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The maximum power principle: An empirical investigation

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Abstract

The maximum power principle is a potential guide to understanding the patterns and processes of ecosystem development and sustainability. The principle predicts the selective persistence of ecosystem designs that capture a previously untapped energy source. This hypothesis was investigated empirically in controlled and replicated tests conducted in planktonic microcosms. Microecosystems that developed under a pH-controlled light regime, in which light duration was altered based on changes in an ecosystem-controllable variable (water column pH), were compared with those that developed under fixed photoperiods. According to the principle, pH-decreasing (and power-increasing) organization should selectively persist under pH-controlled light. To assess changes in pH dynamics that occurred under the alternative selection regime, in which photoperiods were not linked with pH-affecting selection or organization, the microecosystems that developed under fixed photoperiods were subjected to pH-controlled light on the last day of each test. The daily light duration increased 506 min on average in microecosystems that developed under pH-controlled light and 412 min on average in microecosystems that developed under fixed photoperiods. Selective reinforcement of acid-secreting blue-green algae in response to CO_2 and nutrient limitations could account for the greater increase in power acquisition in microecosystems that developed under pH-controlled light.

Keywords: Maximum power principle; Ecosystem development; Autocatalytic energetics; Microcosm experiments; Ecosystem theory

1. Introduction

The orderly pattern of succession within a typical landscape has led many to search for ecosystem-level principles of self-organization. Several of the proposed principles, which include minimum specific energy flow (Margalef, 1963), maximum exergy storage (Jorgensen, 1997), optimum ascendency (Ulanowicz, 1997), etc., hypothesize that one or more ecosystem-level properties are optimized during the self-organization of ecosystems, subject to relevant environmental constraints or tradeoffs. The maximum

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power principle is one of the earliest and most general of these proposed optimization (or extremal) principles. Its use as a potential criterion for understanding the direction and outcome of ecosystem development and for assessing the likelihood of ecosystem sustainability has done much to inspire the systems approach among ecologists. No direct, empirical test of this principle of ecosystem development has been reported in the peer-reviewed literature, however, since its initial proposal in 1922.

1.1. General applicability and prerequisites of the proposed principle

The maximum power principle was initially formulated by Lotka (1922a, p. 148) as "natural selection tends to make the [available] energy flux through the system a maximum, so far as is compatible with the constraints to which the system is subject." This hypothesis was subsequently augmented by Odum and Pinkerton (1955), who suggested that selection for maximum power output could determine the efficiencies at which a wide variety of biological systems operate. Odum (1994, 1996) provided possible applications to ecological engineering, economic planning, and the study of long-term human impacts on the biosphere.

The principle predicts the selective persistence of ecosystem designs that exploit previously untapped energy (Lotka, 1922a; Odum, 1995), where "design" refers to the configuration of the ecosystem's network of energy flow. An ecosystem then, for our purposes, is any network that is organized, in part, by energy flow through both biotic and abiotic components and that includes multiple interacting populations. Such organized networks have properties, or traits, which include system performance and organization measures; energy flow and transformation parameters; status and dynamics of bulk media properties such as water column or soil pH, temperature, redox potential, etc.; and other composites of the traits of the networks' components and interactions. Ecosystem identity is a function of the persistent coherence of the energy flow network and the historically conserved nature of the traits that such coherence provides, rather than of an arbitrary choice of static spatial boundaries.

This coherence results from the autocatalytic nature of some of the flows associated with these networks. These flows drive the replication of the biological structure through which they are reinforced, and both the structures and the trait variants associated with autocatalytic flow recur and persist along with the flow. Because of this association with autocatalytic flow, such trait variants possess differing probabilities of both recurrence and persistence that are dependent upon the properties of the networks that bear them and the environments in which these networks occur. Thus, networks, at each level of biological organization, bear trait variants, the conservation of which is subject to a process of natural selection. More specifically, the dynamics of emergence and recurrence among the many actual and potential autocatalytic cycles of energy flow that are selectively reinforced within ecosystems (Lonergan, 1957; Odum, 1983) provide ecosystems with the trait variation and conservation required for natural selection (Lotka, 1922b; Depew and Weber, 1995). Differences among trait variants in their respective probabilities of recurrence and persistence could then potentially result in the optimization of an ecosystem trait such as power acquisition. Given the theoretical arguments, however, against any substantive effect on biological systems of selection among trait variants born by multiple-organism entities (Gould, 1998), empirical assessments of such proposed optimization processes are needed.

1.2. Detection of selective persistence

The emphasis of the maximum power principle is on selective persistence of network designs that increase power acquisition by the systems possessing them. Thus, in the case of ecosystems, the primary trait-bearing unit is the ecosystem itself rather than the individual organisms or autocatalytic cycles within it, although the selection associated with trait variant persistence might occur among the alternative flows and network designs within this experimental unit. An important implication of the nature of the trait-bearing unit is that the variability of this unit with respect to the trait affects the ability to detect a selection-induced difference in the trait. In typical selection experiments based on the phenotypic traits of organisms, sample sizes in the hundreds or thousands are often required to empirically detect moderate selective forces at the conventional type I error rate of 0.05 (Lewontin, 1974; Manly, 1985). When the studied trait is an ecosystem-

level property and directional selection is assessed using a standard *t*-test for differences in this property under alternative selection regimes (Endler, 1986), the sample size is the number of ecosystems subjected to each selection regime, and the power to detect a selection-induced difference is limited by the residual variability of the ecosystems with respect to the trait.

Like individual organisms, individual ecosystems that develop under similar conditions can display great variability, as shown repeatedly in microcosm research. Therefore, experiments with large sample sizes and long durations might be necessary to produce statistically significant selective events. If ecosystem phenotypic variability is similar to that of organisms, the requirement for such large sample sizes could make detection of selection practical only for extremely strongly selected traits—in any but the smallest ecosystems. Use of small, microbial ecosystems (microecosystems or microcosms) thus provides the best chance for detection of selection because generation times are short and most include species that are resilient to strong selection pressures. Furthermore, a possibility for selection among laboratory microecosystems under strong selection regimes has been demonstrated through artificial ecosystem selection experiments (Swenson et al., 2000a,b) and through investigation of differences in response to toxicity between preexposed and non-preexposed microecosystems (Genoni et al., 2001; Montague et al., 2001).

General advantages of microcosms for practical tests of ecosystem theory include both rapid ecosystem development and the controllability of their environments, initial conditions, and the exchanges across their boundaries (Beyers and Odum, 1993; Fraser and Keddy, 1997). More specifically, the study of the relation between power acquisition and other ecosystem-level attributes and behaviors is greatly facilitated by the precise monitoring of energy inputs and ecosystem-level responses made manageable by a microcosm-based investigation. Finally, the suitability of microcosms for initial testing of general principles of ecosystem self-organization is uncompromised by attributes related to scale or boundary effects insofar as the conditions established within them conform to the conditions under which the principles are hypothesized to operate.

The principle we tested, for instance, predicts increased power acquisition by any ecosystem in which an increased influx of available energy can be coupled with existing or potential energy flow pathways, given an adequate period of adaptation and within thermodynamic and material constraints. Such increases should be observable in microcosms that are given access to and control of a source of additional photosynthetically active radiation at a physiologically usable intensity if adequate space and nutrients are available to support increased photosynthetic production. As long as light period duration (relative to dark period) limits production, a relatively longer light period represents an additional source of available energy. Furthermore, the extant variation in metabolic pathways within aquatic microcosms permits rapid physiological adaptation to changing light regimes. Thus, the conditions required for selection of power-increasing ecosystem designs within the time frame of an empirical investigation, which might be otherwise unavailable, are possible in aquatic microcosms.

1.3. A specific property of development predicted by the maximum power principle

Under the above conditions and with a sufficiently precise monitoring of energy influx, the proposed selective persistence of pathways of energy flow that permit an ecosystem to capture previously untapped available energy predicts an empirically detectable increase in power acquisition. We were able then to test this prediction by supplying light to microcosms at a constant daily duration, thus allowing the ecosystems to develop under a fixed energy-input regime. By subsequently introducing a mechanism to adjust the daily light duration based on the changing level of a measurable ecosystem property, a source of untapped energy was placed under the potential control of the ecosystem. An increase in net biomass production tended to decrease the energy influx under the introduced mechanism. Thus, any increase in energy influx (i.e., daily light duration) subsequent to its introduction indicated a power-increasing reorganization of the energy flow pathways, as predicted by the maximum power principle.

Detection of an increased energy influx is possible under the above conditions without determining whether power acquisition has actually been maximized within the constraints of the environment. Results simply indicate whether a tendency occurred

toward power maximization. The degree of increase or decrease in power acquisition occurring within any period of observation depends on the pathways for ecosystem organization available, their time-dependent probabilities of realization, and their selective persistence upon realization. Whether power acquisition actually achieves the maximum possible within the prevailing constraints remains difficult to determine due to the innumerable alternative configurations of the energy flow network that might be assumed by the components of an ecosystem. Such a determination is unnecessary, however, for testing the hypothesis deduced from the maximum power principle that systems tend to develop in a power-increasing manner when an untapped source of available energy and adequate material resources are provided (Lotka, 1925). Such a test requires monitoring the energy acquisition by the ecosystem but does not require characterizing all the energy flow paths within it.

1.4. Relations with other optimization principles

Although this hypothesis is explicitly required by the maximum power principle, it is not incompatible with most other proposed optimization or extremal principles. Many of the properties optimized according to these other principles are such close correlates of system power acquisition that increases in their respective values are expected to regularly coincide during at least some stages of ecosystem development (Lotka, 1922a; Odum, 1983; Patten, 1995). Often, for instance, capture of available energy by a system becomes closely correlated with the system's dissipation of this energy. Accordingly, Lotka (1922a) and Schneider and Kay (1994) have proposed that maximizations of available-energy capture and dissipation rates occur (ultimately) in conjunction. Furthermore, the mutual dependence in ecosystems between power acquisition and biomass (and thus chemical exergy storage) establishes a correlation between these properties. Maximization of total system exergy throughflux, which has recently been suggested as an alternative version of the maximum power principle (Jorgensen et al., 2000; Fath et al., 2001), is compatible with multilevel selection for maximum system power acquisition. Increases in efficiency-related measures, such as a dissipation-specific exergy storage or flux, can also coincide with increased power acquisition to the extent, for instance, that a relative increase in storage or flux enhances processes that contribute to the capture of available energy from a system's (external) sources (Odum, 1983, 1994; Jorgensen et al., 2000).

Although a system's power acquisition, dissipation rate, and exergy storage are closely related through the mutual association of these properties with the presence of thermodynamic gradients, their correlation is limited by tradeoffs among alternative possible applications of available energy within the system. Increases in dissipation rate can occur at the expense of, rather than in conjunction with, power acquisition and exergy storage, and divergence between the long-term average dissipation rate and power acquisition of a system result from export or from the tradeoff between power acquisition (i.e., output) and dissipation by the processes through which the acquisition occurs (Odum, 1994). Likewise, exergy storage does not always reinforce a system's power acquisition but can, instead, occur at the expense of such reinforcement. Along with these tradeoffs, differences in exergy-specific contributions to ecosystem power acquisition exist among the many forms of exergy storage or flow (with dissipation) that do so contribute, further limiting the correlation of these properties. The concurrence or divergence of the changes in these properties during successive stages of ecosystem development thus remains an object of active theoretical and, to a lesser extent, empirical inquiry (Nielsen and Ulanowicz, 2000; Fath et al., 2001, 2004; Jorgensen et al., 2004), and methods for adjusting standard exergy-based calculations to account for differences among exergy types have been suggested based on their production requirements (Odum, 1988, 1996) and the information associated with biotic organization (Jorgensen et al., 1995; Bastianoni et al., 2005).

The maximum power principle predicts selective persistence of the (dissipative) processes and exergy storages that maximize power acquisition, whether or not this selection also maximizes dissipation rate and exergy storage. Because additional production-enhancing power increases a system's potential for exergy storage, maximization of this storage might be dependent on power maximization, even if the converse condition does not apply. If ecosystem development is nonetheless oriented towards maximum exergy storage, then system power might prove a more sensitive indicator of ecosystem development during early stages

of development, with exergy storage becoming the more sensitive indicator during later stages (Jorgensen et al., 2000). We did not test these latter propositions or investigate whether power or storage increases predominate in cases where these two properties are negatively correlated. Nor did we test other alternative theoretical perspectives on the relations among proposed optimization principles or all hypotheses derivable from or required by the maximum power principle. We tested only one such hypothesis (described above); suitable modification of the methods described below, however, could permit testing other hypothesized relations and dynamics of system properties during ecosystem development. Such testing might help us identify scientifically sound and ecologically meaningful measures of ecosystem development based on one or more of the above system properties. A more immediate goal, however, is a more precise explanatory characterization of the common basis for these properties and their relations in ecosystems—i.e., the selective persistence among networks of coupled thermodynamic fluxes that results from differential (exergy-consuming) production of autocatalytic structures (that sustain the underlying thermodynamic gradients).

2. Materials and methods

The empirical investigation was conducted using aquatic microcosms in which predominantly planktonic communities were established on January 19, 1998. Development of the microecosystems was monitored for 847 days, within which two tests of the effects of a pH-controlled light regime on ecosystem properties were performed. The first test occurred from day 119 to day 177 of the experiment and the second from day 517 to day 561. Other intervals provided time for preparation of forthcoming tests, for stabilization of community metabolism, and for further investigation of trends observed during the tests.

2.1. Microcosm construction and setup

Six microcosm tanks (Fig. 1) were constructed of mirror glass reflecting inward with interior dimensions of 15 cm × 10 cm × 10 cm ($L \times W \times H$). Smaller tanks of clear glass (5 cm in height with the same bottom dimensions) were situated above the microcosm tanks and filled with water to absorb heat when the microcosms were receiving light. Plastic frames maintained the 2.5-cm air space between the microcosm and heat-absorbing tanks to permit circulation of air to the microcosms. Temperature fluctuations between the light and dark periods were thus maintained at less than 2 °C. Each microcosm received light from an 18-cm section of a 60-cm, 20-W cool-white fluorescent tube of 3.8-cm diameter positioned diagonally above the clear tanks (Fig. 1). These lights provided 70–100 μE m^{-2} s^{-1} at the water surface, depending on the age of the tubes and ballasts. A light-excluding cover (a box of poster board with aluminum foil on the inside surfaces) enclosed each microcosm tank unit (Fig. 1).

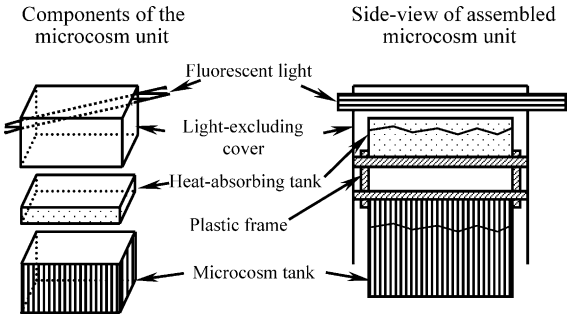

Fig. 1. Components and side view of the microcosm units.

2.2. Linkage of energy input with an ecosystem-level property

Each microcosm tank had a pH electrode (Orion Low-Maintenance Triode Model) attached to a computer through an Orion model 290A pH/ISE meter, with the electrode sensor 2 cm below the water surface. The computer logged pH readings throughout the experiment at 5-min intervals, both during and between the pH-controlled light tests. The pH electrodes were rinsed daily with deionized water and calibrated biweekly until day 486 and weekly thereafter. Adequate stirring for stable pH readings was maintained using a magnetic stirring bar in each microcosm and a stirring platform (Multi-Magnestir No. 1278, Lab-line Instruments, with a speed setting of 4.5). The computer also controlled the fluorescent lamp and recorded the length of each light and dark period as a measure of total energy influx. The computer program permitted choice of either a fixed photoperiod or a pH-controlled light regime for each tank. During

the light periods, the lights in all tanks were switched off for 5 min in each 65-min interval in an attempt to estimate light-period respiration via changes in pH (Beyers, 1963a).

A stabilization stage, during which a uniform light regime consisting of fixed photoperiods was maintained in all microcosms until the daily highest and lowest pH values showed no consistent upward or downward trend, preceded each test. The timing of initiation of the tests was thus dependent on the time required for pH dynamics to stabilize. A 4-h light:4-h dark cycle was used in Test 1 and a 12-h light:12-h dark cycle in Test 2. (The 4-h light:4-h dark cycle was originally employed to shorten the time required for detection of changes in the pH dynamics, especially in terms of the highest and lowest values attained during each cycle. The rapidity of pH stabilization and response to pH-controlled light in Test 1 indicated that a more natural 12-h light:12-h dark cycle, which would permit cell cycles to coincide with the photoperiods to which they had historically adapted, was feasible within the timeframe available.) Subsequently, under the pH-controlled regime, the light was switched on when water column pH fell below a predefined value, and switched off when water column pH rose above another predefined value. For each microcosm in each test, the average highest and lowest pH values obtained at the end of the stabilization stage were used to determine the pH threshold values above and below which the lights would be switched off and on, respectively, throughout the test period for the treatment tanks and on the last day of each test for the fixed-photoperiod control tanks. The pH-controlled light regime was maintained for 4–8 weeks in each test to allow enough time for pH-controlled light to affect and be affected by ecosystem organization. The time that the pH-controlled light regime was maintained varied due to differences in the durations of the fixed photoperiods and in the time required for the pH dynamic to stabilize prior to the tests. The end of each test was also selected to coincide with a scheduled sample date.

2.3. Experimental design

The six tanks were arranged on the stirring platform in three blocks with two tanks in each block. For each test, one tank from each block was randomly chosen to be the treatment microcosm, in which the duration of light and dark was controlled by microcosm water pH, and the other was the control, which received a fixed photoperiod with light and dark periods of equal duration. (All tanks received this fixed photoperiod during the stabilization stage preceding each test.) Each test thus employed a randomized complete block experimental design. This design minimized temperature differences between tanks within blocks. The control tanks indicated whether changes in pH dynamics that occurred in microcosms in which pH was not allowed to affect the light regime were similar to those in microcosms that developed under pH-controlled light.

2.4. Chemical analysis

Chemical properties of the initial lake water and of subsequent water samples taken once every 4–5 weeks from each tank were determined as follows. Two 40-mL samples (one filtered through a Whatman 42 filter and the other unfiltered) were analyzed by the University of Florida's Analytical Research Laboratory for P, Ca, Mg, and Fe by inductively coupled argon plasma spectroscopy (Spectro Ciros CCD model) and for NO_3^--N and TKN by air-segmented automated spectrophotometry (Rapid Flow Analyzer, 300 Series). TKN was analyzed following sample digestion using EPA method 351.2. Total alkalinity was obtained by titrating with 0.02N standardized H_2SO_4 to a pH of 4.5. (Titration curves covering a pH range from 8.5 to 2.5 were also obtained in this manner following Test 2 using micropipettes to deliver precise quantities of H_2SO_4 to tank water samples.) Total organic carbon (TOC) was analyzed using a High-Temperature Total Organic Carbon Analyzer (model DC-190 manufactured by Rosemount Analytical) after sonifying the sample to break apart the large algal colonies. Ecosystem nutrient ratios (C:N, C:P, and N:P, in g/g) were calculated using the total nutrient concentrations in the unfiltered samples. Total N was estimated as the TKN in the unfiltered sample because NO_3^--N was below the detection limit throughout the time it was measured (from the beginning of the experiment through day 269).

2.5. Interventions common to all tanks

2.5.1. Initial water and inoculation

The microcosm tanks were filled with 1.1 L of a mixture of plankton-containing waters (from five lakes within 25 km of Gainesville, Florida) that had

been passed through 0.3-mm mesh to remove large particulate debris. Water, collected from the same lakes and maintained in the laboratory for 30 days under a fixed photoperiod, was filtered through Whatman 42 filter paper to produce a concentrated inoculant, 8.5 mL of which was added to each tank at the beginning of the experiment. Two subsequent inoculations (reseedings) were performed, adding 8.5 mL of similarly produced inoculant each time to each tank. These two reseedings were carried out on days 8 and 23. The water was from four of the original five lakes for the first reseeding and from two for the second, rather than from all five, based on proximity and because the reseedings supplemented a base community (that had become successfully established by the dates selected) with species that might require such a community for their own establishment.

2.5.2. *Initial light regime and nutrient supplements*

A light regime of 4-h light:4-h dark cycles was initiated on day 1 of the experiment. Nutrients were added 2 days later, so that light energy, rather than nutrients, would be the limiting factor during ecosystem development. Based on chemical analysis for the initial lake water, nutrients (N, P, Fe, Mg, and S) were added to each microcosm to achieve Medium C concentrations, a standard solution for maintaining algal cultures (Davis, 1967). Deionized water was added daily to a pre-marked water level in each microcosm to replace the water loss to evaporation. Medium C was added after each sampling to replace water taken for biological or chemical analyses.

2.6. *Biological analysis*

Organisms were counted every 2 weeks throughout the first test and weekly throughout the second test. Green and blue-green algae were identified to genus except for small coccoid green algae and blue-green algae, which were recorded as such. Chrysophytes were identified as *Navicula*, *Melosira*, other diatoms, or other chrysophytes because representatives of the latter two categories were too few for more specific identification. Algal density (as cell volume per volume of tank water) was estimated for each taxon by multiplying the number of cells by an estimate of cell volume, and then dividing by sample volume. Cell volume for each taxon was obtained using visual estimates of the dimensions of a typical cell of each type and applying a geometric formula appropriate to the taxon's cell shape (Rott, 1981). An importance value for each algal taxon, as a summary measure of algal dominance and community structure (Barbour et al., 1987), was calculated as the mean of its relative abundance (i.e., the volume of the genus as a fraction of total algal volume) and its frequency of observation, which was the fraction of the number of grids in counting areas in which a member of the genus was observed.

2.7. *Summary measures of light duration*

On the final day of each test, the final daily light duration was calculated for each treatment tank as the actual light duration in its final light:dark cycle divided by the total duration of the cycle and then multiplied by 1440 min to obtain average minutes lighted (per 24-h period) for this final light:dark cycle. Tanks that had been receiving light continuously for more than 24 h at the end of the test were considered to have attained continuous light. For each test, the cumulative light input fraction was also calculated for each tank as the sum of the durations of all lighted periods divided by the total duration of the pH-controlled light regime.

Also on the final day of each test, the control tanks (under a fixed photoperiod until this time) were switched to pH-controlled light with light-off and -on thresholds obtained as described above. This change in light regime permitted an assessment of whether changes in the microcosms that had not been subject to the pH-controlled light regime had affected the pH dynamic therein in a manner similar to that observed in the microcosms that were subject to pH-controlled light during the test. The first light:dark cycle following the switch to pH-controlled light was used to obtain a final daily light duration in the control tanks for comparison with the final daily light duration in the treatment tanks. The cumulative light input fraction in all control tanks was 0.5 (in both tests) because the light and dark cycles were of equal duration.

2.8. *Test 1*

Twice during the stabilization stage for Test 1 (on days 42 and 70 of the experiment, when growing divergence in pH dynamics between paired tanks became apparent), water from the two tanks in each block was mixed and then redistributed into these two tanks to

obtain greater similarity between the treatment and control tanks at the beginning of the test. Algal cells were counted using a hemocytometer of 0.1-mm depth for the 1-mm^2 grid area. An area of 0.2 mm^2 was used for those taxa with about 50 or more cells in that space. This method was used for all counts of planktonic organisms during the first year of the experiment. Alkalinity and TOC were measured monthly. The switch to pH-controlled light was applied to one treatment tank on day 119, while the other two treatment tanks received this treatment on day 146. The test was terminated on the day-177 sampling date.

2.9. Post Test 1 interim and Test 2

The water from all tanks was mixed together on day 393, at which time the biotic communities attached to the side and bottom surfaces of the tanks were scraped into the water. Afterwards, the attached algae on side and bottom surfaces of the tanks were scraped daily into the water column for the duration of the experiment. On day 471, nutrients were added to each tank to reach Medium C concentrations of N, P, and Fe.

The objectives in Test 2 were the same as those in Test 1, with the two tests together providing a larger sample size than would a single test. During Test 2, in addition to the monthly element analyses, alkalinity was measured biweekly and TOC weekly. Beginning on day 483, a settling-chamber (2.5 mL in volume with 2.8 cm^2 of settling area) was used to improve the accuracy of organism counts. Diluted tank water with one drop of Lugol's solution was allowed to settle for at least 8 h prior to counting. Organisms within a superimposed 10×10 eyepiece grid were counted at each of the 30 (randomly selected) locations using an inverted microscope. The more abundant organisms (those with 100 cells or more per location) were counted only at the first five locations.

The 12-h light:12-h dark cycles began on day 486. The pH electrodes were calibrated weekly from this time forward using two low ionic strength pH buffers (pH 4.71 and 7.05) to reduce potential error in pH readings. On day 491, the water from all six tanks was again mixed together and redistributed to each tank, and each tank was then reseeded with 40 mL of a mixture of water from two of the original five lakes. The tanks were randomly reassigned to positions on the stirring platform in the three previously selected blocks. The test began on day 517, when the same treatment used in Test 1 (light controlled by pH) was randomly applied to one tank from each block, and ended on day 561.

2.10. Investigation of the possible causes of pH plateaus

To investigate potential remedies for pH plateaus, which developed during light periods at the end of Tests 1 and 2, nutrients and alkalinity were added after these tests to tanks in which these plateaus occurred. On day 223, 15 mL of Medium C was added to two of these tanks. Micronutrients (B, Zn, Mn, Mo, Cu, and Co) to reach concentrations in Microcosm Medium T82MV (ASTM, 1997) and 100 mL of Medium C were added on days 592 and 594, respectively, to all tanks. Two Medium C stock solutions (40 mL KNO_3 and 5 mL K_2HPO_4 solutions, the amounts required to reach Medium C concentrations of N and P in 1 L of tank water) were added on day 597 to all tanks. On day 600, sufficient Fe, Ca, and Mg to reach Medium C concentrations in 1 L of tank water was added to all tanks. On days 651 and 653, respectively, 2.5 mL of the K_2HPO_4 Medium C stock solution and 20 mL of 0.00988 M NH_4Cl were added to two of the tanks. Alkalinity as $NaHCO_3$ (1 mL of 0.14 M $NaHCO_3$) was added to all tanks on day 713 and daily from day 720 through day 748. Medium C (10 mL) was added daily from day 753 through day 847.

2.11. Data analysis

All statistical analyses were performed on the combined data from both tests. The primary test for the predicted increase in power acquisition under pH-controlled light was based on a comparison of the final daily light duration in the treatment microcosms (pH-controlled light) versus that in the controls (fixed photoperiod). The null hypothesis was that ecosystem control of the light by pH would not affect pH dynamics in a manner that resulted in more daily light input to the treatments than that which the controls received when they were switched to pH-controlled light on the final day of each test. Thus, the final daily light durations in treatment and control under pH-controlled light were compared using a one-tailed randomization test for matched pairs (Siegel, 1956). The power of this test at $\alpha = 0.05$ for detecting a difference in final daily light duration of a magnitude equal to 10% of the mean

final daily light duration was also calculated based on the observed variability among experimental units in Tests 1 and 2. Given a difference of this magnitude, the approximate number of microcosm pairs required for a power of 0.95 was estimated by solving the *t* statistic for sample size. This calculation used an initial power equivalent to that obtained from the randomization test, a difference of the observed magnitude, and an initial sample size of six. A *t*-test was also performed on the difference in the cumulative light fraction in the treatments from the fraction of 0.5 in the controls.

Exploratory statistical analyses of the data were also performed to uncover possible effects of the treatment on community structure and chemical properties, and to examine correlation among these properties. Measured and derived properties included the importance values of the algal divisions and dominant genera present in both Tests 1 and 2, alkalinity, the C:N, C:P, and N:P ratios, TOC, unfiltered TKN, and filtered TKN, P, Ca, and Mg. The variables assessed included the values of these properties at the end of the tests and the overall changes in their values during the tests. Paired *t*-tests were used to assess the effects of treatment on these variables. Partial correlation coefficients were computed to assess the strength and probability of relations among the properties. The cumulative light fraction and final daily light duration were also included in the partial correlation analysis to assess their relations with the other variables.

The randomization test was performed using Microsoft Excel. The *t*-tests and partial correlation coefficient calculations were performed in SAS using PROC MEANS and PROC GLM, respectively (SAS Institute, 1988a). The power of the *t*-tests was calculated using the SAS function PROBT (SAS Institute, 1988b), as was the required number of blocks to achieve a power of 0.95. All power calculations used $\alpha = 0.05$ and were based on the probability of detecting a difference greater than or equal to 10% of the mean absolute value of the tested variable. The factors in the model used in obtaining the partial correlations were test (1 or 2), block (on the stirring platform), and the test by block interaction. The partial correlation coefficients for pairs of the analyzed variables were obtained from the type-III sum of squares, the sign of the estimated linear regression coefficient, and the error sum of squares, all provided by PROC GLM, as described in Kleinbaum et al. (1988).

3. Results

3.1. Power maximization test

Trends in photoperiods in the treatment tanks and in highest and lowest pH values attained during each light:dark cycle in the control tanks are depicted in Figs. 2 and 3 for Tests 1 and 2, respectively. Considering both tests, the pH dynamics in five of the six treatment tanks changed in a manner that produced continuous light. The exceptional tank (Fig. 3, bottom left panel) developed no consistent trend in daily light duration. It was lighted for 47% of the final light:dark cycle. The average cumulative light fraction in the six treatment tanks was 0.71; i.e., the tanks were lighted 71% of the total duration of the tests, or 42% more ($P = 0.0124$) than the light duration fraction of 0.5 that was maintained before the switch to pH-controlled light in these tanks and until the final day of each test in the paired controls. In four of the six control microcosms, the pH dynamic resulted in continuous light as soon as pH-controlled light was applied, as indicated in Fig. 2, upper right panel, and Fig. 3, right side panels, by the final highest pH values in these tanks, which were all lower than the respective thresholds for switching light

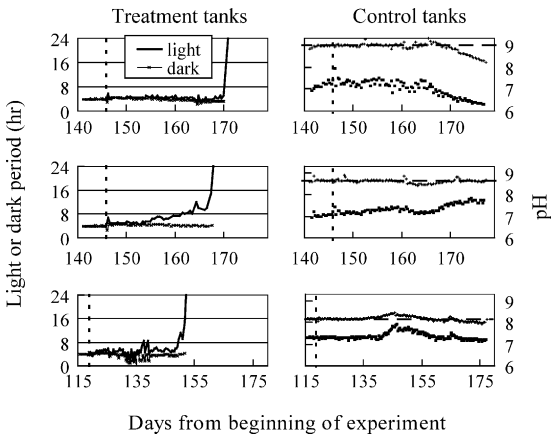

Fig. 2. Test 1: Actual durations of light and dark periods in treatment tanks and the highest and lowest pH values attained during each light:dark cycle in corresponding paired control tanks. Treatment tanks attained continuous light at 24, 22, and 33 days, respectively, from the time at which they began receiving pH-controlled light in this test. Dashed vertical lines indicate the time at which the switch to pH-controlled light in the respective treatment tank was made. Dashed horizontal lines for the control tanks indicate the pH thresholds for switching lights off during their final light:dark cycle.

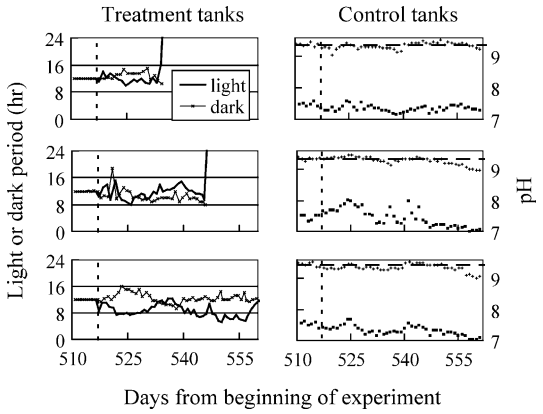

Fig. 3. Test 2: Actual durations of light and dark periods in treatment tanks and the highest and lowest pH values attained during each light:dark cycle in corresponding paired control tanks. Two treatment tanks (top and middle left panels) attained continuous light at 18 and 29 days, respectively, from the time at which they began receiving pH-controlled light in this test. Dashed vertical lines indicate the time at which the switch to pH-controlled light in the respective treatment tank was made. Dashed horizontal lines for the control tanks indicate the pH thresholds for switching lights off during their final light:dark cycle.

off during this final light:dark cycle. In one of the other control tanks, highest pH values remained relatively stable under fixed photoperiods while lowest pH values increased (Fig. 2, middle right panel), producing a decline in daily light duration, i.e., the light was on only 32% of the first light:dark cycle following its switch to pH-controlled light, down from 50%. In the other control tank, both highest and lowest pH values decreased slightly (Fig. 2, bottom right panel), and daily light duration increased from 50 to 68% in the first pH-controlled light:dark cycle on the final day of the test in this tank.

The tendency towards increased available energy influx was more pronounced in the treatments than in the controls, with daily light duration in treatment tanks increasing by an average of 506 min while the average in controls increased by 412 min based on their first light:dark cycle (or immediate attainment of continuous light) under pH-controlled light. The probability of no treatment effect, however, was 0.375, as determined by the randomization test. This high *P*-value was obtained despite the 23% greater increase in average daily light duration in the treatments than in the controls. The power for this randomization test was estimated at only 0.078 given a difference of 10% of the mean final daily light duration. Given the high residual variation in these tests, achieving a power of 0.95 was estimated to require 600 microcosm pairs.

3.2. pH plateaus

Near the end of Test 1, a new pH dynamic developed in two of the treatment tanks and in one of the control tanks (Fig. 4). The rate of pH increase under light tapered to zero or became slightly negative, creating a plateau or gradual decline in pH in a microcosm still receiving light. This plateauing dynamic also developed toward the end of Test 2 in the three control tanks. The effect of this plateauing of pH resulted in the light staying on continuously under the pH-controlled light. Plateauing under fixed photoperiods occurred repeatedly during each light period at progressively lower pH values until the switch to pH-controlled light at the end of the test, after which light remained on continuously. The other control tanks, in which plateauing did not occur, did not attain continuous light upon their switch to the pH-controlled light regime.

The addition of 15 mL Medium C did not have any effect on the pH plateaus. Larger additions of

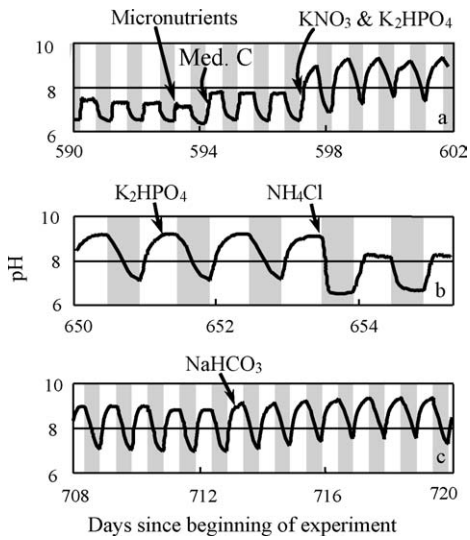

Fig. 4. Response of plateauing pH dynamic to addition of (a) micronutrients (B, Zn, Mn, Mo, Cu, and Co), Medium C (containing 0.55 mg KNO_3-N), and 5.5 mg KNO_3-N with 0.89 mg K_2HPO_4-P; (b) 0.44 mg K_2HPO_4-P and 2.77 mg NH_4Cl-N; (c) 0.14 meq of alkalinity as $NaHCO_3$. Shaded areas indicate the periods when light was off.

Table 1
Changes in chemical and community-structure measures during Tests 1 and 2

	Ctrl	Trt	$P(\|T\|)$	Power	RN
TOC (mg/L)	191.1	320.5	**0.057**	0.071	290
TN (mg/L)	−19.5	−15.3	0.506	0.062	528
Filtered N (mg/L)	0.5	0.4	0.717	0.054	2e3
Filtered P (mg/L)	−0.217	0.033	0.336	0.050	1e4
Filtered Ca (mg/L)	−0.4	−2.5	0.112	0.054	2e3
Filtered Mg (mg/L)	−0.8	−1.3	**0.081**	0.063	467
C:N (g/g)	4.7	6.3	0.345	0.061	576
C:P (g/g)	55.3	94.6	**0.056**	0.068	351
N:P (g/g)	−5.8	−5.3	0.692	0.076	240
Alk (meq/L)	−0.27	−0.41	**0.099**	0.066	397
Apha IV	0.167	0.161	0.929	0.055	1e3
Nost IV	−0.009	0.100	0.204	0.052	3e3
Osci IV	0.152	0.104	0.212	0.062	524
Syne IV	−0.006	−0.007	0.944	0.052	4e3
BG IV sum	0.313	0.389	0.782	0.074	257
Green IV sum	0.232	0.085	**0.031**	0.064	437

Ctrl: mean from control tanks; Trt: treatment mean; $P(|T|)$: probability from two-tailed paired t-test of difference between treatment and control (with P-values ≤ 0.1 in bold); Power $= 1 - \beta$ (β being the type II error rate given $\alpha = 0.05$, an actual mean difference of 10% of the overall mean of the absolute values for the tested variable, and variability as estimated from the current experiment); RN: number of microcosm pairs required to achieve $\beta = 0.05$ given the above conditions; TN: total measured N (TKN from unfiltered samples); Alk: titratable alkalinity; Apha: *Aphanothece*; Nost: *Nostoc*; Osci: *Oscillatoria*; Syne: *Synechococcus*; BG: blue-green algae; IV: importance value; Green: green algae.

Medium C and of other solutions containing KNO_3 (which increases alkalinity through assimilatory reduction) shortened or eliminated them (Fig. 4a). Addition of N as NH_4Cl (which decreases alkalinity), on the other hand, had the opposite effect, with plateaus developing sooner and at lower pH after lights switched on (Fig. 4b). Addition of alkalinity as $NaHCO_3$ eliminated the plateaus (Fig. 4c), which did not recur after the daily $NaHCO_3$ additions following Test 2.

3.3. Exploratory data analysis

The analyses of chemical measures from both tests produced few significant relations between the treatment (pH-controlled light) and the chemical measures or their changes during the tests (Table 1). At the end of the tests, none of the 10 chemical measures differed even marginally significantly between the treatment tanks and controls (data not shown). The power of these tests for detecting a difference equal to 10% of the mean at $\alpha = 0.05$ averaged only 0.18, however. Differences between treatments and controls in the changes in these measures during the tests were marginally significant in four of the 10 cases (Table 1). For these measures, the average power was even lower, at 0.06. The mean increases in TOC and C:P were, respectively, 68 and 71% greater in treatments than in controls, while the mean decreases in alkalinity and in filtered Mg were, respectively, 52 and 62% greater in treatments than in controls. The decrease in filtered Ca was greater in the treatments by a factor of six.

Among the community-structure measures, only the sum of the green algal importance values differed marginally significantly between light regimes, increasing by 173% more in controls than treatments (Table 1). For the six community-structure measures, the power for detecting a difference equal to 10% of the overall mean at $\alpha = 0.05$ averaged 0.57 for the final values (data not shown) and 0.06 for the corresponding changes in values during the tests (Table 1). The sums of both the green and the blue-green algal importance values increased under both light regimes.

Final daily light duration and cumulative light fraction were positively correlated with changes in TOC, C:P, and blue-green algal importance but negatively correlated with changes in alkalinity and filtered Mg and Ca (Table 2). Change in alkalinity was also negatively correlated with changes in TOC, total N, and blue-green algal importance, and positively correlated with changes in filtered Ca and Mg.

Table 2
Partial correlation coefficients for changes in chemical and community-structure measures during Tests 1 and 2 along with cumulative light fraction and final daily light duration

	TOC	Alk	BG IV sum	Green IV sum	Cumul. light	Final light
TOC (mg/L)	1.000	**−0.722**	**0.673**	−0.286	**0.804**	0.557
TN (mg/L)	0.629	**−0.745**	0.586	−0.044	0.347	**0.722**
Filtered N (mg/L)	−0.146	−0.285	−0.056	−0.128	−0.554	−0.432
Filtered P (mg/L)	0.576	**−0.931**	**0.785**	−0.173	0.379	0.607
Filtered Ca (mg/L)	**−0.715**	**0.859**	**−0.760**	0.313	**−0.699**	**−0.779**
Filtered Mg (mg/L)	**−0.725**	**0.875**	**−0.708**	0.400	**−0.721**	**−0.727**
C:N (g/g)	0.198	0.237	0.091	−0.174	0.531	0.166
C:P (g/g)	0.502	−0.225	0.424	−0.409	**0.772**	0.363
N:P (g/g)	0.166	**−0.715**	0.286	−0.336	−0.101	−0.100
Alk (meq/L)	**−0.722**	1.000	**−0.782**	0.417	−0.542	−0.435
Apha IV	0.336	**−0.705**	**0.686**	0.271	−0.058	0.438
Nost IV	0.364	−0.082	−0.286	**−0.698**	0.290	−0.387
Osci IV	−0.391	0.447	0.063	0.652	−0.530	−0.299
Syne IV	−0.463	0.441	−0.452	−0.191	0.093	0.070
BG IV sum	**0.673**	**−0.782**	1.000	0.048	0.493	0.634
Green IV sum	−0.286	0.417	0.048	1.000	−0.499	0.244
Cumul. light	**0.804**	−0.542	0.493	−0.499	1.000	0.556
Final light (min)	0.557	−0.435	0.634	0.244	0.556	1.000

Alk: titratable alkalinity; BG: blue-green algae; IV: importance value; Cumul. light: cumulative light fraction; Final light: final daily light duration; Green: green algae; TN: total measured N (TKN from unfiltered samples); Apha: *Aphanothece*; Nost: *Nostoc*; Osci: *Oscillatoria*; Syne: *Synechococcus*. Values in bold indicate partial correlations with $P \leq 0.1$.

Blue-green algal importance at the end of the tests was also positively correlated with both cumulative light fraction ($r = 0.857$) and final daily light duration ($r = 0.772$).

3.4. Other trends in measured properties during Tests 1 and 2

Consistent trends in the chemical measures among both treatment and control tanks during the two tests included a decrease in alkalinity and increase in C:N and C:P mass ratios in all 12 tanks and, in 11 of 12 tanks, an increase in TOC accompanied by decreases in filtered Ca and Mg. The exceptional tank in the latter case was the one tank with a final daily light duration substantially less than 12 h. This tank also had the lowest final and initial C:P and N:P, the lowest C:P increase, and the highest final filtered Ca and Mg concentrations. Alkalinity decreased by 4% in this tank while decreasing by 15–49% in the other tanks. The average C:N and C:P mass ratios at the end of the two tests were 11.2 and 225, respectively. The dominant algal genera as indicated by importance values were *Synechococcus*, *Oscillatoria*, and *Aphanothece* during Test 1 and *Nostoc*, *Synechococcus*, and *Aphanothece* during Test 2.

4. Discussion

The general trends in light duration and TOC were consistent with the selective persistence of power-maximizing ecosystem designs, as hypothesized. The greater increase in TOC in the treatment tanks than in the controls, for example, is a reasonable consequence of the higher productivity expected with increased light duration in treatment tanks. The greater final daily light duration in microcosms that developed under pH-controlled light relative to that in microcosms that developed under fixed photoperiods is also an expected result given selective persistence of power-increasing pathways. The statistically unresolved question of whether selection or some other source of variation in ecosystem attributes was responsible for the greater final light duration under this treatment is characteristic of small-sample statistical tests for natural selection. The need for an estimated 600 microcosm pairs to detect a 10% difference is comparable to the

sample sizes required in selection trials with individual organisms as the trait-bearing units (Manly, 1985). In all such studies adequate replication is at issue.

If a single study with adequate replication is unattainable, the strength of the results of small-sample selection studies must be inferred through a series of tests of predictions from the same hypothesis over a long period of time in conjunction, if possible, with tests of any proposed mechanism that could be responsible for differences in prevalence or persistence. Our results are a beginning for such a process that can now be continued. Furthermore, we have demonstrated how an ecosystem principle can be tested by connecting what is usually taken as an exogenous variable (photoperiod) and placing its control within the ecosystem itself. By establishing a novel feedback loop with the help of a computer, a potential for autocatalytic cooperation through a previously inaccessible energy flow coupling was introduced to evaluate whether greater energy influx and production would result, something the maximum power principle predicts. Our results agree with this prediction, and this demonstrated capacity for empirical agreement (or disagreement) with an ecosystem theory is one of their chief strengths.

4.1. Factors contributing to pH decline

Interpreting the power-increasing pH dynamics under pH-controlled light is complicated by the overall downward trend in highest pH values under fixed photoperiods (Figs. 2 and 3). The association of this trend with the development of pH plateaus in these tanks suggests that another systematic factor—in addition to any light-increasing feedback loop—was partly responsible for the power-increasing pH dynamics. Factors that could have contributed to a decline in the highest pH values attained during light periods include nutrient limitation, a decrease in light intensity as the fluorescent lights aged, an increase in detritus, etc. A mechanism that would simultaneously explain both the greater tendency to power-increasing dynamics under pH-controlled light and the systematic pH decline can be offered, however, based on the exploratory data analysis. The following evaluation of factors responsible for the pH declines is thus important both to the identification of a likely mechanism and to the selection of a modified experimental design that will diminish the systematic pH decline.

A slow and progressive decrease in light absorption by algae, which could have occurred as the fluorescent lights aged or as detritus increased, could account for the gradual decrease in pH values that occurred under both light regimes. The daily pH plateaus (which resulted in continuous final light in the control tanks when switched to pH-controlled light on the last day of each test), however, cannot be explained by these factors alone, as both alkalinity and some nutrient additions ended the plateauing dynamic. Nutrient deficiencies could retard pH increase during light periods by reducing algal growth rates. Such deficiencies might develop regularly toward the end of each light period, as observed in previous microcosm metabolism studies as well as in natural systems (Beyers, 1963b; Nixon, 1969). Although the high C:N and C:P mass ratios at the end of the tests do indicate possible N and P deficiencies, it is unlikely that nutrient deficiency alone produced the pH plateaus, as addition of macronutrients (including N and P) and micronutrients failed to affect the plateaus in some instances. Furthermore, NO_3^--N was the only nutrient addition that independently eliminated the plateaus, while NH_4^+-N had the opposite effect.

An overview of potential direct and indirect effects of alkalinity on light duration is provided in Fig. 5. The decrease in alkalinity during the tests (Table 1) would lower pH values at all concentrations of dissolved inorganic carbon (DIC), which could have contributed to the increased light durations. If the rates of CO_2 assimilation and generation were unaltered, both the highest

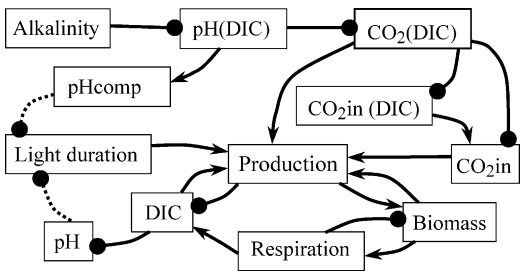

Fig. 5. An influence diagram of relations among productivity, light duration, alkalinity, pH, and inorganic C dynamics. CO_2in: net influx of CO_2 from the atmosphere; (DIC): associated property as a function of dissolved inorganic carbon. pHcomp: pH at DIC compensation concentration. Arrows indicate positive and solid circles negative influences. Dotted lines indicate influences introduced by pH-controlled light.

and lowest pH values attained during fixed light and dark periods would be lowered. The pH at which the DIC compensation concentration (and thus a stable pH) was reached would likewise decline. Because CO_2 accounts for more of the DIC at lower pH, net influx of CO_2 from the atmosphere would decline, and DIC concentrations would be lowered, potentially to the DIC compensation concentration during the light period. Thus, a decrease in alkalinity could have resulted in the daily pH plateaus in the fixed-photoperiod tanks, which in turn produced continuous light in these tanks when switched to pH-controlled light.

Under pH-controlled light, a decrease in alkalinity would result in lower DIC concentrations throughout the fixed pH range. Net primary productivity could increase in this case, as relatively less respiration would be required to reach the low pH threshold given that CO_2 efflux would be lower. Consequently, the light would turn on sooner and the dark period would be shorter. Reaching the low DIC concentration required to reach the high pH threshold and end the light period could take longer, however, as this low DIC concentration approached the DIC compensation point. If DIC limited primary productivity, lower DIC concentrations would reduce the instantaneous rate of light energy capture by the biota and slow the rate of increase of pH, particularly toward the end of the light period. This could account for the plateau effect and for the slow declines in pH that occurred in some tanks while lights were on under pH-controlled light. The daily average rate of light energy capture, if limited by daily CO_2 influx, could increase under these conditions with the increase in the fraction of the day under light. Nevertheless, even greater production could be possible if CO_2 levels were enhanced. A pH-controlled valve on a CO_2 pump together with light control could thus provide a further test of the maximum power principle.

Although CO_2 limitation induced by an alkalinity decline alone might account for the pH plateaus at the end of Test 1, the pH plateaus in Test 2 occurred at alkalinities similar to those after the end of Test 2 when no pH plateau occurred. This difference is not easily explained by a shift in community composition because the dominant algal groups were very similar during and after Test 2. The combination of nutrient and alkalinity additions might have prevented recurrence of the plateaus. Finally, the positive correlation of biomass production with alkalinity decline suggests a mechanism for decreasing alkalinity, and thus for the pH decline, in which production is an important feature. Alkalinity is sometimes assumed to be constant in aquatic systems. Here it clearly is not. The mechanism of its decline is central to any explanation of the results.

4.2. Possible causes of alkalinity decline

The major nutrients N and P are primarily responsible for nutrient-related alkalinity changes (Morel and Hering, 1993). The N inputs to the tanks were limited to N_2 influx and NO_3^- additions, however, and N_2 assimilation does not affect alkalinity while NO_3^- assimilation increases it. Addition of P as K_2HPO_4 also increases alkalinity. Thus, nutrients are unlikely to account for the decreases in alkalinity. Localized $CaCO_3$ precipitation in association with photosynthesis and H^+ excretion is common under alkaline conditions and can function to alleviate both CO_2 and nutrient limitations, with substantial calcification occurring in cyanobacterial mats during periods of nutrient deficiency (McConnaughey and Whelan, 1997). The localized $CaCO_3$ precipitation produces a long-term decrease in alkalinity in the external medium. Although no precipitate was observed, $CaCO_3$ could have been deposited within cells or in mucilaginous sheaths or aggregates without being observed under the microscope in this study.

Another possible cause for decreased alkalinity is excretion of organic acids. The measured alkalinity would be particularly sensitive to low-pK_a organic acids (such as glycolic and lactic), which remain largely dissociated at pH 4.5, the endpoint of the alkalinity measurements. The increase in both C:N and C:P in all tanks could be attributable to the excretion of substantial quantities of organic acids from the cells. Furthermore, the high buffer capacity at low pH values and the lack of a clear peak in the pH titration curve obtained from alkalinity measurements during this study are both compatible with substantial concentrations of several organic acids, if these include some with low pK_a values. The H^+ from these acids would lower pH at any given DIC concentration, and thus increase light period duration under pH-controlled light. The lower pH would also increase DIC availability under either light regime by increasing the proportion of DIC that was present as CO_2. Although this increased availability would be beneficial under conditions of CO_2

limitation, excretion of organic acid was not listed as a CO_2-concentrating mechanism in any of the reviewed literature, perhaps because the carbon cost would typically outweigh the immediate benefit (Tolbert et al., 1985).

Although the above mechanism might be counterproductive in most natural settings, the components of such a mechanism have been observed. The capacity for substantial organic acid/anion excretion by algae is well documented (Chang and Tolbert, 1970; Hosmani et al., 1999), although the form of the compound excreted is often not determined. Organic acid metabolism plays an important role in regulating other metabolic processes, including the maintenance of intracellular pH. Thus, processes that increase intracellular pH, such as photoassimilation of HCO_3^-, can produce compensating reactions that increase organic acid content (Sakano et al., 1998; Foyer et al., 2000). Such compensation for the OH^- produced during HCO_3^- assimilation could have become important during the portions of the light periods in which HCO_3^- was the predominant form of DIC in the microcosms.

Because biological membranes are typically much less permeable to the organic anion than to the organic acid, diffusion out of the cell favors the acid. Dissociation of the excreted acid then occurs outside the cell until equilibrium with the extracellular medium is attained. Such equilibration of undissociated propionic and acetic acid has been demonstrated for blue-green algae and *Chlorella*, with acetic acid equilibration occurring within 25 s (Raven, 1984). In particular, glycolic acid excretion can account for 35–40% of the C fixed during periods of high CO_2 fixation. The dynamics of glycolic acid excretion by *Ankistrodesmus* and *Scenedesmus* have been linked to the cell cycle, with high excretion and low uptake during rapid cell growth followed by low excretion and high uptake preceding and during cell division (Chang and Tolbert, 1970; Sakevich and Bespalko, 1994). Thus, the loss of C with the organic acid during the light period is compensated both by the increased CO_2 fixation during the light period and by the reacquisition of the organic acid during the dark period (or otherwise during periods in which metabolic processes are dedicated to cell division).

Organic acid excretion might have increased with light duration in treatment tanks. As the duration of the light period increased and predominance of HCO_3^- became increasingly common, organic acid production could have increased to compensate for the increased HCO_3^- photoassimilation. Excretion of this acid would further increase the duration of the light period, resulting in an autocatalytic cycle promoting overall net carbon fixation, as expected in a power maximization process in which a previously inaccessible energy source is tapped.

4.3. Other possible selective advantages of acid excretion

Coprecipitation of P within a $CaCO_3$ lattice (Woodruff et al., 1999) could have contributed to the observed P limitation and to the benefits derived from H^+ or organic acid excretion. The excretion of chelating and solubilizing agents, including organic acids, by blue-green algae can increase P availability in the presence of Ca-associated precipitates (Mandal et al., 1992). When P is more limiting than C, the benefit derived from increased P availability could outweigh the cost of organic acid excretion. Such a mechanism might have contributed to the higher blue-green algal importance in tanks with longer light periods and to the negative relation between alkalinity change and change in blue-green algal importance (Table 2), thus further reinforcing the power-increasing pH dynamics. The increased light resulting from such a mechanism under pH-controlled light would have intensified the competition for CO_2 and P, providing greater selective advantage to the blue-green algae that utilized these mechanisms under pH-controlled light than under fixed photoperiods.

Attaining greater CO_2- and P-assimilation rates through excretion of organic acids or H^+ would be costly for the individual organisms employing such mechanisms, and some of the derived benefit would also be exploitable by other phototrophs without such a mechanism. If other phototrophs received, on average, equal benefit from the acidification, natural selection operating among the individual organisms under such highly competitive conditions would tend to reduce the populations of acidifying organisms, and thus suppress the acidification and its accompanying increase in light duration. Most algae alter their immediate environment by producing mucilage (Boney, 1981; Gibson and Smith, 1982), however, and thus the benefits of acid excretion could be more pronounced for the organisms

closest to the acid excretion. Blue-green algal mucilage can contribute to the localization of the effects of acidification not only by serving as a flocculating agent (Choi et al., 1998), but also by providing microhabitats with decreased diffusion rates and microsites for precipitation (Arp et al., 1999).

Increases in CO_2 concentration due to acidification within a mucilaginous environment would be especially pronounced near the acidifying organisms, as would the dissolved P concentrations in the case of P coprecipitation at high pH. Thus, increased photosynthesis would be expected primarily for these acidifying organisms and for other phototrophs in close proximity to them. The increased light duration would benefit all phototrophs within the tank that had sufficient nutrients for continued photosynthesis. Given CO_2 and P limitations, however, the increased CO_2 and P near the acidifying organisms could allow all nearby organisms to benefit to a greater extent, on average, from increased light than similar organisms that were not located in a mucilage-aggregated biotic assemblage possessing the acidifying organisms.

Mucilage-aggregated assemblages with some organisms that perform a community-wide enhancement of production would meet the requirements for groups acting as units subject to natural selection (Wilson, 1980; Sober and Wilson, 1998; Gould and Lloyd, 1999). As the aggregates broke apart due to the continuous stirring and intermittent disturbances within the tanks, they would re-form in association with other precipitate and detritus particles. Thus, the organisms and groups associated with these aggregates would obtain fresh supplies of otherwise limiting nutrients that would not be readily utilizable by those groups with few or no acidifying organisms. The proportion of acidifying organisms would be expected to increase as P and CO_2 limitations became more critical with increased light duration and biomass concentration and as a new balance between individual and group selection was established. The energy flow through these organisms would in turn be selectively reinforced due to their greater capacity for using the additional available energy to diminish the existing constraints imposed by the CO_2 and P limitations. Selective persistence of acidifying organisms would thus result from selective reinforcement of autocatalytic cycles of energy flow established through the positive feedback between acidifying metabolic processes and light energy influx and acquisition.

Wilson (1997) proposed a similar mechanism by which group selection among microecosystems associated with organic-matter aggregates could affect the functional organization of energy flow through open-water ecosystems. He reasoned that open-water ecosystems could contain billions of these microecosystems, which would vary in their productivity based on their taxonomic and genetic composition. If more productive microecosystems also contribute more organisms to the colonization of new aggregates, such an advantage would provide a mechanism for the selective persistence of microecosystems with nutrient cycles and energy flows organized in a productivity-maximizing manner.

Organic acid or H^+ excretion thus could be an important mechanism by which pH was lowered under both light regimes and available energy influx increased under pH-controlled light. The evidence for organic acid excretion under both light regimes suggests that increased light input was not the only basis for the organic acid excretion. Selective benefit from acid excretion within mucilage-aggregated assemblages under CO_2 and/or P limitation can indeed account for such excretion and for an associated pH decline under both light regimes. With increased light input under pH-control, however, acid-excreting organisms could multiply more rapidly, thus further decreasing pH. Thus, the selective benefit of the increased light obtained under pH-control could have contributed to the trend towards power-maximizing pH dynamics being more pronounced in tanks with pH-controlled light than in those receiving fixed photoperiods.

5. Conclusions

Four implications can be derived from the results of this study, based on the evidence of selective reinforcement of power-increasing ecosystem designs, of high variability in pH dynamics among similarly maintained microcosms, of systematic alkalinity decline associated with ecosystem development, and of P and CO_2 limitations to algal productivity. First, the evidence for selective reinforcement of power-maximizing ecosystem designs within the microcosms was strong enough to recommend additional testing using the methods

employed in this study. It was not strong enough to warrant a repetition of the tests, however, without modification. More specifically, the tests provide evidence of variability with respect to pH dynamics that renders detection of moderate selection pressure acting on this property highly improbable unless the number of microcosms is increased by a factor of 10 or more. Third, the systematic alkalinity decline during the tests, irrespective of whether energy influx to the ecosystems was affected by pH (or alkalinity), reduced the likelihood of detection of selective reinforcement or persistence of power-maximizing designs. Alleviation of this systematic decline might reduce the number of tested microcosms required in future experiments. Finally, the relationship among blue-green algal importance, alkalinity, and final daily light duration along with the evidence for P and CO_2 limitation of algal productivity suggest a mechanism for selective reinforcement of power-enhancing designs based on competition among mucilage-aggregated microecosystems within the microcosms. Elucidating that mechanism can serve as a basis for future research.

The method is also applicable to a more general study of the interaction of ecosystem energetics with natural selection. Empirical investigation of the interaction of these fundamental determinants of the structure and function of biological systems has seldom been attempted at the ecosystem level, yet the importance of natural selection and of autocatalytic energy flow in determining the traits and organization of biological systems is seldom disputed. Thus, the specific connections between ecosystem characteristics and their fundamental determinants remain largely unidentified. The potential for examining the efficacy of principles such as power maximization and natural selection in the process of ecosystem development is thus ample justification for expanded investigation of ecosystem theory using computer-mediated couplings of ecosystem processes and forcing functions.

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