EVOLUTIONARY INTERPRETATIONS OF ALLELOCHEMICAL INTERACTIONS IN PHYTOPLANKTON ALGAE

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Organic metabolites of one organism can suppress or stimulate the growth of other organisms. These so-called allelochemical interactions are thus potentially an important cause of adaptation in many kinds of biotic associations (E. Rice 1974, 1979). Furthermore, because allelochemicals are organic molecules, they can show much structural variety, thereby proving an evolutionary basis for specialization. Allelochemicals can be responsible not only for the unitary effect of one organism on another, but also, under the right conditions, for binary interactions of a coevolutionary nature, in which an adaptively significant allelochemical released by one kind of organism creates selection pressures leading to counteradaptations in another kind of organism. Allelochemistry, therefore, may help explain complexity in biological systems.

The evolutionary mechanisms of allelochemical interaction are in principle most obvious for sedentary terrestrial organisms such as higher plants, even though the frequency of significant allelochemical effects in nature, especially in the context of competition, is still open to question (Harper 1977). For example, a tree may produce an allelochemical that suppresses the growth of other kinds of trees. The selection pressures acting against this include the cost of the allelochemical and other more subtle matters such as undesirable side effects on symbionts or propagules. The benefit of producing the allelochemical is a reduction of competition in the immediate environment of the tree. Reduced competition in turn results in a richer resource pool that will support faster growth and reproduction. The balance of costs and benefits is not static because of the possibility that defenses may evolve in the populations of suppressed organisms; such defenses could reduce or neutralize allelochemical effects. Nevertheless, allelochemical interactions arising from competition among higher plants or other sedentary terrestrial organisms are at least feasible in principle.

Allelochemical interaction is possible in aquatic environments as well as terrestrial ones. There are, however, some categorical differences between allelopathy in an aqueous medium and allelopathy on a terrestrial substrate. Most important, the continuous movement of water disperses any water-soluble allelochemical

from its point of release, thus diluting it rapidly. It is possible for aquatic organisms living on substrates to interact allelochemically with adjacent or nearby organisms; examples include corals, which ensure efficient transfer of a toxic chemical by establishing direct contact with the target organisms (Sheppard 1979). However, for the plankton environment, whose allelochemistry has been much studied and discussed, the lack of contact between competing organisms combined with the dispersion of allelochemicals through the water essentially invalidates evolutionary analogies with terrestrial systems or aquatic systems that have a fixed spatial structure. This difficulty has been passed over by students of plankton allelochemistry. As a result, plankton allelochemistry has been consistently viewed in the wrong evolutionary context; the purpose of this paper is to show how this has happened and to propose alternative viewpoints.

HISTORICAL BACKGROUND

The first recognition that allelochemicals might play a role in the succession of individual species in plankton systems should probably be credited to protozoologists working on the problem of allelopathy (negative allelochemical effects) in the early twentieth century. For example, Woodruff (1912) proposed that the competitive balance between species in protozoan cultures could be at least partly explained by allelochemicals, although he was subsequently unable to demonstrate this experimentally (Woodruff 1913).

Despite the early role of protozoologists, most analysis and discussion of allelochemistry in plankton systems has dealt specifically with phytoplankton. A historical landmark for studies of this type is the work of Akehurst (1931), who attempted to explain the complex patterns of phytoplankton species replacements in several London ponds by invoking both suppressive and stimulatory allelochemicals. Akehurst proposed that two broad physiological groups of taxa (an oil group and a starch group) have predictable, consistent influences on each other. However, Akehurst's theory was essentially indefensible insofar as it was devoid of experimental or observational validation beyond the data set from which it was developed and because it failed to take into account equally reasonable kinds of explanations that would not require a role for allelochemicals.

A second historical landmark is the classical work of Pratt (e.g., Pratt 1940; Pratt and Fong 1940), who demonstrated for algae under laboratory conditions the existence of interspecific and intraspecific allelochemical interactions and the connection of allelochemical effects with particular classes of organic molecules. In the tradition of Pratt's work, many subsequent investigations have been done with laboratory cultures (e.g., Lefèvre et al. 1952; T. Rice 1954).

The frequency with which allelochemical interactions are observed under laboratory conditions may give the impression that allelochemistry is a potent force affecting the competition of species in nature. Any such conclusion is unwarranted, however, because laboratory studies have almost always been done completely outside the evolutionary context of the organisms that were being tested. Such experiments have typically involved high concentrations of algae, use of

algal strains that have been in culture for hundreds of generations, and random pairing of taxa that do not occur together in nature. Allelochemical effects observed under these conditions support very little ecological interpretation; they show only that allelochemical interactions can occur, and not that they do occur. In the case of negative interactions (allelopathy), an organism would have no evolutionary incentive to maintain an armory of defenses against metabolites produced by other kinds of organisms with which it does not occur; the frequent observation of suppression between randomly paired taxa is thus not surprising. Although some students of allelochemistry may have lost sight of this principle, others have not (Phelps 1935; Parker and Bold 1961; Keating 1978).

Yet another landmark in the history of plankton allelopathy is a paper by Hutchinson (1944) based on observations of the seasonal phytoplankton succession in Linsley Pond, Connecticut. Hutchinson pointed out that the complex sequence of events would be very difficult to explain on the basis of a few factors such as nutrient availability and amount of light, and that much more plausible theories of control could be formulated with reference to allelochemical interactions. A similar viewpoint for the marine environment was expressed by Lucas (1955). However, it remained for studies of allelochemical interactions under natural conditions to test this theory.

Few studies have yet been done of allelochemistry in phytoplankton associations under natural conditions or in the laboratory under conditions that reasonably mimic those in nature. In some instances, evidence of allelochemistry has been sought either experimentally or statistically and has not been found (Talling 1957; Smayda 1963; Lewis 1977; Reynolds 1978; Holm and Armstrong 1981; Bailey-Watts 1982). Other studies at least suggest that allelochemical effects occur under field conditions (e.g., Proctor 1957). The most extensive study of allelopathy under natural conditions is that of Keating (1977, 1978), which showed consistent evidence of allelopathic interactions in Linsley Pond.

Keating's studies of Linsley Pond were well suited for the interpretation of natural interactions. First, although Keating did her work in the laboratory, the concentrations of metabolites were low enough to be reflective of the natural concentrations. In addition, the stocks of algae that Keating tested for allelochemical interactions were cultured directly from the environment, and therefore consisted of coexisting genetic strains. Finally, because Keating observed the natural successional sequence, the results of experiments could be related to events in the lake.

Keating's initial study on Linsley Pond demonstrated positive, negative, and null effects for species pairs. These effects occurred according to a definite pattern: metabolites produced by a given species were in all instances either repressive or neutral to species occurring earlier in the sequence, but were either stimulatory or neutral to species occurring later in the sequence. In subsequent studies, Keating (1978) also showed that metabolites produced by blue-green algae were consistently inhibitory to diatoms. Keating interpreted her data as indicating that allelochemicals play a major role in controlling the seasonal succession of taxa, at least in Linsley Pond.

THE PROBLEM OF DISTRIBUTED BENEFITS

Negative allelochemical interactions among phytoplankton have received much attention because they are widely supposed to indicate the existence of interference competition. According to this line of reasoning, an algal cell that releases an antibiotic metabolite benefits from this release in the same way that a tree might benefit from such a release, that is, by suppressing the growth of competitors. Four important points must be taken into account, however: (1) an organic substance released by an algal cell is left behind as the cell moves by sinking or flagellar propulsion rather than remaining near the cell; (2) an algal cell competes diffusely with millions of other cells, all of which lack stable spatial associations with it or with each other; (3) individual cells or colonies are separated from each other by large relative distances (dozens to hundreds of cell diameters), even in dense populations; and (4) viscous forces are so large within the size range of phytoplankton that transmission of dissolved substances between two cells separated by many cell diameters is very inefficient. Because of these peculiarities of the plankton environment, any benefits that might come to the releasing algal cell as a result of an antibiotic effect will also accrue to all other cells that are not negatively affected, including all cells of similar genotype, probably all cells of the same species, and possibly cells of many other species. In other words, the benefits of the metabolite are not captured either uniquely or even with significantly higher probability by the cell that produces the metabolite; rather, the benefits are distributed among many cells. This inevitably creates an advantage for any cell that is of similar genetic constitution to the releasing organism but does not synthesize the allelochemical. Such a "cheater" saves the metabolic cost of the allelochemical while benefiting from its production by other cells. Thus, for phytoplankton cells, the production of allelochemicals as agents of interference competition is not an evolutionarily stable strategy.

Although the release of antibiotic allelochemicals caused by natural selection operating through the benefits of interference competition cannot be explained from the viewpoint of individual cells or clones of a given genotype, one could possibly resort to group selection as a means of explaining this phenomenon. It could be argued that only populations with this type of interference-competition mechanism have survived; other populations have consistently become extinct. In general, however, group selection is considered a weak vehicle for the explanation of adaptation (Williams 1966; Maynard Smith 1976). Group selection seems most feasible when organisms are tightly integrated in fixed spatial arrangements (Wilson 1980). Plankton communities do often have spatial structure (Steele 1978), but the structure is ephemeral. Since phytoplankton lack fixed spatial associations, group selection is not likely to resolve the problem of distributed benefits.

THE PROBLEM OF ADAPTIVE INCOMPETENCE

If antibiotic allelochemicals cannot be explained as adaptations associated with interference competition, then we must view them as fortuitous by-products of

metabolism, that is, excreta. If antibiotic metabolites are in fact merely excreta and thus without selective value to the organisms that release them, a logical question is whether or not antibiotic substances can still be expected to play a role in controlling successional sequences. If so, then it is necessary to assume that the receptor taxa in general show a high degree of adaptive incompetence where antibiotic substances are concerned. If two kinds of organism occur routinely in sequence, and the first of these two releases some kind of antibiotic, the second taxon will experience steady selection pressure for metabolic mechanisms that would counter the antibiotic effect. There is little doubt that this type of selection pressure can result in immunity to a given antibiotic substance; striking examples can be taken from the literature on DDT and medicinal antibiotics. In fact, it has been shown that mutants resistant to antibiosis arise readily in laboratory algal populations (Sager 1974; Fogg 1975; Gowans 1976). Thus, a persistent antibiotic effect originating from a releasing organism that does not continually alter the antibiotic as part of an interference-competition strategy implies an improbable degree of adaptive incompetence in the populations of receptor organisms.

As long as a releasing organism is producing an allelochemical as part of an interference-competition strategy maintained by natural selection, any counteradaptation on the part of the target organism simply leads to further selection favoring changes in the antibiotic so that it retains its effectiveness. For this reason, it would be quite reasonable (although by no means inevitable) to find antibiosis in some communities, such as forests, despite the existence of selection pressures for defenses against it. Such reasoning does not apply, however, if the releasing organism is merely disposing of a metabolic by-product and not producing a toxin whose adaptive purpose is interference competition. In this case, a defense against the toxin on the part of the receptor organism will not lead to selective pressures favoring changes in the nature of the toxin. Thus, toxic effects can be effectively countered, and the incidence of toxicity will be low. The only alternative is to postulate adaptive incompetence on the part of the receptor organisms. For phytoplankton populations, such a postulate would imply that the metabolic permutations possible in a large population of phytoplankton cells will never lead to the development of a defense against a particular antibiotic; this seems unreasonable.

ALTERNATIVE INTERPRETATIONS OF ALLELOCHEMICAL INTERACTIONS

Given the problem of distributed benefits and the problem of adaptive incompetence, it seems impossible to salvage traditional interpretations of phytoplankton allelochemistry without being in conflict with some basic principles of natural selection. Other interpretations more consistent with natural selection are possible, however. The first possibility is that the importance of allelochemistry, and particularly allelopathy, under natural conditions has been greatly overestimated. This could be explained by the preponderance of unrealistic laboratory studies among the demonstrations of allelopathy. Furthermore, as mentioned above, a number of studies have sought evidence of allelopathy under natural conditions and failed to find it. The difficulty with this viewpoint, however, is that some

studies, notably those of Keating, seem to present definite evidence of allelopathy under field conditions.

Very irregular occurrences of allelopathy would be consistent with the principles of natural selection and would not present the problems of distributed benefits or adaptive incompetence. Unusual bloom conditions, caused by the appearance of a particular taxon in atypically great abundance, could result in allelopathic suppression of co-occurring taxa, as in the case of certain highly toxic blooms of blue-green algae and dinoflagellates (Collins 1978), simply because the receptor taxa would not have been challenged frequently enough with the metabolites in question to show selection for a specific resistance. This would be an instance of passive toxicity; the antibiotics could be produced simply as a by-product of required physiological processes and not as part of an interference-competition strategy. Under these conditions the problem of distributed benefits is not an issue; yet the symptoms of allelopathy in the community would be no less real than if the allelopathic substances had developed as an interference-competition strategy. Despite the possibility that unusual circumstances could lead to allelopathic interactions of this type, however, unusual circumstances cannot provide a satisfactory explanation of regular seasonal sequences such as those observed in Linsley Pond by Keating. Although the failure of receptor organisms to be adapted to extraordinary doses of antibiotics may explain some effects that accompany unusual blooms, an explanation is still needed for the more important routine species interactions involving allelochemicals.

One possible explanation of allelochemical interactions is consistent with the routine occurrence of such interactions in phytoplankton seasonal succession, and it is also consistent with the basic principles of natural selection. This explanation, which can be called the allelochemical-signal hypothesis, is essentially the mirror image of the traditional explanation of allelochemistry. According to the allelochemical-signal hypothesis, allelochemicals have no selective value whatever to the releasing organisms except insofar as they represent a mechanism of excretion. The significance of these chemical compounds lies entirely with the receptor organisms. Receptor organisms may be adversely affected by allelochemicals to which they have had no opportunity to adapt. This could well explain the frequency of negative effects in randomly paired laboratory stocks, but it is not relevant to co-occurring populations. Because the receptor organisms have the capacity to evolve defenses against antibiotic allelochemicals, they are not routinely repressed by co-occurring populations in a fashion detrimental to their growth and reproduction. The receptor organisms are often sensitive to allelochemicals released by co-occurring populations, as shown by studies such as that of Keating, but the sensitivity represents the use of the allelochemicals by the receptor organism as an environmental cue. The feasibility of chemical cues being transmitted through water is shown by sexual chemotaxis in some algae (e.g., Muller 1974). The value of the cue to the receptor organism is that it signals very reliably the occurrence of specific conditions matching the beginning or ending of appropriate growth periods for the receptor organism. In effect, the receptor organism uses the specific metabolic products of other organisms as an indication of position in the niche space.

It is widely acknowledged that organisms have evolved responses to various environmental cues that trigger critical events in their life cycles. Most of the examples of such phenomena, however, are centered around simple inorganic chemical or physical cues such as temperature, light, or nutrient concentrations. In certain contexts, possibly including the one relevant to phytoplankton, an allelochemical signal might offer advantages over an abiotic signal. In general, an organism derives the greatest benefit from a signal that predicts the phenomenon of interest with the greatest possible reliability. Thus, it is logical for day length to serve as a cue for certain flowering plants (short-day plants) that require a mechanism to anticipate the end of the growing season. A simple abiotic signal of this type might be less satisfactory for phytoplankton species, however. Net growth in phytoplankton is regulated by a complex of abiotic and biotic factors that are not tightly coupled and that are not clearly predictable in many instances on the basis of fundamental climatic variables such as day length or air temperature. Furthermore, timing for phytoplankton must be much more precise on an absolute time scale than for larger organisms, such as vascular plants, because phytoplankton populations often rise and decline over a period of only a few weeks. If taxa are specialized, as they seem to be, to take advantage of relatively narrow ranges of nutrients, light availability, and temperature, a cuing system based on any single abiotic factor would probably be very imprecise with respect to the other factors. In fact, the narrower the niche with respect to abiotic factors, the more difficult it is to anticipate such factors by sensitivity to particular abiotic conditions. The allelochemical signal, which is based on the presence of certain critical quantities of other kinds of organisms, may thus be the most reliable indicator of the position of the environment with respect to a particular organism's niche space.

The allelochemical-signal hypothesis requires that individual phytoplankton cells have distinct physiological strategies associated with growth and maintenance. For much of the year, any given phytoplankton cell is in a maintenance mode; that is, the environmental conditions do not support a net increase in biomass. The physiological strategies typical of cells under these conditions are likely to be very different from the strategies of the growth phase, when environmental conditions will support a rapid increase in biomass. It is not clear on the basis of present evidence whether or not there is typically a recognizable switch from one strategy to another, as there would have to be in order for the allelochemical-signal hypothesis to be valid. However, among taxa that pass the maintenance phase in a discrete physical location where they can be obtained for study (such as sediment), major physiological and morphological differences have been demonstrated between the maintenance phase and the growth phase of populations (e.g., Lund 1954, 1955; Reynolds et al. 1981). In these taxa, and quite possibly in phytoplankton generally, the cell holds a reserve from the preceding growth period. The reserve allows the cell to make future commitments to growth. The allelochemical-signal hypothesis requires that this commitment be selectively important; if the cell makes the commitment at the wrong time, it will be disadvantageous, and possibly fatal, because no additional reserves are available.

The concept of the individual phytoplankton cell favored by the allelochemical-

signal hypothesis is somewhat different from the prevailing rheostat concept, according to which phytoplankton show a long continuum of growth rates governed by a corresponding continuum of nutrients and light. The rheostat concept may well be accurate for growing cells, which are most often studied, but inaccurate for cells that cannot photosynthesize rapidly enough to grow. The allelochemical-signal hypothesis credits phytoplankton cells with physiological recognition mechanisms, implying that cells contain a certain amount of physiological programming based on environmental cues. Although detailed verification of this idea is necessary, the concept is consistent with what is known of short-term rhythms in phytoplankton cells (Chisholm 1981) and with changes of physiological state that accompany sexuality or encystment.

The allelochemical-signal hypothesis would be consistent with varied strategies involving allelochemistry. Abiotic cues might be most useful to some organisms. For example, certain diatoms characteristic of early succession, such as *Melosira* in freshwater lakes, would be most likely to rely on abiotic cues because of the coincidence of their growth with major abiotic changes. In the case of *Melosira*, resting cells come up from the sediment at the spring mixing and grow in the water column as long as the entire water volume is turbulent (Lund 1954, 1955). In contrast, taxa that thrive later in the successional sequence are not coordinated with discrete abiotic events and would thus be more likely to evolve responses to an allelochemical signal. The seasonal sequence of phytoplankton taxa might begin under the influence of certain abiotic cues; this would then be followed by a succession of species cued to each other. Of course, there is no reason why a particular species of phytoplankton would have to be cued only to one other taxon; a phytoplankton species could be programmed by natural selection to respond to the presence of a number of other species, any one of which would indicate an approaching transition in the conditions for growth. In addition, it is entirely possible that specific phytoplankton taxa respond to different allelochemicals in different lakes. The allelochemical-signal hypothesis is thus consistent with considerable complexity in community dynamics.

The allelochemical-signal hypothesis helps explain an interesting peculiarity in Keating's study on Linsley Pond. Her study showed that allelochemicals secreted by individual taxa always affected succeeding taxa in a positive (stimulatory) way, if any effects were observable. According to traditional interpretations of allelochemistry, releases of metabolites are of selective advantage to the releaser as agents of interference competition, or they may be neutral to the releaser and have inadvertent effects on the receptor organisms. If allelochemicals are selectively advantageous to the releaser, there is no reason whatever for the occurrence of stimulatory responses under natural conditions. Furthermore, even if the releases are selectively neutral with regard to the releaser, no response is expected in the receptor; a stimulatory response is hard to explain in evolutionary terms. This difficulty is resolved by the allelochemical-signal hypothesis: the allelochemical is significant only to the receptor organism, which responds to signals from preceding species by a physiological commitment to growth and to signals from a succeeding species in the opposite way. Thus, the allelochemical-signal hypothesis not only conforms with the general principles of natural selection, but also fits the empirical data better than present hypotheses.

CONCLUSIONS

Traditional interpretations of phytoplankton allelochemistry, which are based essentially on an analogy between allelochemical effects in phytoplankton and in sedentary organisms, are attractive because they help explain the complexity of phytoplankton dynamics and are consistent with most of the empirical information on phytoplankton allelochemistry. Traditional interpretations of phytoplankton allelochemistry are, however, at variance with some basic principles of natural selection and are therefore untenable. The null hypothesis, which would hold that there are no routine allelochemical effects in nature among phytoplankton, seems inconsistent with some observations of allelochemical interactions under essentially natural conditions. An alternative hypothesis based on the significance of allelochemicals as signals is consistent with the principles of natural selection, preserves the possibility that allelochemicals may play a major role in plankton communities (although as signals rather than as controllers), and is as consistent with experimental evidence, or slightly more consistent with it, than traditional interpretations. Although the allelochemical-signal hypothesis departs from the traditional view of allelochemistry in phytoplankton, it seems the most parsimonious, and therefore the most defensible, explanation of the phenomenon.

SUMMARY

Although allelochemistry among phytoplankton species has been studied relatively little under natural conditions, it is widely thought to influence the increase and decrease of individual species in the course of a growing season in plankton systems. Some direct evidence supports this view. Allelochemistry involving growth suppression has often been viewed as beneficial to the releaser of allelochemicals, and thus as being maintained by selection pressures deriving from competition. This interpretation is indefensible, however, insofar as individual phytoplankton cells are unable, because of the movement of both the cells and the allelochemicals, to capture selectively the benefit of suppressing other individuals by means of allelochemicals; any such benefits would be shared by many other organisms. Other explanations must therefore be sought. Allelopathy can be considered passive from the viewpoint of the releaser but still capable of having detrimental effects on receptor organisms. This explanation also seems untenable in that it requires receptor organisms to be unable, even over many thousands of generations of exposure, to develop defenses against specific, passively released organic substances. An alternative explanation that avoids these difficulties, while allowing for the possibility that allelochemicals are important in natural systems, is based on the idea that the significance of allelochemicals lies strictly in the receptor and not the releaser. According to this explanation, allelochemicals are significant to the receptor organisms as cues that trigger physiological responses to an improving or deteriorating environment. This interpretation, unlike the traditional one, is consistent with observational and experimental evidence of allelochemical interactions and with the basic principles of natural selection.

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