrys* zygotes (Gunnill 1986). Zygotes of *Ascophyllum* attached to pottery chips and out-planted into and around adult beds containing high *Littorina* density exhibited high mortality relative to controls (Vadas *et al.* 1982; Miller and Vadas 1984). One of the postulated negative effects of mussels on *Postelsia* recruitment was deposition of silt on spores (Dayton 1973). Mixing spores and silts together resulted in low survival. Experimental removal of sea urchins resulted in rapid algal recruitment (Sousa *et al.* 1981). Water-borne exudates of reef anthozoan *Condylactis gigantea* inhibited SG of green, red and brown algae (Bak and Borsboom 1984). GRM of settled spores and growth of germlings of *Pilayella littoralis* and *Enteromorpha* spp. was reduced by the presence of grazers *Idotea chelipes* and *Gammarus locusta* (Lotze *et al.* 1999). *Siphonaria pectinata* graze superficial, soft algae including spores and emerging germlings (Ocana and Fa 2003).

8 WATER MOVEMENT

Water movement increases the uptake of nutrients and exchange of gases in algae (Whitford and Schumacher 1961). Water movement has been suspected of influencing settlement, attachment, survival, and GRM of spores; they usually need adherence to a substratum before GRM, while they also germinate when suspended in water like spores in *Macrocystis* and *Pterygophora* (Reed *et al.* 1992). Christie *et al.* (1970) found that *Enteromorpha* zoospores adhere to a substratum within minutes of contact by means of a mucopolysaccharide. Types of substratum also influenced SG, *e.g.*, α-spores of *Porphyra schizophylla* required 2 d to germinate on glass, but ≤12 h on cotton thread (Boney 1978). About 70 % aplanospores of *Prasiola* were attached and germinated in culture (Bingham and Schiff 1979). Water movement prevented spore settlement and smothered the gametophytes of *Macrocystis pyrifera* (Devinny and Volse 1978). With *Ascophyllum*, one low-energy wave (of 200–500 mm in height) dislodged 90 % of the zygotes (settled for 15 min) on smooth pottery plates (Vadas *et al*. 1992). A higher reproductive vitality (zoospore release, spore attachment, and GRM) was observed in *Lessonia trabeculata* living in an environment with an active water movement than plants growing in a sheltered environment (Edding *et al.* 1993). *Macrocystis* populations showed higher spore release and GRM at the wave-protected southern Chile coast (Buschmann *et al.* 2004). Water movement keeps spores suspended in water or brings a mass of settled spores from deep sediments to the

upper layer of water where they germinate in the presence of light. More work is needed in this line of research.

9 WATER STRESS

Akinetes, zygospores, oospores or cysts can torelate dryness of different extent and period (Proctor 1967; Lippert 1967; Yamamoto 1975; Tanoue and Aruga 1975; Livingstone and Jaworski 1980; Sili *et al.* 1994; Agrawal and Singh 1999*a*,*b*) but they all need water to germinate. Spores of some algae need drying or alternate drying and soaking prior to GRM (Table VII; p. 289). Water stress of both physical and physiological nature decreased or altogether inhibited SG. Akinete GRM in *Pithophora oedogonia* was more sensitive to water stress than zoospore GRM in *Cladophora glomerata* and *Rhizoclonium hieroglyphicum*; it was probably due to larger size, more dense contents, or thicker cell wall of akinetes than zoospores (Agrawal and Singh 1999*a*). Akinetes of *P. oedogonia*, *A. iyengarii*, *W. prolifica* and *N. lobatus* formed under water stress or no water stress were equally viable; but zoosporangia of *C. glomerata* and *R. hieroglyphicum* formed under water stress were not viable (not releasing any zoospore) while those formed under normal conditions were viable (Agrawal and Singh 1999*a*,*b*, 2000). Sediment drying in reservoirs is considered to be a useful measure to reduce periods and scales of *Anabaena* blooms, and its effect will be enhanced by performance during the warmer seasons (Shigeo 2004). Desiccation stress can be extremely damaging to cells, causing protein denaturation, DNA strand breaks and membrane leakage upon rehydration (Potts 1994; Shirkey *et al.* 2003).

10 ANTIBIOTICS

All antibiotics used decrease or totally suppress SG (Table VIII; p. 290). Even pretreatment of spores with different antibiotics proved inhibitory for SG; this indicates that fresh protein synthesis is necessary for GRM of spores. The blocking of protein synthesis in chloroplasts and mitochondria may secondarily lead to interference with several other essential reactions inside the cell. Agrawal and Sarma (1980) observed that penicillin increased akinete GRM in *Stigeoclonium pascheri* up to 2 ‰. Any probable biochemical and/or physiological reason behind the above observation is not known. Penicillin has been found to inhibit the growth of bacteria by accumulating the immediate precursors in the terminal reaction of cell wall synthesis (Strominger 1969). Nothing is known about its mode of action on the cell wall of eukaryotic organisms.

Preservation of algal spores of *Ulva fasciata* and *U. pertusa* was enhanced by the addition of antibiotic ampicillin to the culture medium at 4 °C. Addition of ampicillin (100 ppm) to the culture medium, increased the viability of *Ulva* spores for several days. Spore preservation was heavily dependent on the bacterial contamination and subsequent degradation in stock solutions (Bhattarai *et al.* 2007).

11 UV LIGHT, X-RAYS, γ-RAYS

Spores subjected to UV-B or UV-C irradiation of any dose showed a delay and decrease in GRM (Table IX; p. 290). UV light causes dimerization of DNA bases, particularly the formation of cyclobutane pyrimidine dimers (Setlow and Setlow 1962; Setlow and Carrier 1963; Karentz *et al*. 1991; Karentz 1999; Wiencke *et al.* 2000; Roleda *et al.* 2004–2006*b*). The dimers prevent DNA replication, thus arresting the cell cycle in DNA synthesis phase. UV light also causes damage to essential enzymes or proteins involved in membrane transport processes (Holm-Hansen *et al.* 1993) and destruction of phycobiliproteins and a loss of linker polypeptides (Sinha *et al.* 2005). In this study, the GRM gradually declined with an increase in UV dose, indicating that dimerization was dose-dependent. In seaweeds, spores and gametes were more vulnerable to environmental stress than juvenile and adult macrothalli (Coelho *et al.* 2000). Spores of *Porphyra schizophylla* germinated but developed abnormally when exposed to direct sunlight (Boney 1978). Spores of *Alaria marginata* were unable to survive at 10 °C in the presence of high levels of UV radiations (Hoffman *et al.* 2003). UV light reversed pheromone-induced sexual reproduction in *Volvox carteri* (Kochert and Crump 2005). Tolerance to UV may be an important determinant of kelp zonation on rocky coasts (Swanson and Druehl 2000; Oiencke *et al.* 2000).

Nutrient medium irradiated with UV light decreased akinete GRM. Stone *et al.* (1947) stated that either or both of the following physical or chemical changes occurred during irradiation of a culture medium: (*i*) some mechanism involving a shift to a higher energy level by the absorption of a quantum of

energy and subsequent effect of this energy transfer, and (*ii*) the production of different chemical compounds under the influence of irradiation. The UV radiation was found to produce H_2O_2 in μmol/L level but at such level it was not likely to contribute to growth control (Bin Alam *et al.* 2001). Moharikar *et al.* (2006) observed that spent medium recovered from UV-C exposed *Chlamydomonas reinhardtii* cells exhibited a protective effect against cell killing of fresh cultures of *C. reinhardtii* cells by UV irradiation, probably an adaptive response.

Various photoprotective strategies have evolved to tolerate UV exposure, such as chemical sunscreens and repair of essential biomolecules. Extracellularly (cell wall) and intracellularly formed UV-absorbing compounds act as a sunscreen. Important UV screening compounds are mycosporine-like amino acids (MAAs) and scytonemin (Franklin *et al*. 2003). They are proposed to function as passive shielding solutes by dissipating the absorbed short wavelength radiation energy in the harmless form of heat without generating photochemical reaction. The accumulation of MAAs is induced by both UV radiation and by blue light (Korbee *et al.* 2006). In brown algae, exudation of phlorotannins and phloroglucinal into water can also reduce the impact of UV-B radiation on UV-sensitive spores (Schoenwaelder 2002; Wiencke *et al.* 2004; Roleda *et al.* 2006*a*). Biofilters containing zoospore suspensions act as a buffer and showed variable UV-protection properties on the GRM of its conspecies. At higher zoospore concentration ($\approx 4 \times 10^6$/mL), zoospores were observed to screen UV radiation, maintaining viability among shielded spores in *Saccorhiza*, *Alaria* and *Laminaria* (Roleda *et al.* 2006*a*). Within a plume of zoospores, each cell can buffer each other and protect the lower layer of spores from excessive radiation (Roleda *et al.* 2006*a*). The light dependent repair, probably photoreactivation, compensated for a large fraction of sunlight-induced DNA damage by UV radiation through photoenzymatic repair using the enzyme photolyase, in the presence of photorepair radiation, UV-A, and visible light (Grad *et al.* 2001).

X-Rays (0.64–2.6 C/kg) and γ-rays (0.64–1.9 C/kg) increased the percentage GRM of akinetes in *Stigeoclonium pascheri*. The maximum stimulatory effect was observed at 2.6 C/kg of X-rays and at 1.3 C/kg of γ-rays. The GRM of akinetes decreased with an increase in the dose rate – 1.9–7.7 C/kg of γ-rays (Agrawal 1986*b*,*c*, 1987). Increase in GRM percentage at lower dose of γ-rays may be due to structural changes in the membrane of akinetes as it was in slime mold spores (Hashimoto and Yanagisawa 1970), or it may be due to a rise in oxygen consumption rate as it was in *Bacillus megaterium* spores (Levinson and Hyatt 1960), or to some changes in the tertiary structure of proteins which might expose previously masked reactive sites which are important for GRM, as, *e.g.*, in *B. cereus* spores (Gould and Ordal 1968). However, no exact mechanism of activation of akinetes following X-rays and γ-rays at low level has as yet been established. Decline in the percentage of GRM at higher doses of γ radiation may be due to γ-induced injury to cell DNA.

12 POLLUTION

Pollutants, such as heavy metals (Hg, Cu, Cr, Co, Zn, Pb, *etc*.), pesticides or insecticides (carbofuran, 2,4-D, dithane, phorate, bavistin, parathion, *etc*.), sewage effluent, crude oil, acetylene, ethylene, ammonium, *etc*. at various levels decreased spore liberation, motility, settlement, and GRM in different algae (Table X; p. 291). Similarly, the vegetative survival in blue-green algae *Lyngbya birgei*, *L. major*, *Phormidium bohneri*, *P. foveolarum*, *Microcoleus chthonoplastes*, *Scytonema millei*, *Myxosarcina burmensis*, *Aphanothece pallida*, *Gloeocapsa atrata*, and green algae *Scenedemus quadricauda*, *Cosmarium granatum*, *Hormidium flaccidum*, *Rhizoclonium crassipellitum*, and *Oedogonium* sp. was greatly affected by agents such as sewage water, fertilizer factory effluent, brassica oil, phenol, toluene and benzene. These agents exhibited an important effect on the reproductive features of the algae, influencing thus their growth properties (Agrawal and Gupta 2009).

Anoxic conditions (low oxygen concentration) in water and sediment also disturb GRM in dinoflagellate cysts. Akinete GRM in *Anabaena cylindrica* was stimulated by the presence of oxygen (Yamamoto 1976). Cu, Fe, Zn, Hg, Ni, Co and organic substances captan, DDT, 2,4-D, and thiourea decreased the speed and motility period of zoospores in *Rhizoclonium hieroglyphicum* (Gupta and Agrawal 2004). When pH was decreased from 8.0 to 5.5, more Cu and Zn were required to inhibit the growth rate of *Chlorella* sp. (Wilde *et al.* 2006). Growth inhibition after exposure to heavy metals has been attributed to inhibition of the function of photosynthetic pigments, to enzyme inhibition, uptake of nutrients or damage to cell membrane (Stokes 1983; De Filippis and Pallaghy 1994). Pesticides are considered to alter cell membrane permeability, inhibit the activity of some enzymes and interfere with photosynthesis and with the synthesis of nucleic acids and proteins (Stratton 1987).

13 DORMANCY OF SPORES

(*i*) *Zoospores*. Of different kinds of spores, zoospores in all algae, *e.g. Stigeoclonium pascheri*, *Cladophora glomerata*, and *Rhizoclonium hieroglyphicum* (Agrawal 1985*a*; Agrawal and Singh 1999*a*) had no cell wall or very thin cell wall and germinated immediate by after formation without any dormancy.

(*ii*) *Akinetes*. Akinetes of all algae have slightly thicker cell wall than vegetative cells and are slightly more resistant to different environmental stresses than vegetative cells (Table XI; p. 292). They are not dormant and can germinate after formation immediate by or after a short or longer time period. Akinetes of green algae *Stigeoclonium pascheri* and *Pithophora oedogonia* (Agrawal 1984; Agrawal and Singh 1999*a*, 2000) and of blue-green algae *Anabaena iyengarii*, *Nostochopsis lobatus* and *Westiellopsis prolifica* (Agrawal and Singh 2000) germinated immediate by after formation when transferred to fresh culture media under suitable culture conditions. They can also be stored in the laboratory for several months either wet or dry or in the presence or absence of light. The viability of stored akinetes decreased with storage time, but more drastically at lower temperatures of 12 and 0 °C than at 20 °C; thus they can tolerate desiccation but not frost (Agrawal and Singh 2000). Reynolds (1972) reported mass GRM of akinetes of *Anabaena* after over-wintering in the sediments of Crose-Mere, but this was not always consistent (Reynolds 1975). Wildman *et al.* (1975) found akinetes of *Aphanizomenon* in the sediment in winter and noted that akinete GRM did not take place until spring. Lembi and Spencer (1981) proposed that akinetes of *Pithophora oedogonia* ensured survival during periods of desiccation caused by fluctuating water level. Although, not heat-resistant like endospores of G^+ bacteria, the desiccated akinetes of *Anabaena cylindrica* (Yamamoto 1975) and *Cyanospira* spp. (Sili *et al.* 1994) retained GRM ability after storage in darkness for 5 and 7 years, respectively. Akinetes of *Nostoc* sp. have been reported to tolerate months of cold (4 °C) and dark conditions (Sutherland *et al.* 1979). Rother and Fay (1977) observed that the bulk of akinetes of *Anabaena* and *Aphanizomenon* germinated shortly after sporulation and that the over-wintering population was as vegetative filaments. Akinetes of blue-green algae may not only have a temporary or over-wintering function but also ensure long-term survival. Livingstone and Jaworski (1980) recovered *Anabaena* akinetes from a 1-m sediment core from Rostherne Mere at depths of up to 270 mm below the mud surface and deposited up to 64 years previously. Laboratory incubation of these akinetes under continuous illumination (40 μmol m^{-2} s^{-1}) at 18 °C induced GRM within 20–30 d. Little is known about the molecular basis for such resistance to environmental extremes. Coleman (1983) reported a system of osmotic control for survival of thick-walled akinetes. Viable akinetes of *Nodularia spumigena* were found in the sediments of the Peel–Harvey estuary (Australia) even at 350 mm depth. They have the potential to germinate to form new filaments given appropriate conditions (Hüber 1984). Akinetes of *Cylindrospermopsis raciborskii* may persist in sediments as spores for long periods (Moore *et al.* 2003, 2005). The GRM of akinetes occured more or less synchronously in response to water temperature rising to 22–24 °C in temperate regions (Padisak 2003; Hong *et al.* 2006).

(*iii*) *Oospores, zygospores, cysts*. Oospores and zygospores of green algae, *e.g.*, of *Oedogonium*, *Chlamydomonas*, *Closterium*, *Cosmarium*, *Pandorina*, *Spirogyra*, *Chara*, *etc*., cysts of *Acetabularia* and of various dinoflagellates, and resting spores of diatoms usually did not germinate immediate by after formation and required a period of dormancy or an endogenous clock (of a few days to many months or years) before GRM in suitable conditions (Table XII; p. 293). It seems probable that in nature they may remain viable for long periods (may easily endure drought and other environmental rigors which destroy the vegetative cells). Nipkow (1927) found *Ceratium hirundinella* cysts in 5–6 years old carves in lake. Oospores of *Chara* spp. may easily endure drought of several years duration when buried in pond or lake bottom deposits. Oospores deposited in bird droppings may survive for several years, while being carried down the slopes of the watershed to a permanent body of water (Proctor 1967). On storage of *Chara* spp. oospores dry at 3 °C, some (2–70 %) remain viable for periods of at least 4 years and probably much longer (Proctor 1967). Desiccated cysts of fresh-water members of *Prasinophyceae* remain viable after exposure to 100 °C for 1 h (Belcher 1970). The dried cysts of *Platymonas* sp. stored in a refrigerator at 5 °C and in a growth chamber at 20 °C in darkness for 10 months germinated well when they were transferred to the culture medium under favorable conditions in the presence of light (Tanoue and Aruga 1975). The zygospores of *Pandorina* sp. are the preferable form of storage of the alga and remain viable for at least 15 years (Colemen 1975). Lembi *et al.* (1988) stated that *Spirogyra* zygospores over-winter in benthos and germinate thereafter.

The zygotes and other spores (*e.g.*, monospores, carpospores, tetraspores, *etc*.) of the majority of seaweeds investigated had no resistant wall and had high metabolic rates and germinated soon after formation (with no obvious resting stages apparent). However, *Nemalion helminthoides* formed thick-walled, over-wintering carpospores (Martin 1969), while *Acetabularia* sp., formed thick-walled cysts (Tanner 1981).

Marine dinoflagellates formed dormant hypnozygotes (Dale 1983), and marine centric diatoms resting spores (Hargraves and French 1983). Cysts of dinoflagellates *Diplopsalis* sp., *Gymnodinium nolleri*, *Oblea rotunda* and *Protoceratium reticulatum* were viable down to 150 mm depth or for a period of 37 years in

sediments in Koljo Fjord on the west coast of Sweden (Mcquoid *et al.* 2002). Spores and resting cells of the diatoms *Chaetoceros* spp., *Detonula confervacea* and *Skeletonema costatum* were viable to >400 mm depth and may have been buried for many decades (Mcquoid *et al.* 2002). The oxygen-deficient sediments in Koljo Fjord appeared to be a natural preservatives of cells viability. Spores and cysts were able to repopulate water if suspended and exposed to suitable light, temperature and nutrients (Mcquoid *et al.* 2002).

14 BREAKAGE OF DORMANCY

The environmental and physiological factors governing the GRM of dormant oospores, zygospores or cysts have been examined in a few forms. In many of them, a change in temperature to some lower or higher level from the existing level within the temperature tolerance limit of the spores was found to break the dormancy and induce GRM (Table XIII; p. 293). Oospores of *Oedogonium* sp. germinated easily when subjected to frost (Mainx 1931). The zygospores of *Chlamydomonas chlamydogama* required an incubation of 2 d at 37 °C to germinate (Starr 1949). The zygospores of *Cosmarium* could be made to germinate effectively by immersing them in a fresh medium after a prior freezing and drying (Starr 1955, 1959). The oospores of *Chara* spp. were induced to germinate rapidly after cold treatment or storage at 5–7 °C (Imahori and Iwasa 1965; Shen 1966*a*,*b*). The cold-conditioned hypnocysts of *Gonyaulax tamarensis* excysted when exposed to high temperature and *vice-versa* (Anderson 1980). The hypnozygotes of *Gyrodinium uncatenum* collected in late winter germinated when exposed to >15 °C (Coats *et al.* 1984). Dinoflagellates cysts are known to be viable in sediments (under certain conditions at low oxygen and low temperature) for at least 6 years (Matsuoka and Fukuyo 2000). Temperature change, exposure to light, and floating up by water turbulence are thought as triggering factors for induction of GRM but an internal mechanism, *i.e.*, biological clock, also controls the GRM (Matsuoka and Fukuyo 2000).

Zygospores or cysts in some algae need a change in light conditions to break dormancy and induce GRM. Zygospores of *Chlamydomonas* sp. (Lewin 1949), *Gonium pectorale* (Stein 1958) and *Chlamydomonas eugametos* (Gowans 1960) can be regularly induced to germinate by providing alternate conditions of illumination and darkness (Table I). Lewin (1949) stated that starvation of zygotes of *Chlamydomonas moewusii* during their formation might reduce the amount of stored material and shorten the period of dormancy. The zygotes of *C. reinhardtii* need a period of rest in darkness and in nitrogen-free medium to germinate (Van Winkle-Swift 1977).

Drying of zygospores in some algae shortens the dormancy and induces GRM. The alternate soaking and drying of spores of *Furcilla stigmatophora* breaks the dormancy and induces GRM (Belcher 1967). Drying of zygospores of *Closterium* spp. was prerequisite to induce their GRM (Lippert 1967; Table VII).

Gussewa (1931) opined that bacteria in natural water cooperate in GRM of oospores of *Oedogonium* by digesting their cell wall. Cook (1962) observed that oospores in *Bulbochaete hiloensis* germinate when placed in tightly closed containers for several weeks and subjected to relatively warm temperature (bacterial and fungal decomposition was also observed under these conditions); Kremp *et al.* (2003) found that deposit-feeder gut passage may enhance GRM of dinoflagellate cysts.

Oospores of *Sphaeroplea annulina* of various age groups failed to germinate when subjected to any of different physical or chemical changes of temperature, light, drying-flooding, UV light, pH, or hormones (Chaudhary 1979). Probably, oospores required some natural conditions and/or substances or other unknown treatments to germinate or their GRM was not at all inducible before the natural dormancy period expired. The mandatory dormancy period of *Scrippsiella* cysts was *ca.* 60 d and was not affected by cold and dark storage of the cysts (Olli and Anderson 2001). Matrai *et al.* (2005) have shown that excystment of *Alexandrium* populations from the eastern Gulf of Maine exhibited a circannual endogenous rhythm with an average period of 11 months. This indicates self-regulation and internal-feedback mechanisms whether they include levels of reserves or time lapses in relation to a specific-sensed variable. The minimum dormancy period of *Gymnodinium catenatum* cysts (with an average value of 13.3 ± 5.5 d) was not affected by any of the nutritional conditions (Figueroa *et al.* 2006).

15 ROLE OF VEGETATIVE CELLS IN TOLERANCE TO ENVIRONMENTAL STRESS

Bristol-Roach (1919) reported that some herbarium specimens of blue-green algae *Schizothrix calcicola*, *Nostoc ellipsosporum*, and *Microcoleus* sp. were preserved for 70 years. Fritsch (1922) pointed out that the striking characteristic feature of terrestrial algae is the capacity of the ordinary vegetative cell to withstand prolonged drought without any marked change or special thickening of the cell wall. Further, the

change from the resting to active condition is accomplished in a very short time, apparently because the terrestrial algae require only small amounts of moisture to reactivate them (Stokes 1940). Hedlund (1913) showed that small organisms are in a better position to withstand desiccation. Lund (1945) opined that with the reduction in cell size, the forms are in a better position to lie apposed to the soil particles from which they can absorb moisture. Tolerance of *Chlorella vulgaris* vegetative cells to dryness for >1 month might be due to their small cell size or due to chemical composition of the cell wall containing sporopollenin (Agrawal and Singh 2001; Agrawal and Manisha 2007). 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, so that they could resist desiccation (Petersen 1935). 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. But it was not clear whether the survival of dried algae was due to the presence of spores in stored materials (Davis 1972).

Many species of *Nostocales* over-winter as vegetative filaments rather than akinetes (Reynolds 1972; Kappers 1976; Barbiero and Welch 1992). *Aphanizomenon flos-aquae* over-wintered in Kinnego Bay as vegetative filaments and the production of akinetes was not necessary for perennation of the species (Jones 1979). Under natural conditions, *Pithophora oedogonia* over-winters as vegetative filaments and akinetes, and is still photosynthetically competent (Spencer *et al.* 1981).

Filaments of *Stigeoclonium pascheri* died without any akinete formation at ≥45 °C (Agrawal and Sarma 1982*b*). No vegetative cells of *Pithophora oedogonia*, *Anabaena iyengarii*, *Westiellopsis prolifica* and *Nostochopsis lobatus* filaments survived and formed akinetes, and no akinete germinated, at 41 °C (Agrawal and Singh 2000). Since akinetes are not formed at high temperature, the akinete-forming blue-green algae are generally absent from the hot spring flora (Anagnostidis 1961). Spore-forming blue-green algae are generally absent from desert floras (Cameron and Blank 1966). A unicellular red alga *Cyanidium caldarium* grows in acid hot-springs throughout the world. It has the ability to grow in water of pH as low as 2 (Ascione *et al.* 1965) and has a temperature optimum for ^{14}C incorporation of 45 °C (Doemel and Brock 1970).

Evans (1958) had shown that survival of desiccation by pond algae has no relation to the production of spores. Fogg (1969) has rightly pointed out that the formation of akinetes is a relatively unimportant means of survival under adverse conditions by most algae. This is also supported by the observations on sub-aerial blue-green algae. The large majority of them are not spore forming and survive environmental stress due to the high by reducing state of cytoplasm coupled with the presence of a thick sheath (Tripathi and Talpasayi 1980). Extensive extracellular polysaccharide sheaths produced by some blue-green algae help to stabilize the cell membrane during desiccation and enhance water retention and water absorption (Caiola *et al.* 1993, 1996; Tamaru *et al.* 2005). Many blue-green algae have been shown to be tolerant to cellular water loss and counteract damage through the production of polyhydroxy saccharides (Potts 1994). These saccharides most likely replace the water shell around cellular macromolecules, *e.g.*, proteins, DNA, and lipids and prevent their denaturation (Potts 1994, 1999). The vegetative cells of blue-green algae *Scytonema millei* and *Lyngbya major* (both growing on wall and bark surfaces) and *L. mesotricha* and *Phormidium bohneri* (both growing on soil surface) survived atmospheric temperature of 48 °C (Gupta and Agrawal 2006, 2008). Soil blue-green algae resume physiological activity soon after rewetting with atmospheric water (Lange *et al.* 1992). Trainor and Gladych (1995) found that even after soils had air-dried for 35 years, green algae (which had survived in an unknown form) could be cultured from them. A non-sporeforming *Microcoleus* occuring within the crust sample collected in desert can tolerate extremes of temperature, light and diurnal desiccation cycle. The alga was able to rapidly activate photosynthesis when rehydrated (Harel *et al.* 2004). The ability of *Lyngbya* mats to tolerate desiccation and take advantage of hydration periods enables these mats to predominate in the intertidal environment (Fleming *et al.* 2007). The surface of *Lyngbya* mat is a dark-brown color due to a high scytonemin content in the extracellular polysaccharide sheaths, which is an extracellular UV radiation screening compound (Garcia-Pichel and Castenholz 1991). Green algae isolated from desert habitats were *Scenedesmus rotundus*, *Cylindrocystis* sp., *Myrmecia* sp. and *Chlorosarcinopsis* sp. (Cardon *et al.* 2008). The vegetative cells of these algae can tolerate rapid dehydration, and the cellular functions such as photosynthesis can recover upon rehydration very quickly within 1 h (Gray *et al.* 2007). Desiccation recovery can be an energetically expensive process involving protein and lipid biosynthesis as well as various cellular repair mechanisms (Angeloni and Potts 1986; Taranto *et al.* 1993).

16 CONCLUSIONS

Very little is known on the effects of different factors on the SG. This is because that (*i*) many algae did not reproduce and form any spore in culture, (*ii*) the life cycle of many algae is not monitored in nature,

and (*iii*) many algae survive in nature most of the time as vegetative cells without forming any spore. But in spite of that it is possible to draw certain conclusions from the data in this line of research.

(*a*) GRM takes place more in light than in darkness. In darkness, GRM occurs in the presence of suitable organic carbon in the medium serving as energy source, or it may be due to storage reserve compounds of spores. Storage of algal spores usually decreases their viability (because of respiratory utilization of reserve substances during storage). Certain minimum light intensity level is required to trigger algal SG and percentage SG increases with an increase in light intensity level. The presence of silt and sediments in water column reduces light penetration and prevents algal SG. White light is most favored for SG, but it is red light in some algae. Photo-reversible phenomena mediated by pigment functionally similar to the phytochrome of higher plants are reported to occur in some algae.

(*b*) Temperature is one of the important factors controlling SG. In blue-green algae, akinete GRM was found to be optimal at 22–27 °C (GRM usually occurred in spring or in early summer). In green algae, SG was optimal at ≈20 °C (spores collected from warmer regions germinated at somewhat higher temperature than those collected from colder regions). In *Vaucheria* sp., zoospores and oospores germinated optimal at 12 and 15 °C, respectively. Dinoflagellate cysts germinated optimally at ≥17 °C. Zoospores and zygotes of brown algae were reported to germinate within a wide range of temperature (3–30 °C), depending upon the type and place of occurrence of alga.

(*c*) Lack of N, P or Mg decreased SG (indicating the synthesis of proteins, nucleic acids and chlorophylls during SG). The presence of microelements (such as Zn, Mn, Mo, Cu, Co, B) in the culture media decreased SG. High level of N, P or Mg also decreased SG, indicating that it was sensitive to nutrient concentrations.

(*d*) The presence of plant hormones (IAA, IBA, NAA, GA_3), kinetin, tryptophan (a precursor of IAA), vitamins B_2, C, serine (at certain level), pretreatment (of spores) with caffeine, crystal violet or methylene blue induced SG. Dyes produced changes in membrane permeability and active transport processes.

(*e*) In some green and blue-green algae, spores germinated optimally at pH 7 or 8 (at which the algae also grew optimally).

(*f*) Biotic factors (including algal and bacterial extracellular products, animal grazing and extracellular products), water stress (except for the need of prior drying for some algal spores), antibiotics (except penicillin at some low level), UV light, and pollution (including heavy metals, pesticides, insecticides, sewage effluents, crude oil, acetylene, ethylene, ammonia or anoxic conditions) at various levels decreased or totally suppressed SG.

(*g*) X-Rays and γ-rays at low doses stimulated akinete GRM in green alga *Stigeoclonium pascheri.* The exact mechanism of activation of akinetes at low levels of X-rays and γ-rays is not known.

(*h*) Water movements help to release zoospores in some brown algae but prevent spore settlement and GRM. Water movement keeps spores suspended in water and brings settled spores to the upper layer of water where they can germinate in the presence of light.

(*i*) Zoospores (having very thin or no cell wall) had no dormancy and germinated immediate by after formation; akinetes (with thicker cell wall and more resistant to environmental stresses than vegetative cells) germinated either immediately or after a shorter or longer time period following formation (both in the laboratory and in natural conditions); zygospores, oospores and cysts (of terrestrial and freshwater algae having much thicker cell wall than vegetative cells) did not germinate immediately after formation and required a period of dormancy (when they easily endure drought and other environmental rigors before GRM). Dormancy in some of them (but not in all) can be broken by a change in temperature, light, or other factors. More work is needed to know which external or internal factors govern the dormancy of spores and how it can be broken.

(*j*) Seaweed zygotes (with no resistant cell wall and high metabolic rate) had no resting period and germinated soon after formation. However, marine diatoms and dinoflagellates may have thick-wall resting spores and cysts, respectively.

(*k*) Desert algae, hot-water spring algae, and many terrestrial algae did not form any spore-like structure, and their vegetative cells (usually covered with extracellular polysaccharide sheath or having a reduced state of cytoplasm) survived environmental stresses similarly to or more than any dormant spores of other algae. These dry vegetative cells resume physiological activity soon after rewetting with atmospheric water.

TABLES I–XIII

Abbreviations (for all tables)

A	akinete	M	monospore	OS	old spore	RS	resting spore	ZoS	zoospore
C	cyst	MZS	microzoospore	PRS	physiological resting stage	S	spore	Zy	zygote
DGC	dormant green cells	O	oospore	QS	quiescent spores	SS	statospore	ZyS	zygospore
HC	hypnocyst								

Table I. Light is required for spore germination in algae

Alga or flora	Spore	Light quality[a,b]	Reference
No germination occurred in darkness			
Anabaena azollae	A	R	Kezhi and Cheng 1985
A. cylindrica	A	R	Yamamoto 1976
A. doliolum	A	G, BY, R, W, all equal	Kaushik and Kumar 1970, Rai *et al.* 1988
A. fertilissima	A	R	Reddy *et al.* 1975
A. iyengarii	A	W	Agrawal and Singh 2000
A. ucrainica	A	W	Tsujimura and Okubo 2003
A. vaginicola	A	R	Rai and Pandey 1981
A. variabilis	A	R	Braune 1979
Anabaenopsis arnoldii	A	R	Reddy *et al.* 1975
Asterionella formosa	PRS	W	Lund 1954, Sicko-Goad *et al.* 1989
Bangia fuscopurpurea	M	W	Charnofsky *et al.* 1980
Chaetoceros sp.	S	W	Hollibaugh *et al.* 1981
Chlamydomonas reinhardtii	Zy	W	Hudock and Rosen 1976
C. eugametos	ZyS	alternate W and D	Lewin 1949, Gowans 1960
Chlamydomonas sp.	ZyS	alternate W and D	Lewin 1949, Gowans 1960
Cylindrospermum sp.	A	W	Pandey *et al.* 1989
Dinobryon divergens	SS	W	Sheath *et al.* 1975
Eudorina sp.	O	W	Schreiber 1925
Fischerella muscicola	A	G, BY, R, W, all equal	Kaushik and Kumar 1970, Rai *et al.* 1988
Gloeotrichia echinulata	A	W	Roelofs and Oglesby 1970, Barbiero 1993, Karlsson-Elfgren (2003)
Gonium pectorale	ZyS	alternate W and D	Stein 1958
Melosira sp.	PRS	W	Lund 1954, Sicko-Goad *et al.* 1989
Nodularia spumigena	A	R	Pandey and Talpasayi 1981, Hüber 1985

Nostoc ellipsosporum	A	R	Ahluwalia and Kumar 1980
Nostoc PCC 7524	A	W	Chauvat *et al.* 1982
Nostochopsis lobatus	A	W	Agrawal and Singh 2000
Oedogonium foveolatum	O	W	Hoffman 1965
Pandorina sp.	Zy	W	Coleman 1975
Pithophora kewensis	A	G and B	Patel 1971
Platymonas sp.	C	W	Tanoue and Aruga 1975
Spirogyra hyalina	ZyS	R	Agrawal and Chaudhary 1994
Stigeoclonium pascheri	A	R	Agrawal 1984
ditto	ZoS	W	Agrawal 1985*a*
Volvox sp.	O	W	Pocock 1933, Metzner 1945
Westiellopsis prolifica	A	W	Agrawal and Sharma 1994*a*
Germination can occur both in the presence or absence of light, but was more intensive in the light than in darkness			
Acetabularia sp.	C	W	Koop 1975
Anabaena circinalis	A	W (with suitable organic carbon in the dark)	Van Dok and Hart 1997
A. solitaria	A	W	Cmiech *et al.* 1984
Aphanizomenon flos-aquae	A	W	Rose 1934
Ascophyllum nodosum	Zy	W	Sheader and Moss 1975
Aulacoseira skvortzowii	RS	W	Jewson *et al.* 2008
Chara spp.	O	W	Forsberg 1965, Proctor 1967
Chlamydomonas moewusii	Zy	W	Lewin 1951
Enteromorpha flexuosa	S	W	Kolwalkar *et al.* 2007
Many *Floridae* members	S	W	Chemin 1937
Furcilla stigmatophora	S	W	Belcher 1967
Halidrys siliquosa	Zy	W	Moss and Sheader 1973
Himanthalia elongata	S	W	Moss *et al.* 1973
Nostoc punctiforme	A	W (in presence of sugar in dark)	Harder 1917*a*,*b*
Pithophora oedogonia	A	G and B	Neal and Herndon 1968, Agrawal 1986*a*, Chaudhary and Singh 1987

[a]Condition favored for germination.

[b]B – blue, BY – blue-yellow, D – darkness, G – green, R – red, W – white.

Table II. Temperature (°C) optimal for spore germination in algae

Alga	Spore	°C	Reference
Cyanophyceae			
Anabaena cylindrica	A	27	Yamamoto 1976
A. solitaria	A	17	Rengefors *et al.* 2004
A. vaginicola	A	25	Rai and Pandey 1981
A. ucrainica	A	23	Tsujimura and Okubo 2003
Cylindrospermopsis raciborskii	A	22–24	Gorzo 1987, Padisak 2003, Hong *et al.* 2006
Gloeotrichia echinulata	A	17	Karlsson-Elfgren 2003
Nodularia spumigena	A	≥22	Hüber 1985
Chlorophyceae			
Acetabularia sp.	C	21	Koop 1975
Botrytis cinerea	S	20	Bernard 1973
Chara contraria	O	18–24 or 28	Proctor 1967
C. zeylanica	O	28–24	Proctor 1967
Cladophora sp.	A	11.5–13.8	Mason 1965
Enteromorpha sp.	ZoS	20	Woodhead and Moss 1975
ditto		10–15	Lotze *et al.* 1999
Pithophora oedogonia	A	20–25	Spencer *et al.* 1980, 1981, Agrawal 1986*a*
Stigeoclonium pascheri	A	25	Agrawal 1984
ditto	ZoS	20–30	Agrawal 1985*a*
Rhizoclonium riparium	A, ZoS	15–20	Hall and Walmsley 1991
Spirogyra hyalina	ZyS	25	Agrawal and Chaudhary 1994
Ulothrix sp.	MZS	≤10	Klebs 1896
Xanthophyceae			
Vaucheria sessilis	ZoS	12	League and Greulach 1955
ditto	O	15	
Dinophyceae			
Ceratium hirundinella	C	17	Rengefors and Anderson 1998
Peridinium cinctum	C	20	Pfiester 1975
Scrippsiella trochoidea	C	22–25	Binder and Anderson 1987

Phaeophyceae			
Ascophyllum nodosum	Zy	10	Sheader and Moss 1975
Ecklonia stolonifera	ZoS	10–30	Notoya and Asuke 1983
Halidrys siliquosa	Zy	3–10	Moss and Sheader 1973
Macrocystis integrifolia	ZoS	18	Buschmann *et al.* 2004
Pilayella littoralis	ZoS	5	Lotze *et al.* 1999
Spermatochnus paradoxus	Zy	9–20	Müller 1981
Bacillariophyceae			
Aulacoseira skvortzowii	S	4	Jewson *et al.* 2008

Table III. Need of inorganic nutrients[a] for spore germination in algae

Alga	Spore	Inorganic nutrients[b]	Reference
Anabaena circinalis	A	phosphate	Van Dok and Hart 1997
A. fertilissima	A	phosphate	Reddy 1976*a*
A. iyengarii	A	nitrate, phosphate	Agrawal and Misra 2002
A. vaginicola	A	nitrate	Rai and Pandey 1981
Blastocladiella emersonii	ZyS	brief exposure to KCl, $CaCl_2$ and $MgCl_2$	Soll and Sonneborn 1972
Chlamydomonas moewusii	ZyS	nitrate	Cain 1980
Cladophora glomerata	ZoS	nitrate, phosphate	Agrawal and Misra 2002
Enteromorpha sp.	S	phosphate	Sousa Ana *et al.* 2007
Gymnodinium catenatum	C	phosphate	Figueroa *et al.* 2006
Nodularia spumigena	A	phosphate	Hüber 1985
Nostochopsis lobatus	A	nitrate, phosphate	Agrawal and Misra 2002
Pithophora oedogonia	A	nitrate, phosphate	Neal and Herndon 1968, Riley and Anderson 1976, Agrawal and Misra 2002
Rhizoclonium hieroglyphicum	ZoS	nitrate, phosphate	Agrawal and Misra 2002
Stigeoclonium pascheri	A	$MgSO_4$, phosphate	Agrawal and Sarma 1982*a*
Westiellopsis prolifica	A	$MgSO_4$, nitrate, phosphate	Agrawal and Sharma 1994*a*, Agrawal and Misra 2002

[a]Present in the culture medium. [b]Needed for spore germination.

Table IV. The chemicals found to be stimulatory for spore germination in algae

Alga	Spore or cell	Chemicals	Reference
Anabaena cylindrica	A	acetate (0.1–1 mmol/L)	Yamamoto 1976
Botrytis cinerea	OS	glucose, maltose or malt extract	Bernard 1973
Chlamydomonas sp.	ZyS	a type of soil solution prepared without heat	Moewus 1940
Hydrodictyon reticulatum	ZyS	IAA, strychnine	Rowan 1937
Pithophora oedogonia	A	IAA, IBA (0.01–1 ppm), NAA (0.01–0.1 ppm), GA_3 (0.01–500 ppm)	Agrawal 1985*b*
Stigeoclonium pascheri	A	IAA (0.01–0.1 ppm), GA_3 (0.01–500 ppm), serine (100–200 ppm), ascorbic acid (100–400 ppm), pretreatment with caffeine (500–1000 ppm) or Crystal violet (2–5 ppm) or Methylene blue (20–50 ppm)	Agrawal and Sarma 1984, Agrawal 1985*c*, 1988*a*, 1992*a*
Ulva sp.	DGC	IAA (0.05 ppm) in the presence of kinetin (0.1 ppm)	Provasoli 1958
Vaucheria sp.	ZoS	IAA, tryptophan	Hustede 1957

Table V. Optimum pH for spore germination of algae

Alga	Spore	pH optima	Reference
Anabaena cylindrica	A	7–8	Yamamoto 1976
A. fertilissima	A	7.0–10.5	Reddy 1984
A. iyengarii	A	7–8	Agrawal and Misra 2002
A. vaginicola	A	7–9	Rai and Pandey 1981
Anabaenopsis arnoldii	A	7.0–8.5	Reddy 1984
Cladophora glomerata	ZoS	7–8	Agrawal and Misra 2002
Cladophora sp.	A	8.1–8.3	Mason 1965
Nostochopsis lobatus	A	7–8	Agrawal and Misra 2002
Pithophora oedogonia	A	7–8	Chaudhary and Singh 1987, Agrawal 1986*a*, Agrawal and Misra 2002
Rhizoclonium hieroglyphicum	ZoS	7–8	Agrawal and Misra 2002
Spirogyra hyalina	ZyS	8	Agrawal and Chaudhary 1994
Stigeoclonium pascheri	A	8	Agrawal 1984
S. pascheri	ZoS	8	Agrawal 1985*a*
Westiellopsis prolifica	A	7.5	Agrawal and Sharma 1994*a*

Table VI. Algal spores formed in old cultures usually need fresh culture medium to germinate and do not germinate in the same medium in which they were formed[a]

Alga or flora	Spore	Medium of germination[b]	Reference
Anabaena cylindrica	A	FCM	Fay 1969*b*
A. iyengarii	A	FCM (did not germinate in medium of its formation)	Agrawal and Sharma 1994*a*, Agrawal and Singh 1999*b*
A. torulosa	A	FCM	Sarma *et al.* 2000
Aulacoseira skvortzowii	RS	FCM	Jewson *et al.* 2008
Chaetophora attenuata	ZoS	in the same medium in which it was formed	Agrawal and Sharma 1994*b*, 1996, 2005
Chara sp.	O	fresh soil-water medium (pure water with sandy loam)	Proctor 1967
Charophyte members	O	fresh soil-water medium (pure water with clay)	Imahori and Iwasa 1965
Cladophora glomerata	ZoS	in the same media in which it was formed	Agrawal and Singh 1999*a*
Cylindrospermum sp.	A	FCM	Miller and Lang 1968
Gonium pectorale	ZyS	fresh Beijernick's soil extract agar	Stein 1958
Gymnodinium pseudopalustre	S	FCM	Stosch 1973
Nostoc spongiaeforme	A	FCM (did not germinate in culture filtrate of its own)	Thiel and Wolk 1982, 1983
Nostochopsis lobatus	A	FCM (did not germinate in medium of its formation)	Agrawal and Sharma 1994*a*, Agrawal and Singh 1999*b*
Pediastrum simplex	RS	fresh Bold's basal medium	Ooshima 1974
Pithophora oedogonia	A	FCM (did not germinate in medium of its formation)	Agrawal 1986*a*, Agrawal and Singh 1999*a*, Gupta and Agrawal 2007
Platymonas sp.	C	FCM (following air exposure of cyst for ½ h)	Tanoue and Aruga 1975
Rhizoclonium hieroglyphicum	ZoS	in the same media in which it was formed	Agrawal and Singh 1999*a*
Scrippsiella trochoidea	C	fresh nutrient replete medium (after dormancy period was over)	Binder and Anderson 1987
Stigeoclonium pascheri	A	fresh Bold's basal medium (did not germinate in medium of its formation)	Agrawal 1990
Westiellopsis prolifica	A	FCM (did not germinate in medium of its formation)	Agrawal and Sharma 1994*a*, Agrawal and Singh 1999*b*
Woloszynskia apiculata	S	FCM	Stosch 1973
Zygnema sp.	ZyS	fresh Godward's culture medium	Prasad 1963

[a]Zoospores formed in the young cultures germinated in the same medium. [b]FCM – fresh culture medium.

Table VII. Water stress was inhibitory for spore germination in algae

Alga	Spore	Observation	Reference
Anabaena circinalis	A	desiccation for short periods decreased the viability	Baker and Bellifemine 2000
A. iyengarii	A	failed to germinate on ≥6 % agarized media or in 0.2 mol/L salinized liquid media	Agrawal and Singh 1999*b*, 2000
Anabaena sp.	A	ability to germinate lost after 3 d of desiccation	Shigeo 2004
Cladophora glomerata	ZoS	failed to germinate on ≥6 % agarized media or in 0.2 mol/L salinized liquid media	Agrawal and Singh 1999*a*
Closterium spp.	ZyS	germinate in wet condition (after prior drying)	Lippert 1967

continued

Cosmarium spp.	ZyS	germinate when immersed in fresh medium (after prior drying and freezing)	Starr 1955, 1959
Furcilla stigmatophora	S	germinate in wet condition (after alternate soaking and and drying)	Belcher 1967
Nodularia spumigena	A	salinity of >20 ‰ inhibited germination	Hüber 1985
Nostochopsis lobatus	A	failed to germinate on ≥6 % agarized media or in 0.2 mol/L salinized liquid media	Agrawal and Singh 1999*b*, 2000
Pithophora oedogonia	A	*ditto*	Agrawal and Singh 1999*a*, 2000
Rhizoclonium hieroglyphicum	ZoS	*ditto*	Agrawal and Singh 1999*a*
Volvox carteri	O	dryness retards germination	Metzner 1945
Westiellopsis prolifica	A	failed to germinate on ≥6 % agarized media or in 0.2 mol/L salinized liquid media	Agrawal and Singh 1999*b*, 2000

Table VIII. Antibiotics inhibit spore germination in algae

Alga	Spore	Antibiotics[a] inhibiting germination	Reference
Anabaena doliolum	A	Pen, Stm, Chl	Kumar and Kaushik 1971
A. doliolum	A	Mtm	Madan and Kumar 1973
Fischerella muscicola	A	Pen, Stm, Chl	Kumar and Kaushik 1971
Nodularia spumigena	A	Pen, Stm or Chl (all 0.2–0.8 ppm)	Pandey and Talpasayi 1982
Oedogonium gunnii	ZoS	Pen (10 U/mL), Stm (10 ppm), Tet (30 ppm), Kan (30 ppm), Nov (30 ppm)	Srivastava and Sarma 1980
Oedogonium sp. VPP 74	ZoS	Erm (15 ppm), Tet (30 ppm), Stm (10 ppm)	Srivastava and Sarma 1980
Schizomeris leibleinii	ZoS	Erm (15 ppm), Nov (30 ppm), Chm (30 ppm), Pen (10 U/mL)	Srivastava and Sarma 1980
Stigeoclonium pascheri	A	Pen (≥4000 ppm), Stm, Chl (12.5–400 ppm)[b]	Agrawal and Sarma 1980
S. tenue	ZoS	Erm (15 ppm), Nov (30 ppm), Chm (30 ppm), Pen (10 U/mL)	Srivastava and Sarma 1980

[a]Chl – chloramphenicol Chm – chloromycetin Erm – erythromycin Kan – kanamycin Mtm – mitomycin-C
Nov – novobiocin Pen – penicillin Stm – streptomycin Tet – tetracycline
[b]Even pretreatment with these antibiotics decreased germination.

Table IX. UV light inhibits spore germination in algae

Alga or flora	Spore	Agents	Reference
Alaria esculenta	ZoS	UV-B	Wiencke *et al.* 2004, 2006, 2007, Roleda *et al.* 2005, 2006*a*
A. marginata	ZoS	high levels of UV radiation	Hoffman *et al.* 2003
Anabaena doliolum	A	UV-C irradiated culture media	Reddy 1976*b*

Anabaena sp.	A	UV-C of any dose (0.96–7.68 kJ/m^2)	Agrawal and Singh 2000
Fischerella muscicola	A	UV-C	Singh and Singh 1972
Kelp and kelp-like brown algae	ZoS	UV-B	Wiencke *et al.* 2000, Swanson and Druehl 2000, Oiencke *et al.* 2000
Laminaria digitata	ZoS	UV-B[a]	Wiencke *et al.* 2004, 2006, 2007, Roleda *et al.* 2005, 2006*a*
L. hyperborea	ZoS	UV-B[a]	Wiencke *et al.* 2004, 2006, 2007, Roleda *et al.* 2005, 2006*a*
L. saccharina	ZoS	UV-B	Makarov and Voskoboinikov 2001
ditto	ZoS	UV-B[a]	Wiencke *et al.* 2004, 2006, 2007, Roleda *et al.* 2005, 2006*a*
Nodularia spumigena	A	UV-C of any dose	Pandey 1985
Nostochopsis sp.	A	UV-C of any dose (0.96–7.68 kJ/m^2)	Agrawal and Singh 2000
Pithophora kewensis	A	UV-C of any dose	Sarma *et al.* 1983
P. oedogonia	A	UV-C of any dose (0.96–7.68 kJ/m^2)	Agrawal and Singh 2000
Saccorhiza dermatodea	ZoS	UV-B	Wiencke *et al.* 2004, 2006, 2007, Roleda *et al.* 2005, 2006*a*
Scenedesmus incrassatulus	A	UV-C irradiated culture media	Reddy 1976*b*
Stigeoclonium pascheri	A	UV-C of any dose (0.032–9.60 kJ/m^2), culture media irradiated with UV-C (1.92–11.52 kJ/m^2)	Sarma and Agrawal 1980, 1981, Agrawal 1987, 1992*b*
Westiellopsis sp.	A	UV-C of any dose (0.96–7.68 kJ/m^2)	Agrawal and Singh 2000

[a]Lower subtidal *L. hyperborea* was more sensitive than upper subtidal *L. saccharina* and *L. digitata*.

Table X. Pollution of any type (*e.g.* heavy metals, pesticides, oil, sewage, *etc.*) inhibits spore germination in algae

Alga or flora	Spore	Inhibition agents	Reference
Anabaena iyengarii	A	heavy metals $Co(NO_3)_2$, $CuSO_4$, ZnO, $HgCl_2$, $Pb(NO_3)_2$ (all at ≥0.5 ppm); pesticides carbofuran, 2,4-D, dithane, phorate or bavistin (all at ≥1 ppm)	Agrawal and Misra 2002
Ceratium hirundinella	C	anoxic conditions, introduction of nitrogen gas into sample vials	Rengefors and Anderson 1998, Kremp and Anderson 2000, Matsuoka and Fukuyo 2000
Cladophora glomerata	ZoS	heavy metals $Co(NO_3)_2$, $CuSO_4$, ZnO, $HgCl_2$, $Pb(NO_3)_2$ (all at ≥0.5 ppm); pesticides carbofuran, 2,4-D, dithane, phorate or bavistin (all at ≥1 ppm)	Agrawal and Misra 2002
Cylindrospermum sp.	A	acetylene, ethylene; H_2, argon when supplied with 1 % CO_2	Pandey *et al.* 1989
ditto	A	insecticide parathion-methyl at ≤8 ppm	Panigrahi *et al.* 2003
Dictyota sp.	S	crude oil at 0.1–10 ppm	Premila and Rao 1997
Dinoflagellates	C	anoxic conditions, introduction of nitrogen gas into sample vials	Rengefors and Anderson 1998, Kremp and Anderson 2000, Matsuoka and Fukuyo 2000
Enteromorpha sp.	S	NH_4-N	Sousa Ana *et al.* 2007
Gracilaria sp.	S	crude oil at 0.1–10 ppm	Premila and Rao 1997
Haematococcus lacustris	QS	chromium ($K_2Cr_2O_7$) at 10 mg/L	Bassi *et al.* 1990
Hormosira banksii	Zy	sewage effluents of different quality	Burridge *et al.* 1996

continued

Hypnea sp.	S	crude oil at 0.1–10 ppm	Premila and Rao 1997
Lessonia nigrescens	S	copper at >7.87 μg/L	Contreras *et al.* 2007
ditto	S	polylysine	Santelices and Aedo 1999
Macrocystis angustifolia	ZoS	sewage effluents of different quality	Burridge *et al.* 1996
M. pyrifera	S	$CuSO_4$ at 10–50 μg/L	Anderson *et al.* 1990
Nostochopsis lobatus	A	heavy metals $Co(NO_3)_2$, $CuSO_4$, ZnO, $HgCl_2$, $Pb(NO_3)_2$ (all at ≥0.5 ppm); pesticides carbofuran, 2,4-D, dithane, phorate or bavistin (all at ≥1 ppm)	Agrawal and Misra 2002
Padina sp.	S	crude oil at 0.1–10 ppm	Premila and Rao 1997
Phyllospora comosa	Zy	sewage effluents of different quality	Burridge *et al.* 1996
Pithophora kewensis	A	organophosphorus insecticide Elalux EC-25 (0.025–0.1 %)	Agrawal and Chaudhary 1989
P. oedogonia	A	heavy metals $Co(NO_3)_2$, $CuSO_4$, ZnO, $HgCl_2$, $Pb(NO_3)_2$ (all at ≥0.5 ppm); pesticides carbofuran, 2,4-D, dithane, phorate or bavistin (all at ≥1 ppm)	Agrawal and Misra 2002
ditto	A	$HgCl_2$ at 1.25–45 ppm (lethal at ≥60 ppm)	Chaudhary and Singh 1986
Rhizoclonium hieroglyphicum	ZoS	heavy metals $Co(NO_3)_2$, $CuSO_4$, ZnO, $HgCl_2$, $Pb(NO_3)_2$ (all at ≥0.5 ppm); pesticides carbofuran, 2,4-D, dithane, phorate or bavistin (all at ≥1 ppm)	Agrawal and Misra 2002
Scenedesmus armatus	QS	chromium ($K_2Cr_2O_7$) at 10 mg/L	Bassi *et al.* 1990
Scrippsiella hangoei	C	anoxic condition, an introduction of nitrogen gas into sample vials	Rengefors and Anderson 1998, Kremp and Anderson 2000, Matsuoka and Fukuyo 2000
Undaria pinnatifida	ZoS	herbicides diuron, simazine and glyphosate; antifoulant seanine 211; red algal extract furanone 281	Burridge and Gorski 1998

Table XI. Algal akinetes are slightly more tolerant to various stress conditions than vegetative cells

Alga or flora	Stress conditions	Reference
Anabaena cylindrica	desiccation and high temperature (55 °C)	Yamamoto 1975, 1976
A. fertilissima	low (0, 7 °C) and high (37, 47 °C) temperature	Reddy 1976*a*
A. iyengarii	dryness, frost, heat shock	Agrawal and Singh 1999*a*,*b*, 2000
Anabaenopsis arnoldii	low (0, 7 °C) and high (37, 47 °C) temperature	Reddy 1976*a*
Blue-green algae (akinetes-forming)	physical extremes	Harder 1917*a*,*b*; Kaushik and Kumar 1970
ditto	lyophilization	Watanabe 1959; Whitton 1962; Holm-Hansen 1963*a*,*b*, 1964
Cyanospira capsulata	long time storage, desiccation	Sili *et al.* 1994
C. rippkae	*ditto*	*ditto*
Cylindrospermum licheniforme	heat	Glade 1914
Nostochopsis lobatus	dryness, frost, heat shock	Agrawal and Singh 1999*a*,*b*, 2000
Pithophora oedogonia	*ditto*	*ditto*
Stigeoclonium pascheri	UV-C light, temperature extremes (0, 45, 50 °C)	Sarma and Agrawal 1980, Agrawal 1985*d*
Westiellopsis prolifica	dryness, frost, heat shock	Agrawal and Singh 1999*a*,*b*, 2000

Table XII. A dormancy period is needed before germination of some spores (mostly zygospores, oospores or cysts) in algae

Alga or flora	Spore	Dormancy period	Reference
Acetabularia mediterranea	C	12–15 weeks	Koop 1975
Chlamydomonas moewusii	Zyg	a period of rest (in darkness and in the presence of nitrogen)	Lewin 1949; Cain 1980
C. reinhardtii	Zyg	a period of rest (in darkness and in nitrogen-free medium)	Van Winkle Swift 1977
Closterium sp.	ZyS	several months	Fox 1958; Kies 1964; Lippert 1967
Cosmarium botrytis	ZyS	2–3 months	De Bary 1858
Dinoflagellates	C	upto even 6 years	Matsuoka and Fukuyo 2000
Gonium pectorale	ZyS	18–21 d	Stein 1958
Gymnodinium catenatum	C	13.3 ± 5.5 d	Figueroa *et al.* 2006
Oedogonium foveolatum	O	22 months	Hoffman 1965
Oedogonium sp.	O	a period of rest	Gussewa 1931; Mainx 1931
Scrippsiella cf. *Lachrymosa*	C	≈60 d	Olli and Anderson 2001
S. trochoidea	C	≈25 d	Binder and Anderson 1987
Spirogyra hyalina	ZyS	90 d	Agrawal and Chaudhary 1994
Spirogyra sp.	Zy	overwinter in benthos	Lembi *et al.* 1988

Table XIII. Treatment used to break dormancy of algal spores and induce germination

Alga or flora	Spore	Treatment	Reference
Bacteriastrum hyalinum	S	cold treatment of different durations	Drebes 1972
Ceratium cornutum	C	incubation at high temperature	Stosch 1965, 1973
C. hirundinella	C	incubation at high temperature	Huber and Nipkow 1922, 1923
Chaetoceros teres	S	cold treatment of different durations	Drebes 1975
Chara contraria	O	storage at 5–7 °C	Shen 1966*a*,*b*
Chara sp.	O	cold treatment of different durations	Imahori and Iwasa 1965
C. zeylanica	O	storage at 5–7 °C	Shen 1966*a*,*b*
Chlamydomonas chlamydogama	ZyS	incubation at 37 °C for 2 d	Starr 1949
Cosmarium botrytis	ZyS	freezing	Starr 1954
Cosmarium spp.	ZyS	drying and freezing	Starr 1955, 1959
Dinoflagellates	C	temperature change, and exposure to light	Matsuoka and Fukuyo 2000
Eunotia soleirolii	S	incubation from 2 to 15 °C	Stosch and Fecher 1979
Gonyaulax sp.	C	an increase in temperature	Wall and Dale 1968, 1969
Gonyaulax spp.	HC	incubation from 5 to 16 °C	Anderson and Wall 1978

continued

G. tamarensis	HC	temperature change (cold-conditioned hypnocyst when exposed to high temperature and *vice versa*)	Anderson 1980
Gymnodinium pseudopalustre	C	incubation at high temperature	Stosch 1965, 1973
G. pseudopalustre	HC	temperature treatment of 3 °C	Stosch 1973
Gyrodinium uncatenum	HC	exposure to >15 °C (cyst collected in late winter)	Coats *et al.* 1984
Oedogonium sp.	O	frost	Mainx 1931
Peridinium cunningtonii	C	incubation at 22 °C (cold and dark treated cyst)	Sako *et al.* 1984
Pyrodinium bahamense	C	an increase in temperature	Wall and Dale 1968, 1969
Spirogyra hyalina	O	storage at 4 °C for 90 d	Agrawal and Chaudhary 1994
Woloszynskia apiculata	C	incubation at high temperature	Stosch 1965, 1973

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