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DO INTERACTIONS OF CELLULAR SLIME MOLD SPECIES REGULATE THEIR DENSITIES IN SOIL?[1]

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Abstract. Studies of the ecology of macroorganisms have produced a body of theory about the nature of biological interactions and their effects on species in the field. This body of theory describes the ways that species affect each other and also predicts the outcome of specific interactions such as competition or predation. It is reasonable to ask whether the same body of theory applies to species of microorganisms.

We performed a simple field experiment to test the hypothesis that biological interactions influence species of cellular slime molds living in forest soils. Members of the guild of cellular slime mold species co-occur on both microhabitat and geographic scales and, in laboratory cultures, the species all consume the same food resources. We experimentally elevated the density of one cellular slime mold species and detected significant population responses in the remaining species in the cellular slime mold guild. Our results clearly show that biological interactions are important to cellular slime molds: (1) we observed resource limitation in the species that we added, and (2) we observed that the densities of cellular slime mold species are interrelated.

Key words: cellular slime mold; competition; Dictyostelium; *forest soil; interspecific interaction; microbial ecology;* Polysphondylium; *predation.*

INTRODUCTION

While community ecologists generally acknowledge that microorganisms are important in the living world, the attention of ecological studies to date has focused almost exclusively upon macroorganisms. This emphasis is understandable: natural populations of microorganisms pose problems of enumeration and identification different from those encountered in the study of directly observable plants and animals. Nonetheless, there are good reasons to incorporate microbes into the repertoire of actively investigated organisms. Their rapid growth rates and elementary life cycles, relative to macroorganisms, offer an opportunity to investigate community responses to experimental perturbation within a shorter time frame than is possible with many macroorganisms. A more fundamental reason to include microorganisms in our investigations of communities is that they almost certainly are involved in interspecific interactions that are important influences on total community structure (Barker 1977, Lopez et al. 1977).

Historically, ecologically minded microbiologists have emphasized the fundamental niches of microbes (Griffin 1972, Smith and Brock 1973, Flanagan and Bunnell 1976, Ghilarov 1977, Brock 1985). For those organisms that can be isolated in pure culture, it is relatively easy to explore the effects of abiotic environmental variables on population growth. While it is reasonable to study the limits of a microbe's fundamental niche in the laboratory, it may be that biotic interactions confine microbial populations to smaller realized niches in the field. Competition and predation may be as important in influencing populations of very small organisms as they are thought to be for larger organisms (Hairston et al. 1960, Salt 1970, Fenchel and Christiansen 1977).

Unfortunately, competition and predation are not amenable to study under the controlled conditions of the laboratory, at least not in a way that can provide meaningful answers to questions of population regulation that (macro)ecologists like to ask. For instance, two types of bacteria, each in pure culture, might be able to grow on the same resource. Growing them together on that sole resource would lead to the elimination of one of them from the culture (Gause 1934, Harder et al. 1977), but would not reveal anything definite about the role of competition between the two in their native habitat, where competitive exclusion may not take place (Fredrickson and Stephanopoulos 1981). To investigate the dynamics of microbial populations requires that experimental work be done in the field, even though that means foregoing some of the sophisticated methods of modern microbiology in favor of the techniques of simple enumeration used for so long in the study of macroorganismic communities.

We began by asking the simple question: do biological interactions influence the cellular slime mold community? The cellular slime molds are a group of species

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that co-occur and utilize the same food resource. We elevated the density of one species in the field. We predicted that experimental elevation of the density of one species would affect the densities of the unmanipulated species if interactions are important in our experimental system. The results of our experiment clearly show that biological interactions do affect the cellular slime mold guild.

Materials and Methods

The system

The guild of cellular slime molds (CSM) is made up of soil-inhabiting bacterial predators (Raper 1984). A few grams of almost any forest soil will yield several to many species of CSM. On a broad scale, species diversity is negatively correlated with latitude (Cavender 1973). Local areas within latitudinal zones seem to have characteristic relative abundances of species (Cavender and Raper 1965, Benson and Mahoney 1977, Traub et al. 1981, Raper 1984). In our area the four most commonly encountered species are: *Dictyostelium mucoroides, Dictyostelium purpureum, Polysphondylium pallidum,* and *Polysphondylium violaceum.* These co-occur on a fine scale, measured in metres (Kuserk 1980), or centimetres (Eisenberg 1976). Two additional species, *Dictyostelium discoideum* and *Dictyostelium minutum,* also occur here, but infrequently. Based on previous sampling experience, either *Dictyostelium mucoroides* or *Polysphondylium pallidum* is the usual numerical dominant in this area (Eisenberg 1976, Olsen 1978, Kuserk 1980).

During active growth the CSM are typical microbes: the single cell (ameba) consumes available resources (soil bacteria) and reproduces by binary fission when it has accumulated sufficient material to become two cells. The unique feature of the CSM is the aggregation of amebae to produce a fruiting body bearing spores (Bonner 1967, Raper 1984). Spore formation is a response to food limitation. The conversion from feeding amebae to dormant spores is completed in a matter of hours. When activated, a spore gives rise to a single ameba once again. Thus the life history of the CSM is a balance between amebae and spores and between solitary and collective activity.

Like the spores of most microbes, those produced by the CSM are resistant to abiotic stresses that are lethal for the vegetative stage (Kuserk et al. 1977). In our laboratory, spores have survived up to 3 yr on agar slants. The length of viability of CSM spores in the environment of moist leaf litter is not known, but it is probably measured in months or years, unless a predator intervenes. Short-term changes in spore densities are useful indicators of conditions in the environment. An increase means resources have become limiting; a decrease means either that resources have become available or that a predator has removed the spores from the population.

In laboratory cultures the CSM are capable of growth on the same species of bacteria (Anscombe and Singh 1948, Horn 1971, Kuserk 1980). This has suggested to some workers that competition is an important factor in CSM ecology (Horn 1971, Kuserk 1980). In the field, the CSM respond rapidly to bacterial food supply. For instance, *Dictyostelium mucoroides* quadrupled its numbers within 1 d after a pulse of *Escherichia coli* was added (Kuserk 1980). Such direct evidence of resource limitation strengthens the idea that competition is important.

Study site

Our study was done in a mixed hardwood forest on the University of Delaware Morris Farm Reserve, New Castle County, Delaware, USA. This woodland, located in the Appalachian Piedmont at its juncture with the Atlantic Coastal Plain of the Delmarva Peninsula, is a remnant of the Eastern deciduous forest. It appears to have been unlogged for more than a century. We established an experimental area of 0.28 ha within the Morris Farm Reserve, choosing a location with reasonably uniform drainage and plant cover.

Thirty experimental sites were selected as follows: a reference point was defined and 30 compass points between 1° and 360° were selected at random. Each of these compass points was then randomly assigned a distance between 3 and 30 m. At each site thus defined, two 0.25-m^2 plots (50 × 50 cm) were established so that the two plots were separated by 1.0–1.5 m, and neither plot contained woody vegetation that would interfere with sampling. After the two plots were marked, a coin toss identified which plot would serve as treatment and which as control.

Field addition

P. pallidum was selected for our addition because it was a co-dominant in our study area. We chose to add amebae rather than spores because amebae are the active, feeding stage of the life history. The *P. pallidum* amebae used in the addition were grown from a clone recently isolated from the Morris Farm site. The experimental clone was inoculated into 30 250-mL DeLong flasks, each containing 100 mL of phosphate buffer (Sorensen's [Gerisch 1960]: M/60, pH 6.0) and $\approx 5 \times 10^{11}$ cells of *E. coli* strain B/r as food. The slime mold was grown at room temperature with constant shaking (100 revolutions/min on a rotary shaker) until the bacterial turbidity disappeared. It was determined by direct microscopic count that each flask contained $\approx 1.4 \times 10^8$ *P. pallidum* amebae/100 mL at the time of use. No spores were observed during the microscopic examination.

In the field, the loose leaf litter was brushed aside from both treatment and control plots before the additions were made. The treatment plot received the *P. pallidum* amebae suspended in 1 L of phosphate buffer; the control plot received 1 L of the same buffer. Liquid

TABLE 1. Mean density, relative abundance, and percent dormancy of cellular slime mold (CSM) populations in control (C) and treatment (T) plots. Totals refer to all species combined.

		Dictyostelium mucoroides		*Polysphondylium pallidum*		*D. purpureum* + *P. violaceum*		Totals	
		C	T	C	T	C	T	C	T
Total density (no. propagules/g dry soil)	May*	172.6	45.7	71.0	1517.4	29.3	21.4	272.9	1584.5
	July†	111.8	34.3	89.6	165.5	117.2	36.1	318.6	235.9
Relative abundance [100 × (species total density/CSM total density)]	May	63.2	2.9	26.0	95.8	10.7	1.4	...	...
	July	35.1	14.5	28.1	70.1	36.8	15.3	...	...
Spore density (no. resistant propagules/g dry soil)	May	69.0	30.6	28.9	849.5	13.4	16.6	111.3	896.7
	July	76.9	21.0	57.3	85.6	72.7	7.1	206.9	113.7
% dormant [100 × (spore density/total density)]	May	40.0	67.0	40.7	56.0	45.7	77.6	40.8	56.6
	July	68.8	61.2	64.0	51.7	62.0	19.7	64.9	48.2

* May values refer to means of 30 paired plots (control + treatment) for samples collected 3 d after the 3 May addition of *P. pallidum* amebae to treatment plots.

† July values refer to means of 5 of the original 30 paired plots chosen at random for resampling 10 wk after the treatment application.

was dispersed on the plots through the sprinkler head of a standard watering can attached to a 2-L suction flask by 30 cm of flexible Tygon tubing. Separate apparatuses were used for treatment and control plots. The leaf litter was replaced on the plots after the additions. All additions were made within 2 h on the morning of 3 May 1985.

Sampling

Three days after the addition all treatment and control plots were sampled. The sampling protocol consisted of taking cores at 20 randomly selected coordinates within each plot. Cores were 2 cm in diameter and 0.5 cm in depth. The 20 cores from each plot were combined in a single, tared, 0.47-L glass container (pint Mason jar).

In the laboratory, each sample was weighed and suspended in phosphate buffer; the volume of buffer added was 8 mL/g wet mass of sample. Each sample jar was subjected to a standardized agitation procedure (Kuserk et al. 1977) that consisted of six inversions, 30-s rest, 3 inversions, and 30-s settling time. An aliquot of 0.5 mL was spread on the surface of a water agar plate (15 g/L) along with 0.5 mL of a thick *E. coli* suspension. Four plates were prepared from each sample. These plates were used to estimate total density (amebae + spores) of each CSM species. After the aliquots for total density determination were removed, the jars were frozen to kill the amebae (Kuserk et al. 1977), and then resampled to determine spore densities. Finally, the jars were dried to constant mass in a 100°C oven and the dry mass of each sample was determined.

Plates were incubated at room temperature and were checked regularly for aggregation. Each aggregation was marked on the underside of the Petri dish using a waterproof marking pen. On the 6th d after inoculation all fruiting structures were identified to species. A substantial fraction of the plates were inspected again after a further 4-d incubation, but no new aggregation or fruiting structures were observed. CSM densities were expressed as numbers per gram dry mass of soil. The unfrozen samples gave estimates of total numbers (i.e., amebae plus spores) for each species. The frozen samples yielded spore densities alone for each species.

The experimental plots were left undisturbed from 6 May 1985 through 12 July 1985, when a set of five randomly selected plots were sampled again, using the same procedures as in the first sampling.

Analysis

The density estimates for *Dictyostelium purpureum* and *Polysphondylium violaceum* were combined, because both of these species occurred at low frequencies in our experimental plots in the first sample. All density estimates were log transformed to assure independence of means and variances. The proportions we calculated, relative abundance and percent dormancy, were transformed using an arcsine transformation (Sokal and Rohlf 1981). Relative abundance was calculated as total density of each species divided by total density of all species combined. Percent dormancy was calculated as spore density (frozen sample) divided by total density (unfrozen sample) for each species or group of species.

Control and treatment comparisons were made using a one-way ANOVA with blocking by plot. Comparisons over time (May vs. July) were made using one-way ANOVA.

RESULTS

May sample

Our addition of *P. pallidum* was effective. Mean *P. pallidum* density in treatment plots was 20 times the *P. pallidum* density in control plots (Table 1). Relative abundance of *P. pallidum* was significantly greater, relative abundances of the other two groups were significantly lower, and total density for all CSM was sig-

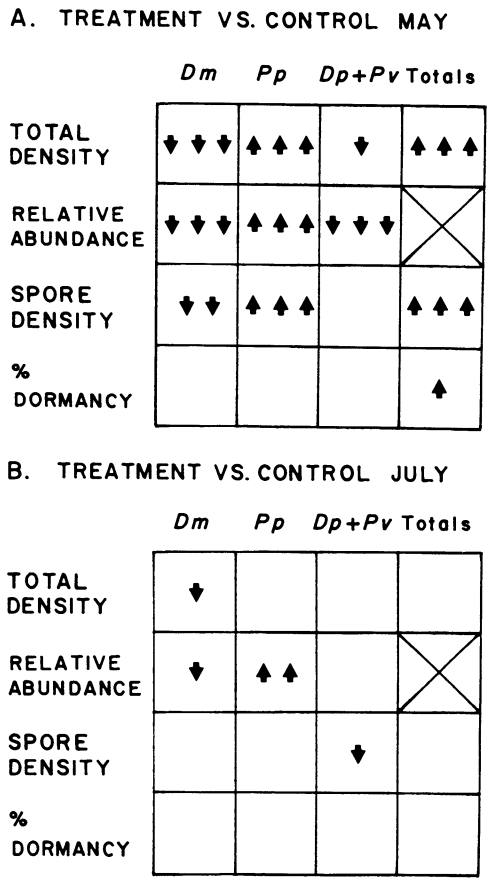

FIG. 1. Significant differences in density, relative abundance, and percent dormancy of cellular slime mold species between control and treatment plots 3 d after treatment (A) and 10 wk after treatment (B). Level of significance is indicated by number of arrows: 1 = $P < .05$; 2 = $P < .01$; 3 = $P < .001$. Direction of difference is indicated by direction of arrows: up means treatment > control. *Dm* = *Dictyostelium mucoroides*, *Pp* = *Polysphondylium pallidum*, *Dp* + *Pv* = *D. purpureum* + *P. violaceum*. Totals refer to all species combined.

nificantly greater in the treatment plots (Fig. 1A). These differences between treatment and control involve no population responses by members of the CSM guild, but result from the increase in *P. pallidum* numbers.

There were six significant population responses to the addition (Fig. 1A). These included three decreases in density: *D. mucoroides* total density, *D. mucoroides* spores, and *D. purpureum* + *P. violaceum* total density. There were also three increases: *P. pallidum* spore density, total spore density (a consequence of the change in *P. pallidum* spore density), and an increase in percent dormancy for all species combined.

July sample

After 10 wk there was no detectable difference between total CSM densities in treatment and control plots (Fig. 1B). Neither was there a significant difference between the total *P. pallidum* densities. Despite the disappearance of *P. pallidum* in treatment plots, there were continued effects of our addition: total *D. mucoroides* density was significantly less in treatment plots, as was *D. purpureum* + *P. violaceum* spore density. There were also two differences involving relative abundance: *P. pallidum* was elevated and *D. mucoroides* was decreased in treatment plots (Fig. 1B).

DISCUSSION

We asked the question: Are there interactions among the members of the CSM guild? The May data (Fig. 1A) clearly show that there are. The impact of our addition upon *Dictyostelium mucoroides* was especially strong. This is interesting because *Polysphondylium pallidum* and *D. mucoroides* are the usual co-dominants in this area. Our addition did provoke a significant response in *D. purpureum* + *P. violaceum* also, but this was not as pronounced as the response of *D. mucoroides*.

Since *P. pallidum* and *D. mucoroides* are the usual co-dominants of the CSM guild in this area, it is reasonable to look for competitive interactions between them. If there was competition based on shared resources, the response in *D. mucoroides* to the removal of resources by our added amebae would have been a life history shift, measurable as an increased spore density. This was not the pattern we observed, however; what we found was a simultaneous reduction in both amebae and spores. Total density of *D. mucoroides* dropped to 26.5% and spore density fell to 44% of control (Table 1). A simultaneous reduction in both life history stages of *D. mucoroides* is inconsistent with a competitive interaction with *P. pallidum*, but it is the expected change if both stages are attacked by a common agent. Therefore, we attribute these changes in *D. mucoroides* to predation.

The observed decrease in total density of *D. purpureum* + *P. violaceum* (Fig. 1A) is best attributed to the same predator stimulation that produced changes in *D. mucoroides*. The evidence in this instance is less convincing, but a common mechanism is the simplest explanation.

Logically, there are two ways other than predation for the observed changes in *D. mucoroides* to take place, but these can be dismissed on the basis of the known biology of the CSM. One possibility is that both densities decreased as a result of spore germination and ameba death due to starvation. This is unreasonable because (1) no stimulus to germination was applied, and (2) the elapsed time was only 3 d, an interval that CSM amebae can survive without food (aggregateless mutants of *P. pallidum* survive without food for >6 wk; D. Francis, personal communication). The other possibility is that the *P. pallidum* clone we added was predatory on *D. mucoroides*. There is one known CSM that is predatory on other CSM. It is *Dictyostelium*

caveatum, known only from Blanchard Springs Cavern, Arkansas, USA (Waddell 1982). It has an easily recognizable effect on the aggregations and pseudoplasmodia of other CSM species. We saw no such effects on any CSM species on our enumeration plates.

Apparently, our addition of *P. pallidum* was a stimulant to a higher trophic level. This is an interesting outcome because it is evidence that the predator is a generalist, taking more than one species of CSM. To date, the identity of the predator (or, very likely, predators) on CSM has remained a mystery. Kuserk (1980) provided circumstantial evidence that there was a rapid predatory response to an increase in a single species of CSM; our results suggest that the predatory response can have repercussions on CSM species other than the one that is increased.

We do not conclude that interspecific competition was absent, either in the case of *D. mucoroides,* or for *D. purpureum* + *P. violaceum.* It may have been present but overwhelmed by the effect of the predator(s). The increased density of *P. pallidum* spores (Fig. 1A) demonstrates that resources were limited in the treatment plots. We added *P. pallidum* as amebae and found that 50% of the survivors were spores on day 3 (Table 1). Since aggregation, fruiting, and spore formation are the response to the absence of food, it is clear that there were not enough bacteria available in the soil to maintain the *P. pallidum* amebae in an active state. There is some indication that the resource limitation extended to the other CSM species: the bottom line of Table 1 (% dormant, May sample) shows that in each case the dormancy was greater in treatment than in control plots. This was marginally significant for *D. mucoroides* ($P = .05$) and it was significant for all the CSM together (Fig. 1A). This pattern is consistent with competitive effects, but it constitutes weak evidence for competition, since predation alone could produce the same pattern through heavier mortality among amebae than among spores. The observed sporulation in the added *P. pallidum* amebae remains the only hard evidence for the importance of resources in producing the effects we observed. If interspecific competition among the CSM is to be given a good field test, it will be necessary to design an experiment so that predation effects are removed.

By the time of the July sample (Fig. 1B), total CSM density had returned to the pretreatment level. This suggests a carrying capacity for the CSM guild. Despite this similarity, there were continued effects of our treatment. These are seen in the significant differences in relative abundance of *P. pallidum* and *D. mucoroides.* Evidently, population events can change the structure of the guild to create patterns that are detectable long after the event itself is over.

Fig. 2A shows a shift in the relative abundance pattern in control plots between May and July. This shift was composed of the growth of *D. purpureum* + *P. violaceum* populations, and of relative inactivity of *D. mucoroides,* as indicated by the increased dormancy of the latter species. Fig. 2B, in conjunction with Table 1, tells a different story about temporal events in the treatment. There are highly significant differences in relative abundances in treatment plots, but they are due to different causes. These differences result from the disappearance of *P. pallidum* rather than from changes in the other species. *D. purpureum* + *P. violaceum* density did not increase significantly, and the life history shift in *D. mucoroides* had already occurred in the 3 d between the time of the addition and the May sample (Table 1). It appears, therefore, that our addition imposed a shift in the guild structure in the treatment plots, and this shift prevented the occurrence of the natural shift seen in the control plots.

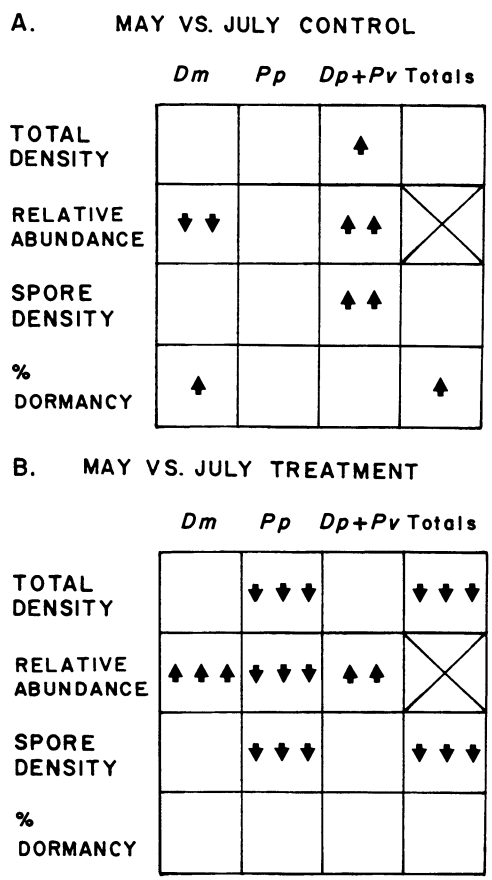

FIG. 2. Significant differences between May and July samples. Up arrow means July > May. Abbreviations and probabilities as in Fig. 1.

In undisturbed forest soils the CSM occur in patches of high density. These are found on a spatial scale of a few cubic centimetres or less (Eisenberg 1976). Our experience, and that of others (Raper 1984), is that any of the CSM species can be found in such local "hot spots," and may exhibit densities in the range of hundreds to thousands of individuals per gram. The reasons for such patchiness must include both oppor-

tunistic growth at bacterial patches and the aggregation response of the CSM. Our experiment can be viewed as the creation of a single-species, high-density patch on a scale large enough to permit repeated sampling. Our results allow us to make some inferences about the dynamics of CSM populations in these patches and, more generally, about the microbial interactions occurring within the soil habitat. We offer the following:

1) There can be two points of control on change in microbial population size, birth rate, and death rate. Each of these can be regulated independently, and each can be regulated in a density-dependent fashion. Birth rate is a function of food availability and so can be influenced by competition from other populations. Death is likely to be due to predation rather than starvation, at least for organisms that can form resting stages. Therefore, both competitive interaction and predation are probably important.

2) By virtue of their growth in colonies, augmented in the CSM by aggregative behavior, microbial distributions are very patchy. A patch is a consequence of a local pulse of food. Patches are ephemeral both in time and in space. These patches are far smaller than any reasonable definition of population size for these organisms that are distributed over vast areas. At a single patch, food may become a limit on growth, or a predator may decimate the patch; the same either/or description is not fairly applied to the population as a whole. To speak of regulation at the population level, we should talk of the frequency with which each biotic limitation occurs at the patch substructure of the population.

3) There are lingering effects of the essentially stochastic events of population growth in patches. These effects are observed in the relative abundances of species and they occur when a carrying capacity is applied to a guild as a whole rather than to single species. Generalist predators can create this effect.

In conclusion, our experimental evidence shows that there is a significant interaction among the members of the cellular slime mold guild. The principal interaction that we observed was between the two co-dominant species, and it was due to stimulation of one or more predators. A common view in the macroecological literature is that competition and predation are mutually exclusive regulators of populations (e.g., Hairston et al. 1960, Paine 1966, Menge and Sutherland 1976). The biology of CSM argues against such a dichotomy. To us, it seems likely that the two factors are interactive in the CSM guild, but more experimental work needs to be done.

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