

Unfavorable environmental conditions induce the production of resting spores in certain organisms. Many algae have successfully developed specialized resistant characteristics, such as thickened cell walls accompanied by decreased metabolic rates, that enable them to resist periods of extreme change in their environment. These strategies give the algae considerable evolutionary advantages over organisms that are unable to withstand changes in temperature, light, or ionic conditions.

Though the resting spore is considered to be an advantageous and primitive trait, the benefits are offset by the great amount of energy needed to produce and maintain the cell in near-dormancy over long periods of time and by the potentially “lost” number of cell divisions that could have occurred during the resting phase. The interesting contrast of advantages and disadvantages has stimulated biologists to investigate the morphology and the underlying processes of the physiology of vegetative cells and thick-walled resting spores.

The chapters in this book provide an excellent background to the ecological conditions and population dynamics of both marine and freshwater algae from diverse habitats and will be particularly useful to biologists and paleoecologists.

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## Survival strategies of the algae

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## Preface

The symposium “Survival Strategies of the Algae” was held in Vancouver, British Columbia, July 15, 1980, and was sponsored by the Phycological Society of America and the Systematic and Phycological Sections of the Botanical Society of America. It provided an opportunity to gather together biologists working on Cyanobacteria (Cyanophytes), Chlorophytes, and Chrysophytes (both Chrysophyceae and Bacillariophyceae) to summarize recent work relating to the production, function, and fate of specialized cells resistant to unfavorable conditions. Often these cells have thickened walls and may have morphologies that are either similar to or markedly different from their vegetative cells. The resting stages may or may not be completely dormant, but they do differ physiologically from the vegetative stage. In some groups, they can be produced by a time- and energy-consuming sequence of determinate divisions, with actual loss of nuclear material. Residual bodies from the cytoplasm often containing cell organelles are sometimes discarded with the old vegetative theca. Schmid (1979) recently reported that the diatom *Navicula cuspidata* (Kützing) Kützing forms a complete endocell nested inside another complete plus a partial theca, probably indicating four mitotic divisions in the resting spore production. In general, germination of resting spores also appears to consist of a series of determinate divisions in a given time sequence. The fact that ungerminated cells of different groups are found in sediment indicates that the individual cell pays a high cost, not only in the energy required to make the additional nuclear divisions and produce the physiological changes from the vegetative state, but also in the “lost” divisions during a resting period, and the possibility of the cell once again being in conditions favorable for germination is finite. Since the production of resting spores or akinetes or statospores is costly to the cell, if not the population, the concept of evolutionary advantage (“strategy”) is interesting to explore.

Unfavorable conditions include a plethora of physical and chemical conditions that may be seasonal: fluctuations of light, temperature, and ionic conditions; ingestion by grazers and subjection to grinding and abrasion plus digestive secretions; presence of poisons in the environment; and poor nutrient conditions, such as the period following a phyto-

plankton bloom. It follows that cells resistant to these changes because of altered metabolic rates, heavy cell walls, and reduced exchange with the surrounding medium, or some combination of these characters, will have an adaptive advantage.

As Coleman (Chapter 1) points out, these problems are shared by marine, freshwater, and terrestrial organisms, but the overriding problem for nonmarine organisms in their survival and dissemination is water loss. In the green algae, specialized thick-walled cells are much more common in freshwater and soil algae than in the sea. Sandgren (Chapter 2) adds that resting stages serve as refuge populations that are able to recolonize a habitat when environmental conditions will again support the growth of vegetative cells. He points out that there may be either sexual or asexual processes involved, with the morphology of the thickened cell wall being typical for a given class and similar to, or different from, the vegetative cell. Recent breakthroughs in our understandings came about because electron microscopy has allowed careful morphological and ultrastructural study of both cultures and field samples.

Although desiccation is a much greater threat to freshwater algae than to most marine algae, Hargraves and French (Chapter 3) indicate that more cases of resting spores in diatoms are reported from the marine habitat than from freshwater and terrestrial habitats. Furthermore, Dale (Chapter 4), working with fossilized as well as living dinoflagellates, deals almost entirely with marine forms, although freshwater resting spores are known (Chapman et al., 1982). The heavy-walled nature of most of the resting spores or statospores of many groups, even those of planktonic species, have an increased sinking rate in both freshwater and marine habitats. However, sinking in coastal waters or the open ocean puts the cells in a different current regime, and although vast numbers of spores are not produced by each cell, this may well serve to be a dissemination mechanism (Garrison, 1980, 1981). In other habitats, viable resting spores spend part of the annual cycle in or on the sediments.

A fine summary of recent work on akinetes of Cyanobacteria was presented at the symposium in Vancouver by Dr. Norma J. Lang, University of California, Davis, but she thought that recent published accounts covered the material very well. Readers are referred to Stanier and Cohen-Dazire (1977), Nichols and Carr (1977), Carr (1979), Wolk (1979), and Carr and Whitton (1982) for summaries of recent work and references.

Resting spore production is considered a primitive trait evolutionarily. It would appear from Dale (Chapter 4) and Hargraves and French (Chapter 3), as well as from our own work (Fryxell et al., 1981), that the evolutionary pressures on vegetative cell and resting spore morphology bring about changes at different rates over geological time. In the case of the dinoflagellates and diatoms thus far reported, the resting spore mor-

phology has diverged to a greater extent than that of the vegetative cells. Thus, early speciation appears to be indicated by divergence of resting spore morphology. However, it may well be true of some lines of descent and not of others that vegetative forms are more conservative.

There are many problems in dealing with resting spores. Coleman (Chapter 1) points out the likelihood of a “population” of resting spores in any one habitat being of markedly different ages. Thus, a gene pool must be considered to extend both temporally and spatially. Another problem deals with correctly associating the distinctive morphology of the resting spore with that of its vegetative cell. Such matching is no problem with field samples when a “bloom” of phytoplankton has occurred, and the resting spores may be found within the vegetative cells in at least some cases. However, on many occasions only suspected resting spores are found – for instance, by geologists studying the fossil record – and biologists have the opportunity (some might call it an obligation) to understand the ecological conditions that produced these cells and the corresponding physiological changes they underwent. This opportunity was the motivation behind this symposium volume, and the authors have excelled in exploring the biology and ecology of resting spores in nature.

Reference was made to field samples of a “bloom” of phytoplankton. A clonal culture is a controlled unialgal bloom, and, like a bloom, it has millions of cells available for study, with the advantage that all are descended from one cell. The large number is needed for understanding life histories, including resting spore formation and germination. Thus, there is no uncertainty involved in relating vegetative and resting stages of the same species. In addition, “foolproof” samples that require little searching are at a premium when working on an expensive instrument, such as an electron microscope, with a crowded schedule for both the operator and the instrument. The following papers point out what has been accomplished, often using clonal cultures as tools. The reader will see that there is more to learn in each group and will find suggestions for research directions. It is only by growing selected species in the laboratory and taking the results back to the field that we can answer questions about the survival strategies of the algae.

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