SimBio Virtual Labs®

EcoBeaker®: Liebig's Barrel and Limiting Nutrients

NOTE TO STUDENTS:

This workbook accompanies the **SimBio Virtual Labs® Liebig's Barrel and Limiting Nutrients** laboratory. *Only registered subscribers are authorized to use this material.* Laboratory subscriptions may not be shared or transferred.

Student's Name: _____

Signature: _____

Date: _____

This and other SimBio Virtual Labs® are accessible through SimBio's SimUText System®.

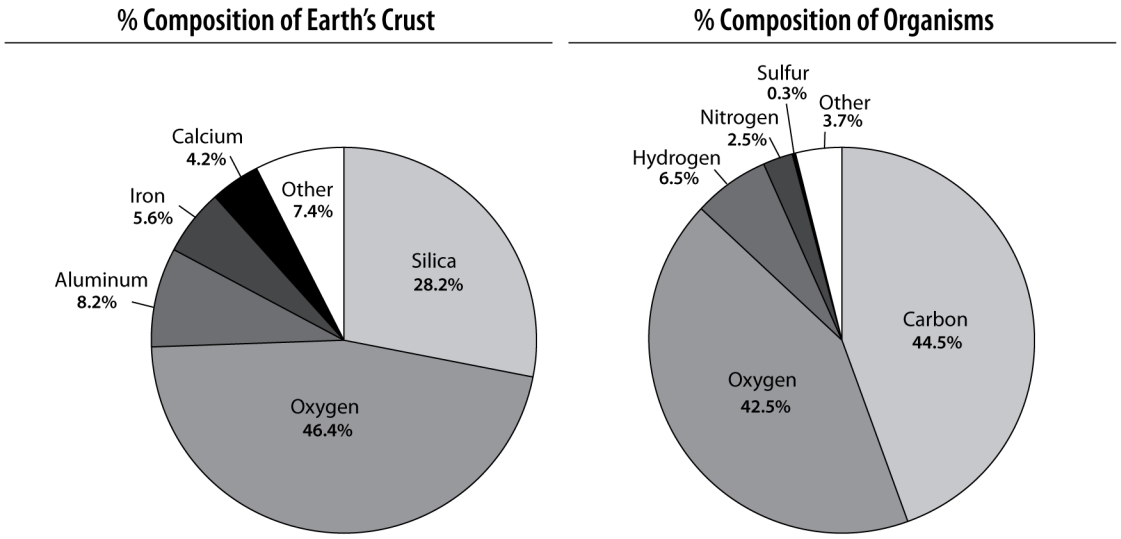
simbio VIRTUAL LABS

SimBio Virtual Labs®: EcoBeaker®

Liebig's Barrel and Limiting Nutrients

Introduction

If you examine the pie charts below, you will see that the composition of the Earth's crust is very different from the composition of the organisms that live in and on Earth. This mismatch means that part of every organism's struggle for existence is acquiring and accumulating needed elements, which sets the stage for a wide range of interesting and important ecological dynamics.



As animals, we can obtain the nutrients we need relatively easily. Directly or indirectly, all of our food comes from plants—and plants (with help from sunlight and some important bacteria) do most of the work of extracting and concentrating the elements they—and we—need to live. However, if plants don't have the nutrients they need, then we won't have the nutrients we need. Understanding nutrient dynamics is important both because they impact us directly and because it helps us understand how communities and ecosystems function. Furthermore, our activities have a tendency to alter nutrient dynamics, often with dramatic results.

We know, for example, that human activities are increasing nitrogen availability in many communities. Could increasing nitrogen affect competitive interactions among plant species in terrestrial and aquatic communities? Could overall productivity change and, if so, could that affect

the animals in the community? Could species composition within the community change? If so, could the community become more susceptible to invasion by exotic species? These are just some of the questions ecologists are currently addressing through field studies, laboratory experiments, mathematical modeling, and other approaches.

In this lab, you will conduct simulated experiments to explore how nutrients can limit population growth and affect competitive interactions among species.

The Nutrient Limitation Model in SimBio Virtual Labs®

This lab uses a simulated chemostat (a device biologists commonly use to grow microorganisms) to explore how changing nutrient levels can affect population growth of individual species of phytoplankton, as well examine as their interactions—especially competition—with other species in aquatic communities. The simulated chemostat consists of a growth chamber, an inflow tube that delivers water and nutrients, and an outflow tube that removes fluid from the growth chamber. The inflow and outflow rates are the same, so the volume of the growth chamber is constant. The investigator can control the delivery rate of nutrients; this, in combination with the volume of the growth chamber, establishes the carrying capacity of the system for the organisms under study. The default nutrient concentration settings for the chemostat approximate those one might find in a North American lake.

Your study system includes three types of phytoplankton: green algae, cyanobacteria (also known as blue-green algae), and diatoms. You will be able to manipulate the simulated chemostat to grow each type individually or in any combination. Three key nutrients—nitrogen, phosphorus, and silica—are added via the inflow tube. You will be able to control these rates. As you conduct your experiments, you will be able to track both population growth and changes in the concentration of each nutrient in the growth chamber over time.

The simulation model works as follows. Each type of phytoplankton has a maximum rate at which it can take up each nutrient it requires. The actual rate at which an individual organism takes up nutrients depends on the concentration of the nutrient in the chemostat. The uptake rates decrease as concentrations decrease. (If you've taken a chemistry class, uptake follows Michaelus-Menton kinetics.) Phytoplankton also photosynthesize to fix carbon and grow, and their growth rate is limited by whichever nutrient is in shortest supply. When an individual grows large enough, it splits in half to reproduce. Individuals constantly use up nutrients via metabolism. If an individual does not grow fast enough to keep up with its metabolism, it will die. There is also a low rate of random death.

Exercise 1: Growing Phytoplankton

Phytoplankton are critical to life on Earth, producing much of the oxygen in the Earth's atmosphere and oceans, and serving as the "base" of aquatic food webs. However, when individual populations of phytoplankton grow too large, serious problems such as toxic shellfish poisoning and massive fish kills can result. Anthropogenic increases in nutrients, especially nitrogen and phosphorus, can contribute to phytoplankton population growth in many aquatic systems. Determining whether adding nutrients to a particular system will adversely impact phytoplankton population sizes requires understanding the nutrient requirements of the organisms involved.

This exercise introduces the populations of organisms in your experimental system and explores their requirements for growth.

[1] If you haven't already, start **SimUText®** by double-clicking the program icon on your computer or by selecting it from the Start menu. When the program opens, enter your Log In information and select the **Liebig's Barrel and Limiting Nutrients** lab from your **My Assignments** window.

You will see a number of different panels on the screen; these will be described as they are needed for the exercises in the lab.

[2] The top menu bar has a drop-down menu from which you will select individual exercises as you proceed through the lab. Be sure that **Growing Phytoplankton** is selected.

[3] Click on the names of each species in the **Organisms** panel to bring up library pages for each group of phytoplankton. Use the library to complete the following questions:

[3.1] Which group of phytoplankton includes species that are capable of fixing nitrogen?

★ *NOTE: Nitrogen fixation does not occur in any organisms modeled in this lab.*

[3.2] Which group of phytoplankton is found in the fur of sloths and contributes to their camouflage?

[3.3] Which group of phytoplankton requires silica and why?

[4] The **Nutrient Input Rates** panel lets you adjust the rate at which nutrients are added to the chemostat. Without changing the default settings, click the **GO** button in the **Control Panel** at the bottom of the screen and examine the data output in the **Nutrient Levels Over Time** panel on the right side of the screen. With these settings, you will only see one line on the graph (plotted at 1.0). There are actually three lines, but they overlap due to the scaling used to produce the nutrient concentration index that is being plotted. The concentrations are scaled relative to the initial input levels. If you set different values in the **Nutrient Input Rates** panel and continue to run the simulation, you will see that scaled data for all three nutrients are actually being plotted.

[5] While running the simulation, try doubling the **Nutrient Input Rate** settings for one nutrient at a time (being sure to click the **SET** button), and watch how the changes are reflected in the Nutrient Levels graph.

★ *NOTE: A scaled concentration index is graphed rather than the actual concentration values displayed to the left of the graph because the three nutrients in the chemostat often occur in widely divergent concentrations. Scaling in this way lets you visualize how they change relative to each other over time on the same graph.*

[6] Next try growing some phytoplankton in the chemostat. First click the **RESET TO DEFAULTS** button in the **Nutrient Input Rate** panel to bring back the initial nutrient input rates.

[7] Click the **RESET** button in the **Control Panel** to start a fresh experiment.

[7.1] Before you run the simulation, fill in the Input Rate and Initial Nutrient Concentration columns in the table below:

DATA TABLE 1:

NUTRIENT	INPUT RATE (UG/HOUR)	INITIAL NUTRIENT CONCENTRATION (UG/L)	FINAL NUTRIENT CONCENTRATION (UG/L)
Nitrogen			
Phosphorus			
Silicon			

[8] Under **Tools**, find the button with the elongated green cell and the plus sign in the upper left corner. This is the **ADD GREEN ALGAE** button; click to select it. You can now add green algae individually by clicking inside your virtual chemostat—the large panel in the upper left—or you can add several at once by clicking in the chemostat and dragging out a box (a number will pop up indicating how many individuals are in the box). Add 10-20 starter algae to the chemostat.

[9] Click the **STEP 100** button (next to the **GO** button) to run the simulation for 100 virtual hours, and watch the action. The **Time Elapsed** display should register 100 hours.

[9.1] Record the final nutrient concentrations in Data Table 1 above.

[9.2] The green algae population initially grows, but then stabilizes (i.e., randomly fluctuates around an equilibrium value). According to the top graph on the screen, at about what size does the green algae population stabilize? (Don't worry about being exact; just approximate based on the graph.)

★ *NOTE: In a real 100 mL chemostat, there would be millions of algae, but that would make this simulation run much too slowly. You can think of each individual as representing many more algae in real life.*

[10] Nutrients are constantly being added to the chemostat, but they are also being removed as they are used by the algae to grow and reproduce. If nutrient availability is restricting growth of the algae population, then the algae population size should increase if the nutrient input rates are increased. **Without resetting the simulation**, double the nutrient input rates for all of the nutrients and click the **SET** button. Click the **STEP 100** button to advance the simulation another 100 hours. When the simulation stops, **Time Elapsed** should be 200 hours.

★ *NOTE: You can speed up or slow down the simulation using* **Speed Slider** *to the right of the* **Control Panel** *buttons.*

[10.1] What is the evidence that nutrient availability was restricting algal population growth?

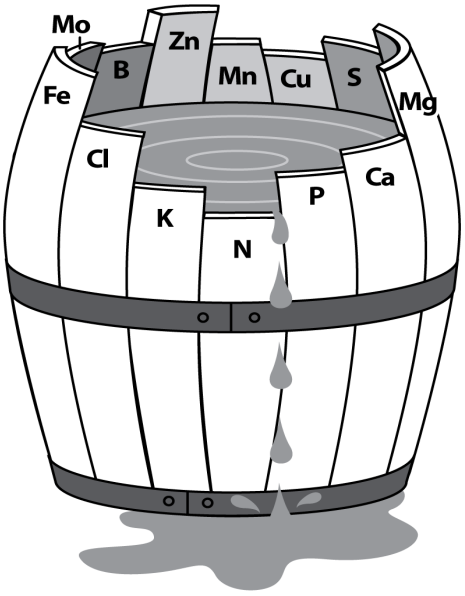
[11] **Without resetting the simulation**, examine the **Nutrient Levels Over Time** graph and look for relationships between this graph and the **Population Sizes Over Time** graph. Then compare the nutrient concentration values on screen to the final nutrient concentration values (@ 100 hours) in **Data Table 1**.

[11.1] One of the three nutrients was limiting the growth of algae under default conditions in your chemostat. Based on patterns in the graphs and in your data, which do you think it is, and why?

[12] Click the **TEST YOUR UNDERSTANDING** button in the bottom right corner of the screen and answer the question in the window that pops up.

Exercise 2: The Law of Liebig

In 1816, crops throughout Northern Europe, the Northeastern U.S. and Canada were destroyed by an unusual series of climatic events. Justus von Liebig was a young teenager in Germany at this time, and living through the global famine is said to have inspired his later work as a chemist: he pioneered the study of plant nutrition and innovated the use of chemical fertilizers in agriculture. Liebig's work helped popularize an important concept in ecology—*that population growth will not be limited by the total amount of resources available, but by the scarcest one*. This idea is referred to as Liebig's **Law of the Minimum**, which is visualized by "Liebig's barrel", depicted below.



Liebig's "Law of the Minimum" is illustrated with the metaphor of Liebig's Barrel—a barrel with staves of varying lengths. Regardless of the capacity of the barrel, it can only hold as much water as allowed by the shortest of its staves. Liebig's Barrel has been used in agriculture to illustrate that if one nutrient is missing or deficient, plant growth will be poor, regardless of the availability of other nutrients, and that if the shortest stave is lengthened sufficiently, then another one will become the *"limiting nutrient"*.

Liebig's research on limiting nutrients in plants applies directly to your study system. In the last exercise, you used chemostat experiments to investigate how nutrient input rates influenced population growth of green algae. *If you concluded that phosphorus was the limiting nutrient for green algae, you were correct!* In this exercise, you will confirm that phosphorus was the limiting nutrient for green algae, and you will explore some intricacies of nutrient limitation in various types of phytoplankton.

[1] Select the **Liebig's Law** exercise from the menu at the top of the screen.

[2] As before, add some starter green algae to the chemostat using the **ADD GREEN ALGAE** button. Make sure that the default nutrient input levels are set and use the **STEP 100** button to run the simulation for 100 virtual hours.

[2.1] Record the green algae population size and nutrient concentrations in the top row of Data Table 2 below. These are your baseline data.

DATA TABLE 2. RESULTS OF NUTRIENT ADDITION EXPERIMENTS

	GREEN ALGAE				CYANOBACTERIA				DIATOMS			
NUTRIENT INPUT RATE	**POP SIZE**	**N (UG/L)**	**P (UG/L)**	**SI (UG/L)**	**POP SIZE**	**N (UG/L)**	**P (UG/L)**	**SI (UG/L)**	**POP SIZE**	**N (UG/L)**	**P (UG/L)**	**SI (UG/L)**
Baseline (1x all)												
2x N												
2x P												
2x Si												

[3] **RESET** the simulation to empty the chemostat and then double the nitrogen input rate. Add some starter green algae and **RUN** the simulation for 100 hours.

[3.1] Record the green algae population size and nutrient concentrations in the second (2x N) row of your data table.

[4] **RESET** the simulation and the default nutrient input rates. Then double the phosphorus input rate. Add some starter green algae and **RUN** the simulation for 100 hours.

[4.1] Record the green algae population size and nutrient concentrations in the third (2x P) row of your data table.

[5] Again, **RESET** both the simulation and the default nutrient input rates. Then double the silicon input rate. Add some starter green algae and **RUN** the simulation for 100 hours.

[5.1] Record the green algae population size and nutrient concentrations in the fourth (2x Si) row of your data table.

[5.2] Based on your results, how do you know that phosphorus was the limiting nutrient in the chemostat, and not nitrogen or silicon?

[5.3] What do you predict would happen to the green algae population size in the chemostat over time if you were to *quadruple* the default input rate of phosphorus? Be as quantitative as possible—approximately how large do you predict the green algae population would grow? Explain your reasoning.

[6] Conduct the experiment. **RESET** the simulation and the default nutrient input rates. Quadruple the default phosphorus input rate and **ADD GREEN ALGAE** to the chemostat. **RUN** the simulation until the green algae population stops growing.

[6.1] Did you predict correctly? What happened?

[7] To help see why your results might not have matched your predictions, try a different version of the experiment. **RESET** the simulation and the default nutrient input rates. Then double the phosphorus input rate, add some green algae, and **RUN** the simulation for 100 hours. Then, *without resetting the simulation*, double the phosphorus input rate *again* (so it is four times the default rate) and **RUN** the simulation for another 100 hours. Examine the graphs, which should now show 200 hours of data.

[7.1] Describe what happened to the concentrations of phosphorus, nitrogen, and silicon in the chemostat during hours 100–200 (after you increased the phosphorus input from 2x to 4x the default rate).

[7.2] Now look at the data you recorded in Data Table 2. When you doubled the input rate of phosphorus, did either of the other two nutrients show a fairly dramatic response? Describe.

[8] If the input rate of a limiting nutrient in a system is increased sufficiently, a different nutrient may limit population growth. In the Liebig's barrel metaphor, this would be analogous to increasing the height of the shortest stave so that it is taller than the next-shortest stave. **A nutrient that**

becomes limiting when a species' primary limiting nutrient is increased is called a *secondarily limiting nutrient*.

[8.1] Between the 2x and 4x phosphorus input rates, another nutrient becomes limiting for green algae. Explain which nutrient you think is secondarily limiting, and why.

[8.2] Rewrite your explanation in the form of a testable hypothesis.

[8.3] Briefly describe an experiment you can conduct to test one prediction of your hypothesis (including the predicted outcome).

[9] Conduct the experiment and record your results below.

[9.1] Experimental Data:

[9.2] Was your hypothesis supported by your experiment? Explain.

[10] Repeat steps 2-5 for cyanobacteria and for diatoms. (The **ADD CYANOBACTERIA** and **ADD DIATOMS** buttons are to the right of the **ADD GREEN ALGAE** button.) Remember to double the nutrient input rates *one at a time*, leaving the other two nutrients at their default rates.

[10.1] Complete Data Table 2 with your results for cyanobacteria and diatoms.

[10.2] What is the limiting nutrient for cyanobacteria, and how do you know this?

[10.3] Can you find any evidence in your data that cyanobacteria has a secondarily limiting nutrient? If so, which nutrient do you predict is secondarily limiting? Justify your prediction.

★ *HINT: Examine the row of data you recorded after doubling the primary limiting nutrient.*

[10.4] What is the limiting nutrient for diatoms, and how do you know this?

[10.5] Do you predict that the diatom population has a secondarily limiting nutrient? If so, which one? Justify your prediction.

[11] (Optional) Test your predictions!

[11.1] Were you right?

[12] Click the **TEST YOUR UNDERSTANDING** button and answer the pop-up question.

Exercise 3: Food Fight!

So far, your experiments have shown that the nutrient that is most scarce for a species will limit its population growth and that different species use nutrients differently. What would happen if you were to grow different species of phytoplankton together in a chemostat, forcing them to compete for nutrients? Could you use your single-species data to predict whether species would coexist or compete? If they competed, could you predict which species would outcompete the other?

In the mid-1970s, David Tilman was a graduate student at the University of Michigan. Tilman reasoned that if he could develop a strong mechanistic model of competition for nutrients—which he called **resource competition**—then information gathered by plant physiologists could be used to predict the outcome of competition among plant species under various conditions of nutrient availability. In developing his model, Tilman studied phytoplankton using a real system similar to your simulated chemostat.

The resource competition model resulting from Tilman's early work on phytoplankton is conceptually straightforward: *given two species competing for the same limiting resource, the species able to survive and reproduce at the lowest concentration of that resource will take over.* In this exercise, you will use your experimental setup to determine whether Tilman's model lets you correctly predict the outcome of competition between species that are competing for the same limiting resource.

[1] Select **Food Fight!** from the drop-down menu of exercises.

[2] **ADD CYANOBACTERIA** to the chemostat and **RUN** the simulation for 100 virtual hours. Notice that the bottom graph now displays phosphorus concentration over time. This experiment focuses on phosphorus, because it is the limiting nutrient for cyanobacteria (and green algae) under the default conditions in your chemostat.

[3] Tilman's model uses the variable **R*** to indicate the lowest concentration of a limiting resource that is required for a population to persist. You can estimate R* for phosphorus from your graphs by finding the concentration of phosphorus at which the cyanobacteria population stops growing over time. Note that the cyanobacteria population fluctuates around a central (equilibrium) value—use the equilibrium value, not an extreme high or low.

[3.1] What is the approximate R* concentration of phosphorus for cyanobacteria?

★ *NOTE: Click on the line on the graph and drag your mouse back and forth to read out the values being plotted.*

[4] **Without resetting the simulation**, examine the values you recorded in **Data Table 2**. You should see that the number you just recorded is in the same ballpark as the phosphorus concentration you recorded under baseline (default) conditions for cyanobacteria.

[4.1] Based on the data you recorded in Data Table 2, what is the R* concentration of phosphorus *for green algae*?

★ *NOTE: DO NOT RESET YOUR SIMULATION TO ANSWER THIS QUESTION—the answer is in Data Table 2!*

[4.2] According to Tilman's resource competition model, if you add some green algae to the chemostat with cyanobacteria, what should happen, and why?

[5] **ADD GREEN ALGAE** to the chemostat with cyanobacteria and **RUN** the simulation for several hundred hours to test your prediction. (If you already reset the simulation, first repeat step #2.)

[5.1] Did you predict correctly? Did the species with the lower R* concentration of phosphorus (the limiting nutrient for both cyanobacteria and green algae) take over?

[5.2] According to Tilman's resource competition model, what do you think would happen if you were to grow green algae, cyanobacteria, and diatoms together in the chemostat (using the default nutrient input rates)?

[6] **RESET** the simulation and **ADD GREEN ALGAE**, **ADD CYANOBACTERIA**, and **ADD DIATOMS** to the chemostat. **RUN** the simulation *for at least 200 hours* to test your prediction.

[6.1] Did you predict correctly? Explain your results in terms of limiting nutrients and Tilman's resource competition model.

★ *HINT: Do all three species share the same limiting nutrient under the conditions in the chemostat?*

[7] Click the **TEST YOUR UNDERSTANDING** button and answer the pop-up question.

Exercise 4: The Plankton Paradox

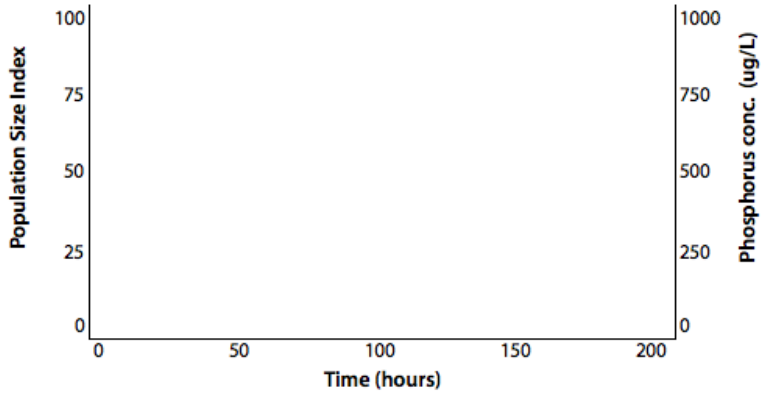
In the real world, aquatic systems often support huge diversities of plankton, many of which share similar nutrient requirements. Based on the experiments you've conducted, this probably doesn't make a lot of sense. Nutrient limitation should lead to competition, which should result in particular species dominating. This conundrum has long intrigued aquatic biologists, who refer to the situation as the "paradox of the plankton". One explanation is that real aquatic environments are not constant over time. Unlike the predictable world inside a chemostat, in real systems, resource inputs and outputs fluctuate over time. Because organisms are adapted to handle different environmental conditions differently, changes in the environment can alter their competitive interactions.

In the previous exercise, you (hopefully) found that R* can be used to predict the outcome of competitive interactions between species. R* reflects the concentration of a population's limiting nutrient at which its population size remains constant. When the concentration of a population's limiting nutrient is above or below R*, how rapidly it grows or shrinks depends on how the species is adapted. Life is a game of adaptive trade-offs; a species that has evolved to be exceptionally efficient at taking up nutrients when they are at high concentrations, may be relatively inefficient at taking up nutrients when they are at low concentrations. This exercise explores how the combination of adaptive trade-offs and variation in the environment can alter the dynamics of species competing for limiting nutrients.

[1] Select **Plankton Paradox** from the drop-down list of exercises.

[2] As before, **ADD GREEN ALGAE** and **ADD CYANOBACTERIA** to the chemostat and use the **STEP 100** button twice to **RUN** the simulation 200 hours.

[2.1] Using the axes below, draw a combined graph of the phytoplankton population sizes and phosphorus concentration over time, labeling your lines. [Note the phosphorus concentration scale on the right side of the plot.]



[3] In the simulation, efficiency at taking up nutrients influences how much energy is available for reproduction.

[3.1] Based on your graph, what is the apparent trade-off for being efficient at taking up nutrients when the phosphorus concentration is high?

[4] Higher reproductive rates produce higher population growth rates, but as long as the death rate exceeds the reproduction rate, a population will shrink. Under default conditions, the death rate in the chemostat is fairly low; on average, only 5% of all phytoplankton die from one hour to the next. One way to determine whether the competitive relationships of green algae and cyanobacteria might change under different environmental conditions is to change the death rate.

Locate the slider that controls **Death Rate** and move the slider, noting the range of death rates available for you to manipulate—the lowest is 0.05, the default level for the other experiments.

[4.1] If the death rate is increased (for all organisms), can you think of any reason why the outcome of growing green algae and cyanobacteria together might change? (Take a stab at answering this; it isn't obvious!)

[5] To see if the outcome changes, **RESET** the simulation and set the death rate to 0.15 using the slider. **ADD GREEN ALGAE** (at least 30) and **ADD CYANOBACTERIA** (at least 30) to the chemostat and **RUN** the simulation. (You need more starter individuals than before, because when populations are small, the combination of a high death rate and random variation in the simulation can lead to chance extinction.) Repeat the experiment a few times to make sure the results are consistent.

[5.1] Briefly describe what happened.

[5.2] **At the higher death rate, do differences in R* explain what happens? If not, what explains the outcome of your experiment?**

★ *HINT: To answer this, you need to determine R* for each species at the higher death rate.*

[5.3] **Consider how cyanobacteria and green algae differ in terms of the tradeoff you identified in question 3.1. At very high death rates, cyanobacteria are at an advantage over green algae. Explain why, in terms of the trade-off you identified.**

[5.4] **What do you predict should happen at an intermediate death rate (e.g., 0.10)?**

[6] Test your prediction. **RUN** the simulation several times (at least 5) for 100 hours at an intermediate death rate, each time initiating the population with at least 30 individuals of each type of phytoplankton.

[6.1] **Did you predict correctly? What happened?**

[7] In natural freshwater lakes and ponds, nutrient input levels and other environmental factors (including ones that kill phytoplankton) often vary seasonally. In temperate climates, for example, nutrients are delivered with runoff associated with spring snowmelt, summer rains, etc., and populations of predators on phytoplankton may grow larger from spring to summer.

[7.1] Using your results from exercises three and four, describe what you might expect to find if you sampled a lake for phytoplankton species. Would there be just one dominant species or many different species? Explain.

[8] Click the **TEST YOUR UNDERSTANDING** button and answer the pop-up question.

Exercise 5: A Barrel of Experiments (Extension)

So far, you've explored the concepts of nutrient limitation, resource-based competition, and the effects of disturbance on competitive interactions. With your new expertise, you're ready to explore extensions of these concepts on your own. You may be assigned one or more of these exercises by your instructor.

[1] **From Coexistence to Competition**

Cyanobacteria and diatoms coexist under default conditions in the chemostat. Under what conditions are cyanobacteria likely to outcompete diatoms? Under what conditions might diatoms outcompete cyanobacteria? Develop and write your hypotheses, predictions, experimental protocols, results, and conclusions.

[2] **Got a Pulse?**

In the chemostat, green algae outcompete cyanobacteria at low death rates and default nutrient input levels. Many real-world freshwater systems, such as lakes and reservoirs, receive periodic short bursts of nutrients. Under what kinds of nutrient pulse conditions might green algae and cyanobacteria coexist? Develop and write your hypotheses, predictions, experimental protocols, results, and conclusions.

★ *NOTE: You can "pulse" nutrients by running the simulation for a while, stopping it, increasing nutrient input levels and running it for a short period, then returning input levels to their default and continuing.*

[3] **Multi-Species Coexistence**

Under what conditions can all 3 species coexist? Develop and write your hypotheses, predictions, experimental protocols, results, and conclusions. Your goal is to achieve coexistence for at least 100 hours.

★ *NOTE: Because of the stochasticity (random variability) inherent in the simulation model, if you can achieve coexistence in 3 out of 5 runs, you're doing great!*

With three species coexisting (using the conditions you established above), what would happen if a large pulse of nutrients were added? (See #2 above for how to simulate this.) Develop and write your hypotheses, predictions, protocols, results, and conclusions.

[4] **Nutrient Co-limitation**

A species can have "colimiting nutrients" if two nutrients equally limit population growth. In such a system, *both* nutrients would have to be increased to significantly increase population growth. Create conditions in the chemostat in which you can experimentally demonstrate that a cyanobacteria population is colimited by two nutrients and not just one. Describe your logic, justify your experimental procedure, and explain how your data support that you have successfully created conditions of colimitation of nutrients for cyanobacteria.

Graded Questions

[1] Use the **SELECT AN EXERCISE** menu to launch "**Graded Questions"**.

[2] Enter your answers for each of the questions and click the **SUBMIT ALL** button. **NOTE**: You must answer all of the questions before you click the **SUBMIT ALL** button.

Wrap-up

Nutrient Limitation in Phytoplankton Communities

As the field of ecosystem ecology blossomed in the 1960s, a growing number of ecologists used phytoplankton communities to try and understand how nutrients affect ecosystems. These ecologists conducted a wide range of studies, some even involving manipulating whole lakes to see what happened when nutrient inputs were changed.

As you have seen, although all phytoplankton need the same kinds of nutrients, each phytoplankton species has unique nutrient demands. Within an algal cell, nutrients are not used independently of one another. Consider nitrogen and phosphorus. Nitrogen and phosphorus are both major components of nucleic acids and proteins. Because these nutrients are used together, they must be acquired in the proper ratios, with those ratios varying among species. So when we consider the nutrients available to a species, we need to consider both absolute amounts of nutrients and the ratios in which they are found. In general, the ratios of nitrogen:phosphorus and, for some species, nitrogen:phosphorus:silica play a major role in determining which species will be present in a given phytoplankton community.

Natural selection has resulted in each species having its own set of adaptations for acquiring the necessary nutrients from the environment. Nutrient acquisition requires energy, and adaptive tradeoffs between nutrient uptake efficiency and reproduction are common. An energetically expensive mechanism for acquiring scarce resources could allow individuals to thrive in a nutrient-limited environment, for example, but could also limit reproduction. What would happen if nutrient levels increased and the habitat were invaded by a species adapted for easy (and energetically inexpensive) uptake of abundant nutrients? If the new species used its energy savings for reproduction, the first species could be outcompeted and replaced.

These sorts of trade-offs occur in many complex ways, even with the types of unicellular organisms you experimented with in this lab. The simulation here modeled cyanobacteria as growing faster than green algae at high phosphorus concentrations, for instance. This happens at low light levels, but the reverse is true at higher light levels. Since large algae blooms will block light to the water underneath, algal blooms tend to favor cyanobacteria over green algae, while open lakes with low nutrient levels favor green algae because of their more efficient uptake of nutrients at low nutrient concentrations. Thus, nutrient levels can impact algal competition both directly, through the R* mechanism you explored in this lab, and indirectly through changing conditions in the lake.

This brings up another important point—namely, that nutrient levels do fluctuate in aquatic habitats. Nutrients are delivered in a number of ways, but consider just one: runoff from surrounding soils and

surfaces. The amount of runoff varies seasonally according to the climate, and the nutrients present in the runoff can change with changes in the terrestrial systems from which the runoff originates. Ratios of nitrogen, phosphorus, and silica will necessarily fluctuate over both short and long terms. Under natural conditions, therefore, phytoplankton communities undergo successional changes that are often quite predictable in space and time.

Anthropogenic Changes in Nutrient Inputs

Human activities are currently changing nutrient inputs to our lakes, rivers, and estuaries dramatically. The fertilizers used in agriculture add phosphate and nitrogen, and use of fertilizers has increased up to eight-fold since the 1960s. Burning fossil fuels increases the levels of nitrogen in the atmosphere, and some industries also release phosphorus into the air. Both of these can settle out into lakes and rivers. The result of these and other changes has been significant nutrient enrichment and changes in nutrient ratios in both freshwater and marine systems.

One of the many consequences of these changes is an increase in the number and extent of harmful algal blooms (HAB)—population explosions of algal species that harm other species. In general, HABs cause harm in one of two ways. First, the species involved can themselves be toxic and lead to deaths of marine organisms, ranging from filter feeding invertebrates to marine birds and mammals. These blooms are often called "red tides" and are generally caused by a group of algae known as dinoflagellates. Second, the phytoplankton themselves may not be toxic, but can affect their habitat and communities simply by their dramatic increase in biomass. When such blooms are at their peak, for example, they may shade submerged aquatic vegetation. As the algae die, decomposition removes oxygen from the water; anoxia can cause fish kills and other problems.

Scientists studying HABs have found that increased nutrient levels alone don't explain patterns of HABs. Instead, changes in nutrient ratios seem to play an important role. Most anthropogenic inputs are high in nitrogen and phosphorus relative to silica. How would you expect that to affect diatom communities? Dinoflagellates often require a high proportion of phosphorus relative to nitrogen; unfortunately, anthropogenic inputs often have low nitrogen:phosphorus. And nutrient inputs themselves aren't the end of the story. Imagine a dam built on a large river. The resulting reservoir is likely to contain relatively high levels of silica initially, favoring diatoms. As diatoms die, they sink, carrying their silica and other nutrients to bottom sediments. How does this affect the ratios of nitrogen, phosphorus, and silica in the estuary below the dam?

Anthropogenic nutrient inputs affect terrestrial plant communities as well. Understanding the interactions between nutrient dynamics and plant communities is critical for developing sound management strategies.

Historical Note

Although Justus von Liebig is credited with formulating the "Law of the Minimum", his countryman and colleague, Carl Sprengel, may have beaten him to the punch. As much as a decade earlier, Sprengel appears to have developed a similar formulation for the Law of the Minimum. Some scholars of science history argue that Sprengel's work should be formally recongnized by referring to the Law of the Minimum as the "Sprengel-Liebig Law of the Minimum" (van der Ploeg et al. 1999).

References

Anderson, D. M., P. M. Gilbert, and J. M. Burkholder. 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries 25(4) Part B:704-726*.

Fenn, M.E., E.B. Allen, S.B. Weiss, S. Jovan, L.H. Geiser, G.S. Tonnesen, R.F. Johnson, L.E. Rao, B.S. Gimeno, F. Yuan, T. Meixner, A. Bytnerowicz. 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *Journal of Environmental Management 91:2404-2423*.

Liebig, J. 1847. Chemistry in its application to agriculture and physiology. T. B. Peterson, Philadelphia.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology 58(2):338-348*.

Tilman, D., S.S. Kilham and P. Kilham. 1982. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics 13:349-372*.

Turner, R. E. 2002. Element ratios and aquatic food webs. *Estuaries 25(4) Part B:694-703*.

van der Ploeg, R.R., W. Böhm, and M.B. Kirkham. 1999. On the origin of the theory of mineral nutrition of plants and the law of the minimum. *Soil Science Society of America Journal 63: 1055–1062*.

