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Chapter 13

Photosynthetic Strategies and Their Consequences for Community Succession

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Introduction

This open-ended investigation involves a combination of field experiences to test predictions derived from observed successional patterns in an eastern deciduous forest. Students discuss several working hypotheses; these focus primarily on how competition for light influences the growth patterns of "pioneer" vs. "primary" forest tree species subjected to different light environments (gaps vs. forest understory). Students then predict how those differences in light would translate into differences in photosynthetic rates of both kinds of trees in gaps vs. understory. Thus, students are challenged to consider how physiological patterns at the organismal level (photosynthesis, growth rates) translate into community-level ecological patterns (forest tree species composition and species turnover during succession). To test their predictions, students measure: (1) annual shoot growth increments in trees, (2) photosynthetically active radiation with light ceptometers in a variety of forest locations, and (3) photosynthetic rates with a portable photosynthesis system (alternative methods and instrumentation are included in Appendix C). Students then statistically test their hypotheses using the student's t-test.

We use this exercise in a sophomore-level course for biology majors entitled: Ecology and Evolutionary Biology. Typically, it is a two-part lab. During the first lab period, students observe successional patterns in the forest, discuss hypotheses, and conduct light and growth measurements on saplings. The second part we structure as a sign-up time (allowing 45 minutes per student group) on a separate day, during which each group conducts their photosynthetic measurements on living trees in the field using the portable photosynthetic system (for which we have just one instrument). Class data are pooled and distributed via a course website, and students receive help with statistical analyses during a course discussion section and/or during lecture.

Student Outline

Conceptual Objectives

1. Natural disturbance regimes (tree death by windthrow, fire, etc.) produce a complex light environment, and different plant species are adapted to photosynthesize most efficiently in the different light environments created.
2. Physiological specialization to different light environments gives rise to different growth and survival responses (hence, different success, or fitness) in species adapted to gap environments vs. those adapted to understory environments.
3. The specialization of different plant species on different (light) microhabitats promotes higher species diversity in the forest through "niche differentiation" than would otherwise be the case.
4. Understand how to state null and alternative hypotheses for purposes of statistical testing, and how these are related to, but different from, the working hypotheses we seek to test.

Skills Objectives

1. Measurement of photosynthetically active radiation with light ceptometers.
2. Measurement of annual shoot growth increments in trees.
3. Measurement of photosynthetic rate with a portable photosynthesis system.
4. Hypothesis testing with Student's t-test.
5. Differences between one-tailed and two-tailed t-tests.
6. How to summarize the results of a statistical test and state conclusions from it.

Background

In a forest undergoing succession, the composition of tree species represented in the canopy changes over time. For example, in certain eastern deciduous forests that were selectively logged 50-100 years ago, Red Oak *(Quercus rubra)* and Black Cherry *(Prunus serotina)* currently represent a greater proportion of the canopy than they are likely to comprise in the future. In contrast, other species (e.g., Black maple, *Acer nigrum*, Sugar Maple, *Acer saccharum,* and American Beech, *Fagus grandifolia*) are projected to become more common in the future than they are now. The resulting projected change in species composition is known as ecological succession.

Prunus serotina is an example of a **"pioneer species"** - trees that establish on a site soon after a disturbance removes the dominant species, and grow rapidly to reproductive size. Most are shade-intolerant, at least after they reach sapling size. Many also produce large numbers of offspring and invest relatively little energy in wood, so the plant is especially susceptible to wind or other damage. As a result, many pioneers don't live very long, and so they are most characteristic of the early stages of ecological succession. Because they are shade-intolerant and often don't persist for very long as succession proceeds, we generally think of them as poor competitors for space in a mature forest.

Ecologists use the term **"primary forest species"** for plants that characterize the mature forest community long after the last disturbance. In southern Michigan, for example, *Fagus grandifolia*, *Acer nigrum*, and *Acer saccharum* are good examples. Most primary species are shade-tolerant, so their seedlings and saplings can persist for long periods in the forest understory. Consequently, they grow more slowly than pioneer species, and many don't reach reproductive size until they are many tens or even hundreds of years old, if ever. These plants also invest more of their energy in a dense wood that can withstand wind stress and insect attack, but expend less energy than pioneers on any

given bout of reproduction. Because they are shade-tolerant and long-lived, we think of primary forest species as superior competitors for space in a mature forest.

Many biological processes at one level of organization (e.g., communities) are actually the result of those occurring at lower levels (e.g., populations). Such properties are known as collective properties. This field exercise will examine factors that might drive the community-level process of succession resulting from physiological processes at the organismal level (within individual plants).

For plants, light is often a limiting resource; most plants can be stimulated to higher photosynthetic rates and higher growth rates by increasing the amount of light they receive. At the same time, many plants are well adapted to living in low-light environments, such as the shaded understory of a forest. In this investigation, we will test some working hypotheses about the photosynthetic responses of representative pioneer and primary forest tree species that might account for the successional patterns we see in the forest. Specifically, these hypotheses are:

a) Light intensity in treefall gaps exceeds that in adjacent forest understory.
b) Pioneer species have faster photosynthetic rates than do primary forest species under gap light conditions.
c) Primary forest species have faster photosynthetic rates than do pioneer species under forest understory light conditions.
d) Growth rates of pioneer species exceed those of primary forest species in gaps.
e) Growth rates of primary forest species exceed those of pioneer species in forest understory.

We will collect the following data:
- light intensity in gap and understory patches (measured with light ceptometers sensitive only to the wavelengths used for photosynthesis: 400-700 nm)
- growth rates of representative pioneer and primary species over the previous year (by measuring the increase in shoot length)
- photosynthetic rates of representative species under gap and understory light conditions (using a portable photosynthesis system)

Measurement of photosynthetic rates with a portable photosynthesis system
Not so long ago, biologists interested in measuring the rate at which plants convert light energy into chemical energy via photosynthesis had to rely on indirect measurements or long-term measurements such as those based on biomass accumulation over time. These methods rely on lots of assumptions that may not hold in all circumstances, and many of them take so long that they're not feasible for understanding the factors that affect photosynthetic rates over short time periods.

Modern techniques for measuring photosynthetic rates make use of the fact that the rate of energy gain via photosynthesis is directly proportional to the rate at which a plant uses CO_2 and produces O_2. Until recently though, such measurements could only be made with the necessary precision in the laboratory, or by taking a truckload of delicate equipment into the field. The advent of small, accurate infrared gas analyzers (IRGAs) has made it possible to construct portable systems that give accurate measurements in the field, since the relationship between the amount of energy incorporated into carbohydrate and the amount of CO_2 used is known. Some systems also measure gas exchange in relation to transpiration, stomatal conductance, etc., as well as photosynthesis in plants, at the level of individual leaves. The machine uses it's own gas analyzers, light source, CO_2 supply, and on-board computer to make all of these measurements, so it is important to use extreme care when transporting or using it.

The basic principle behind most (closed) portable photosynthesis systems is to pump air of known gas composition through a sealed chamber containing a photosynthesizing leaf. By measuring the difference in CO_2 concentration between the air entering and leaving the leaf chamber, and combining this with precise measurements of the rate of air flow through the chamber and the amount of water vapor added to the outgoing air by the leaf, we can determine the rate at which the leaf is using CO_2. Of course, the plant is also respiring at the same time, so it is *producing* CO_2 as well as using it. Since the instrument just measures the *net* change in CO_2 concentration, it is actually measuring *net* photosynthetic rate (i.e., gross photosynthetic rate - gross respiration rate). Recall that:

$$\text{Photosynthesis is essentially:} \quad 6CO_2 + 6H_2O + \text{energy} \longrightarrow C_6H_{12}O_6 + 6O_2$$
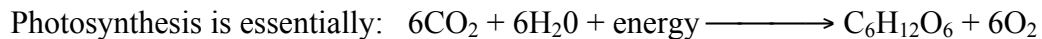
$$\text{While respiration is:} \quad C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + \text{energy}$$

Procedure
During the first part of the investigation, each lab group will collect two types of data in the field: 1) light intensity in gap vs. understory patches, and 2) annual growth increments of pioneer and primary forest tree seedlings in gap vs. understory patches. Groups will also collect data on the photosynthetic responses of seedlings adapted to gap and understory light conditions when subjected to those different light environments in the field or in a greenhouse. Since collecting data on light intensity and photosynthetic rates depends upon complex instruments that we have just a few of, different groups will rotate their use of instruments.

In the field, each lab group will be directed to a particular treefall gap by their lab instructor. All of the data collected by this group will be from this gap and from a nearby forest understory site located 15-20 m south (so as to remain in the same general part of the forest, with the same soil conditions, etc., while minimizing the influence of the gap on local light conditions). Lab groups will take turns with the light ceptometers so that each group can collect both types of data in their gap and understory patches.

Part 1: Light environments in gap vs. understory patches
For this part, you'll need to divide your group into two teams of two students, each with a walkie-talkie and a light ceptometer. The latter is a fancy light meter that is sensitive only in the photosynthetically active portion (400-700 nm) of the electromagnetic spectrum. Recall that chlorophyll absorbs most strongly in this part of the spectrum, which goes roughly from blue (400 nm) to red (700 nm). Using the instructions below, the ceptometers will measure PAR (**p**hotosynthetically **a**ctive **r**adiation) in units of micromoles of photons per meter squared per second ($\mu mol \cdot m^{-2} \cdot s^{-1}$), averaged over the 80 separate sensors on the unit.

We need two ceptometers because we want to express light intensity in the two patch types as percentages of full sunlight, i.e., the light intensity at the top of the canopy, before it passes through leaves, etc. Since the sun moves across the sky, and since clouds blowing across it can change light intensity substantially over very short periods of time, it's important that we measure light intensity in the patch of interest (gap or understory) and in the open at the same instant; hence the walkie-talkies. So before taking any readings, your instructor will direct one of your teams to a location outside the edge of the forest, where the ceptometer will receive the same light intensity as that above the forest canopy. The other team will remain back at the treefall gap.

Each team of your group should take two readings: one at approximately 30 cm above ground level (seedling height) in the middle of your treefall gap, and another at the same height above the ground at your forest understory site. Using the walkie-talkies, the two teams should take their gap measurements at the same instant, recording their PAR readings on the data sheet provided. Then the team in the forest should move to their understory site, and both teams should take and record PAR readings again. Record your group's data in Table 1.

To take readings with the Decagon AccuPAR ceptometer:
- To turn on the unit, press the ON button and wait for the MAIN MENU to display.
- At the main menu select the READ option by pressing F2
- Then select the continuous option by pressing F4
- Then select the full probe option by pressing F3
- Make sure the instrument is level (use the bubble level at the base of the probe) and at the correct height above ground (30 cm), and read the value of PAR from the screen.
- To get back to the main menu, press the up arrow ⇑ key (located in the upper right corner of the keypad) twice.
- To turn the unit off, select F4 from the MAIN MENU.

Part 2: Seedling/sapling growth responses in gap vs. understory patches

If we know something about plant anatomy, we can use a little trick to determine how much a given tree stem has grown during each of the last couple of growing seasons, at least with many species. Every autumn when the tree is about to lose its leaves and go dormant for the winter, it forms several layers of bud scales around each of its terminal buds (the buds at the ends of each shoot). These scales protect the meristematic tissues in the buds from drying out over the winter. The next spring, the bud scales fall off as the bud starts to grow again, and the stem lengthens behind the bud.

If you look carefully, you can see the bud scale scars from one growing season as several close-spaced rings around the stem (Fig. 1). The distance between two sets of such scars is the amount of shoot added during a single growing season. The current season's growth will be the distance between the tip of the terminal bud on a shoot and the first set of bud scale scars on the shoot back from the terminal bud.

Figure 1. Detail of sugar maple shoot, showing rings of bud scale scars left by successive years' terminal bud scales.
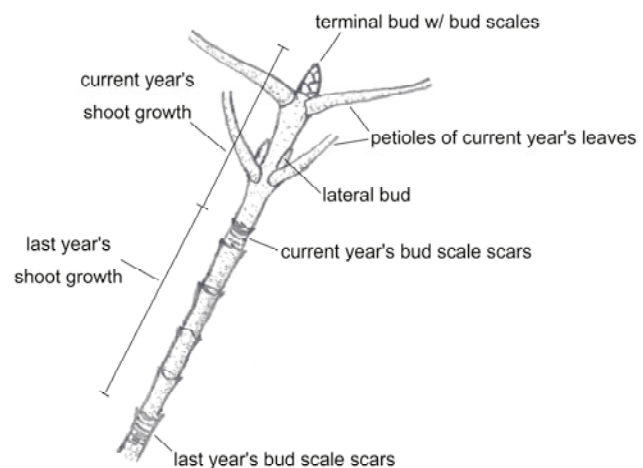
For this part of the lab, you should measure the current year's growth (in mm) of five maples and five cherries in your gap site (near the center is best) and of five maples and five cherries in your understory site. Try to choose seedlings or saplings up to 2 m tall. If the plant has more than one shoot, measure the growth on the most vertically oriented, main shoot.   Report your data in Table 2.

Part 3: Photosynthetic responses of pioneer vs. primary forest trees in gap and understory light environments

For this part of the lab, your group will need to sign up for a 1-hour time slot with your instructor or a TA. We'll have sign-up sheets in the lab - be sure that you sign up for a time slot before leaving lab!

The following is a bare-bones set of instructions on how to take the necessary photosynthesis measurements with a particular instrument called the LI-6400 portable photosynthesis system, assuming that it has already been set up by the instructor.

1. Turn the LI-6400 ON. After 1 or 2 seconds, you will be asked if the infrared gas analyzer (IRGA) is connected:
    Is the chamber/IRGA connected? (Y/N)
2. Press Y. The LI-6400 then scans the file system
    Loading Open System 3.2…
3. If asked, select a Configuration. There may be other configurations available in the display window, but for now, select *"led source"* (use the red arrow keys to highlight your selection, then press enter).
4. After some more messages, the OPEN menu appears. This screen represents the home base for a variety of operations, but the ones we want to use will be accessed via the New Measurements menu. Press the **f4** function key ("New Msmnts"). The New Measurements screen (Fig. 2) displays real time data using text and graphics. The text display shows three rows of four variables (=12 total); each row has highlighted labels above the values. Only twelve variables are displayed at a time, but there are many more available. We'll want to see the variables in groups a, b and c. The display label for variable groups is shown in the left-most part of the window.
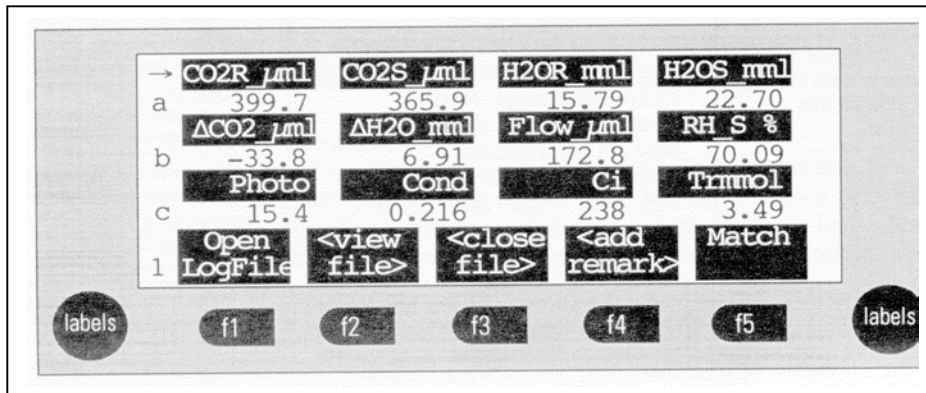
Figure 2. The New Measurements screen of the LI-6400 Portable Photosynthesis System

5. To change a variable group, use the ↑ or ↓ key to move the line marker (→) to the line of the display that you'd like to change, and then press the letter of the variable group you'd like to display there.
6. To set the leaf chamber fan speed:
    a) Press the "labels" key on the keypad to get to level 3 on the function key level indicator (the number to the left of the row of labels in the display above the 5 function keys).
    b) Press f3 to get to the Leaf Fan control menu.
    c) Press f to set the leaf chamber fan speed to fast.

7. Set the Flow control (f2 on level 2 of the function key level indicator) for flow rate of 400 μmol · sec^{-1}, and the desiccant control knob to full bypass. The desiccant control knob is the top knob above the clear plastic tube on the side of the machine that contains a desiccant (a water-absorbing compound). Setting this knob to full bypass allows the air entering the leaf chamber to retain all of its water vapor.

8. Set Mixer (f3 on level 2 of the function key level indicator) to 400 μmol · mol^{-1} and set the CO_2 scrubber control knob (the knob above the other clear plastic tube on the side of the machine) to full scrub. The compound in the scrubber tube will remove all of the CO_2 in the air entering the machine and the mixer will replace it with gas from the on-board CO_2 cylinder to maintain the leaf chamber at a constant CO_2 concentration of 400 μmol · mol^{-1}.

9. Set Temp (f4 on level 2 of the function key level indicator) to 'N) None' (Cooler OFF) to allow the leaf temperature to remain at ambient.

10. To set the light intensity within the leaf chamber:
    a) Press the "labels" key on the keypad to get to level 2 on the function key level indicator.
    b) Press f5 to get to the Lamp control menu.
    c) Select Q) Quantum Flux, then press enter.
    d) Using the keypad, enter the desired PAR intensity, then press enter. IMPORTANT NOTE: the in-chamber light source draws lots of power, so it will run the battery down quickly if left on. Therefore, you should always turn the lamp OFF when you're not taking measurements. The same is true for CO_2 consumption – turn the CO_2 mixer off when you're done with your measurements.

11. To take a measurement of photosynthetic rate:
    a) Choose a leaf that will cover the entire surface area of the leaf chamber (i.e., at least 2 x 3 cm in surface area).
    b) Clamp the leaf chamber onto the leaf, taking care that the knurled adjusting screw has been set to provide enough pressure to seal the upper and lower gaskets against the leaf, but not so much pressure as to prevent the movement of water through the vascular tissues in the leaves.
    c) Turn on the led light source to the desired PAR (1000 μmol·m^{-2}· s^{-1} for gap, 16 for understory; see below).
    d) Set up the LI-6400 to display photosynthetic rate in graphical form in real time:
        • Choose f2 (GRAPH QuikPik) on level 4 of the function key level indicator.
        • Scroll down the choices with the down arrow until you get to "Photo and Cond" and then press enter.
    e) Watch the photosynthetic rate reading on the graph. Since you've just changed the light intensity experienced by the leaf, photosynthetic rate will probably change. It will change rapidly at first, but within a few minutes it should level off. After it levels off, take your reading by pressing escape to get back to the variable groups screen, and reading the value of Photo on variable group c. The units are μmol CO_2 · m^{-2} · s^{-1}. To get back to the graphical display, press 4 to get to level 4 of the function key level indicator and then press f3 (view graph).
    f) When you're ready to change the light level, turn the CO_2 mixer off, etc., you can get back to level 2 of the function key level indicator by pressing 2.

For this part of the lab, your group should take four measurements of net photosynthetic rate: one each from a sun-adapted maple seedling and a sun-adapted cherry seedling at high light intensity,

and one each from a shade-adapted maple and a shade-adapted cherry at low light intensity. For the high light intensity, we'll use 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (about 60% of full sunlight) to simulate conditions near the center of a gap. The low light intensity will be 16 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (about 1% of full sun) to simulate conditions in forest understory. For each plant, be sure to do the high light intensity measurement first. Record your data in Table 3.

Data Analysis
Part 1. Light environments in gap vs. understory patches
    Using class data, test the working hypothesis that light intensity (PAR, expressed as a percentage of incident light above the canopy) is higher in gaps than in adjacent forest understory. Since this is a directional hypothesis (i.e., that PAR is *higher in gaps than in understory*, and not simply that it is *different* in gaps and understory), you will need to do a one-tailed t-test. To use the same table of critical values of the t-distribution for a one-tailed test, you use the column in the table for twice the α level that you want. For example, if you want $\alpha = 0.05$, you use the column labeled $\alpha = 0.1$. Doing this puts the whole rejection region of 5% of the area under the curve below just one tail of the distribution. This is just what we want (and in fact it's why we call this a "one-tailed" test) - we're not even interested in the possibility that mean PAR could be higher in understory than in gaps, because that would make no sense. So we take our whole 5% rejection region and put it in just one tail of the distribution, and are thus able to reject the null hypothesis of no real difference in mean PAR *with a smaller measured difference between them*.

a) State the null (H_0) and alternative (H_A) hypotheses that you will test with the PAR data.
b) Show the means and standard errors of PAR (include units) in gap and understory patches.
c) Show the value of t that you compute from the class data, the number of degrees of freedom for the test, and the critical value with which you compare your computed value.
d) Write a statement to summarize your statistical results and state your conclusion.
e) Construct a bar graph of the PAR data such that the heights of the bars represent the means and the error bars represent one standard error of the means.

Part 2A: Growth rates of pioneer vs. primary forest species in gap conditions
    Do analysis steps a) - e) above to test the working hypothesis that pioneer species have higher growth rates than primary forest species in gap light conditions. Again, use class data.

Part 2B: Growth rates of pioneer vs. primary forest species in understory conditions
    Do analysis steps a) - e) above to test the working hypothesis that primary forest species have higher growth rates than pioneer species in understory light conditions. Again, use class data.

Part 3A: Photosynthetic rates of pioneer vs. primary forest species in gap conditions
    Do analysis steps a) - e) above to test the working hypothesis that pioneer species have higher photosynthetic rates than primary forest species in gap light conditions. Use data only from the sun-adapted plants. Again, use class data.

Part 3B: Photosynthetic rates of pioneer vs. primary forest species in understory light conditions
    Do analysis steps a) - e) above to test the working hypothesis that primary forest species have higher photosynthetic rates than pioneer species in understory light conditions. Here, use data only from shade-adapted plants. Again, use class data.

Data Sheet for Photosynthetic Strategies and Their Consequences for Community Succession

Table 1. Photosynthetically active radiation (PAR, in $\mu mol \cdot m^{-2} \cdot s^{-1}$) in gap and understory patches, relative to that at the top of the forest canopy.

	Gap Site	Understory Site
PAR at forest site (a)		
PAR outside forest (b)		
% sunlight at site (a ÷ b)		

Table 2. Current year's growth (in mm) of Cherry and Maple seedlings and/or saplings in gap and understory patches.

Cherries in gap site	Cherries in understory site	Maples in gap site	Maples in understory site

Table 3. Net photosynthetic rate (in $\mu mol\ CO_2 \cdot m^{-2} \cdot sec^{-1}$) of Cherry and Maple seedlings under gap vs understory light regimes.

Plant #'s used	Growth Condition	Cherries at 16 $\mu mol \cdot m^{-2} \cdot s^{-1}$	Cherries at 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$	Maples at 16 $\mu mol \cdot m^{-2} \cdot s^{-1}$	Maples at 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$
	shade-adapted		-----		-----
	sun-adapted	-----		-----	

Student Worksheet Report for Photosynthetic Strategies and Their Consequences for Community Succession

Part 1. Light environments in gap vs. understory patches
  a. Statement of hypotheses.
    1) Null hypothesis to be tested:
    2) Alternative hypothesis to be tested:

  b. Means and standard errors for % incident PAR in gap and understory patches.

	Mean % PAR	Standard Error
Gap sites		
Understory sites		

  c. Results of t-test

Value of t computed from data	
Degrees of freedom for test	
Critical value of t from table	

  d. Summary statement for statistical results, and biological conclusion.
  e. Attach a copy of your bar graph of mean PAR (± S.E.) in gap vs. understory patches.

Part 2: Seedling/sapling growth responses in gap vs. understory patches
  A. Growth rates of pioneer vs. primary forest species in gap conditions
     a. Statement of hypotheses.
          1) Null hypothesis to be tested:

          2) Alternative hypothesis to be tested:

     b.`Means and standard errors for previous season's shoot growth of pioneer and primary forest species
          in gap patches.

	Mean shoot growth (mm)	Standard Error
Pioneer species		
Primary forest species		

     c. results of t-test

Value of t computed from data	
Degrees of freedom for test	
Critical value of t from table	

     d. Summary statement for statistical results, and biological conclusion.

     e. Attach a copy of your bar graph of mean (± S.E.) shoot growth of pioneer vs. primary forest
          species in gap conditions.

  B. Growth rates of pioneer vs. primary forest species in understory conditions
     a. Statement of hypotheses.
          1) Null hypothesis to be tested:

          2) Alternative hypothesis to be tested:

     b. Means and standard errors for previous season's growth of pioneer and primary forest species in
          understory patches.

	Mean shoot growth (mm)	Standard Error
Pioneer species		
Primary forest species		

     c. results of t-test

Value of t computed from data	
Degrees of freedom for test	
Critical value of t from table	

     d. Summary statement for statistical results, and biological conclusion.

     e. Attach a copy of your bar graph of mean (± S.E.) shoot growth of pioneer vs. primary forest
          species in understory conditions.

Part 3: Photosynthetic responses of pioneer vs. primary forest trees in gap and understory light environments

A. Photosynthetic rates of sun-adapted pioneer vs. primary forest species in gap conditions
   a. Statement of hypotheses.
      1) Null hypothesis to be tested:

      2) Alternative hypothesis to be tested:

   b. Means and standard errors for net photosynthetic rate (in μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) of pioneer and primary forest species under gap light conditions.

	Mean net photosynthetic rate	Standard Error
Pioneer species		
Primary forest species		

   c. results of t-test

Value of t computed from data	
Degrees of freedom for test	
Critical value of t from table	

   d. Summary statement statistical results, and biological conclusion.

   e. Attach a copy of your bar graph of mean ($\pm$ S.E.) photosynthetic rate of pioneer vs. primary forest species in gap light conditions.

B. Photosynthetic rates of shade-adapted pioneer vs. primary forest species in understory light conditions
   a. Statement of hypotheses.
      1) Null hypothesis to be tested:

      2) Alternative hypothesis to be tested:

   b. Means and standard errors for net photosynthetic rate (in μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) of pioneer and primary forest species in understory light conditions.

	Mean net photosynthetic rate	Standard Error
Pioneer species		
Primary forest species		

   c. results of t-test

Value of t computed from data	
Degrees of freedom for test	
Critical value of t from table	

   d. Summary statement for statistical results, and biological conclusion.

   e. Attach a copy of your bar graph of mean ($\pm$ S.E) photosynthetic rate of pioneer vs. primary forest species in understory light conditions.

Address the following questions, based upon the data you analyzed:

1. How did light levels differ between the two patch types (gap vs. forest understory)?
2. Do the results from our experiments on photosynthetic rate support our predictions - i.e., that pioneer species are better adapted to conditions typical of gaps while primary forest species are better adapted to those in shaded forest understory?
3. Do the results from our measurements of annual growth increment support these same predictions? If not, can you suggest possible explanations?
4. Speculate on the likely effects, at the community level (i.e., species composition), of an increased disturbance rate in this forest, such that the proportion of land area in gaps increased, and beneath-tree canopy decreased. (This disturbance could be via increased storm or fire frequency or intensity due to climate change or land management practices).
5. Similary, speculate on the likely effects of a decreased disturbance rate.

Materials

- 2 or more light ceptometers for measuring photosynthetically active radiation (e.g. Decagon AccuPAR); use of the ceptometers is staggered among groups for the entire class; (purchased for approx. $3,000 each in 1998 with NSF-ILI grant DUE 9851665; www.decagon.com
- 2 or more two-way radios (e.g. Motorola Talkabout, approx. $80 each); 1 radio per ceptometer
- 1 or more portable photosynthetic systems (e.g. Li-Cor LI-6400; please see Appendix C for information on alternative methods and systems); use is staggered among groups for the entire class
- data sheets – one set per student group

- clipboards – one set per student group
- cm rulers – one per student group (we prefer flexible plastic)
- hand magnifiers (10X) – one per student group
- regional tree field guides – one per student group (e.g. Little, E.L. 1980. National Audubon Society Field Guide to North American Trees: Eastern Region. Alfred A. Knopf, New York, 714 pages.)

Notes for the Instructor

Successional Patterns

At our institution, this investigation is preceded by one in which students have documented the patterns of forest succession at our study site. In so doing they have determined that early successional species such as Black Cherry (*Prunus serotina*) and Red Oak (Quercus rubra) are becoming less common in the forest, and later successional species, such as American Beech (*Fagus grandifolia*), Black Maple (*Acer nigrum*) and Sugar Maple (*Acer saccharum*) are increasing in proportional occurrence in the forest. Similar patterns of succession in any forest can be qualitatively determined by a quick examination of representation of species in the understory (i.e. what saplings are represented with the greatest frequency in the understory, and hence, will be the replacers of canopy trees that die?) as compared with current canopy species composition (what tree species currently dominant the canopy?). Any noticeable difference in the understory vs. canopy species composition can be interpreted as evidence that the future forest canopy will not have the same composition as the current forest canopy, hence, that successional changes are underway. For the purposes of the photosynthetic strategies lab, the cursory examination is sufficient, but it is still important to discuss successional patterns at the outset, in order to enable students to be able to make reasonable predictions about tree species responses to different light environments.

If a basic, quantitative introduction to forest succession is desired as a precursor to this lab, please refer to "Forest Succession" in Brewer, R. and M. T. McCann (1982) Laboratory and field manual of ecology. CBS College Publishing, Saunders College Publishing, New York, 269 pages. Alternatively, email the authors (Murray et al.) for an electronic copy of a modified version of this lab that we use.

Staggering Use of Instruments

Since there are only a few "copies" of each of the major instruments used (e.g. ceptometers, portable photosynthesis system), it is important to stagger and rotate use of instruments by different student groups for each portion of the lab. For a lab of 24 students divided into groups of 4, some groups can begin with ceptometer measurements, while others begin with either sapling growth measurements or photosynthetic measurements. Because we have found photosynthetic measurements require about 45 minutes per group, we normally schedule a sign-up time for photosynthesis *in addition to* the 3-hour lab during which light and growth measurements are made. On the "photosynthesis day," instructors and undergraduate TAs split up the sign-up times so that one staff member is available to help students set up, interpret and record their measurements. Although this requires additional time for the staff, the payoff is that every group of 4 students receives personalized instruction and *all members of each group* can become proficient with direct use of the instrument. In fact, we routinely evaluate each individual's ability to operate these instruments on lab practicals.

Two ceptometers and two radios are required for one group to complete the light measurements. This is because the "open sky" readings and the "understory" readings must be made simultaneously, in order to calculate understory light as a proportion of what is "available" at that time. Thus, a group of 4 students splits up into 2 teams of 2 people each; one team proceeds to the open sky location, and the second team selects a station in the forest understory. The two teams communicate by way of the radios to "count down" precisely timed simultaneous readings in both

locations. Normally, each team can be finished and ready to rotate with another group of 4 within 15-20 minutes.

Measurement of Growth Rates of Saplings

Not all tree species have well-developed bud scale scars. If you are using alternate species for this lab, make sure to visit your field site first, and confirm that students will be able to easily identify bud scale scars. Measurements will be more reliable if instructors take 5-10 minutes at the beginning of the lab (while in the field) to show bud scale scars on the tree species used, and also to gather suggestions from students about how to standardize the measurement (e.g. will you measure to the proximal or distal scar line where a group occurs clustered together?) Encourage use of hand magnifiers since doing so clarifies most uncertainties about what are bud scale scars vs. other markings along the stem.

Measurement of Photosynthesis and Comparison of Systems

New improvements in technology have made it possible to measure photosynthesis in individual plants and plant leaves under field conditions and a variety of systems are available to choose from to meet your teaching and research needs. The use of portable photosynthesis systems has influenced the field of plant physiological ecology profoundly, and in particular, has been indispensable in tackling pressing questions concerning the impacts of global climate change on ecological systems. Most systems use a portable infrared gas analyzer (IRGA) to measure the change in CO_2 given off by the leaf placed in the chamber. All contain sensors that measure various physiological leaf parameters as well as conditions in the air moving through the leaf chamber (e.g. temperature, humidity, gas concentrations, etc.).   We conduct this lab using the Li-Cor LI-6400 system, which we purchased as part of an NSF-ILI curriculum and laboratory improvement grant (DUE 9851665). Although this enables us to train undergraduates using state-of-the-art research instrumentation, there are less costly systems available through other suppliers that are highly suitable for undergraduate teaching labs. We have included information on a selection of these systems below. Regardless of the system chosen, we highly recommend that instructors who anticipate using a portable photosynthesis system take advantage of the training workshops offered by most vendors and develop their own exercise- and instrument-specific protocols. The particular instructor protocol we use for running the instrument for this lab is included in Appendix A (and student instructions in the Student Outline).

A. LI-COR LI-6400 Portable Photosynthesis System. The research-level portable photosynthetic system used in our laboratory/field exercise was purchased for $26,450 (with CO_2 injector and LED light source) in 1998 from LI-COR environmental biosciences with part of an NSF-ILI grant (DUE 9851665) for "Instrumentation to Integrate Pattern and Process in Organismal Biology and Ecology). The operator can control light intensity, temperature, and relative humidity. The system is available with a variety of leaf chamber options and features an open path design with the optical bench of the sample analyzer open directly to the leaf chamber mixing volume. *<http://www.licor.com/env/Products/li6400/6400.jsp>*

B. CID, Inc. CI-340 Hand-Held Portable Photosynthesis System. This model contains the display, kepad, computer, gas analyzer, flow control system and battery all in a single, hand-held case. LED light source for controlling light intensity and temperature control modules are optional. A variety of leaf chambers for different types of leaves and a chlorophyll fluorescence module can be added. The basic unit is approximately $9,400 (LED light source optional). *<http://www.cid-inc.com>*

C. Qubit Systems, Inc. Photosynthesis Package. Designed specifically for undergraduate laboratories, the Qubit Photosynthesis package sends experimental data to *your* computer in real time, and is equipped with a halogen light source and power regulator, leaf chamber with oxygen sensor, light sensor, LabPro Interface and Logger Pro

Software, and other accessories. It contains no "on-board" LED light source, but is economically priced at approximately $1330 (battery pack is an additional approx. $200). *<www.qubitsystems.com>*

D. PP SystemsTPS-1 Photosynthesis System. This system is smaller than, but similar in components to, the LI-COR 6400. The TPS-1 is designed for "basic research and teaching." As with the Qubit photosynthesis package, the instrument has full data logging capability, allowing transfer of data to PC or printer. It is an "open system" sampling air going into and leaving the leaf chamber. A basic package containing the gas analyzer system and a universal leaf cuvette costs approximately $9,975. *<http://www.ppsystems.com>*

E. Shoestring Budget. ABLE member Paul Willing (*willingp@union.edu*) has designed a homemade respiration system that can potentially be used for animal respiration and photosynthesis measurements. It is based on use of a CO_2 sensor and O_2 electrode from Vernier *<http://www.vernier.com/probes/probes.html?co2-bta&template+standard.html>*. It is designed to run with Vernier's LabPro interface and LoggerPro software (as is the Qubit system above). One station is approx. $500-$700, and, according to Paul, will require that you re-seal the CO_2 sensor, attach LuerLok-type connections for gas flow and the O_2 sensor, and affix your own pump and leaf chamber. When complete, the set-up is quite sensitive and measures photosynthesis in approximately 1 minute.

Additional Ecological Questions to Explore

The combination of techniques introduced in this laboratory can be used to explore a variety of other ecological questions. For example, if your study site does not show strong evidence of successional patterns, you and your students might instead choose to explore differences in growth and photosynthetic rates as a consequence of microhabitat features. These features could be light level, temperature or moisture, proximity to pollution source, degree of herbivory evident on foliage, condition of leaves (e.g., dehydrated vs. hydrated), soil type, competition with other plants, time since disturbance (e.g., fire, treefall, etc.).

One- and Two-tailed t-tests

Most of our students have completed t-tests in other biology core courses prior to conducting this lab. Hence, we use the opportunity in this lab to *expand* on their understanding of inferential statistics by introducing the concept of directional and non-directional alternate hypotheses. Most statistical tables give one-tailed and two-tailed α levels. If the alternative hypothesis is non-directional, i.e. does not specify the direction of the difference, change, etc., then the student is conducting a two-tailed t-test. For example, if H_A was simply that mean photosynthetic rate of maples and cherries differ. On the other hand, the student is conducting a one-tailed t-test when s/he has specified beforehand the direction of the change in the H_A, e.g. if s/he had predicted that mean photosynthetic rate for maples is *greater* than it is for cherries under the same conditions. Then, if the student determines that cherry photosynthetic rates are actually greater, s/he must of course still accept H_O, the null hypothesis. The student must decide whether or not s/he will do a one- or two-tailed t-test at the time s/he sets up the hypothesis, i.e. before even collecting or looking at the data. The reason for this is that α levels for one-tailed tests are *half* those for two-tailed tests, or a t-value insufficient to reject H_O for a two-tailed test might be sufficient to reject H_O for a one-tailed test.

t-tests on a TI graphing calculator

To conduct a t-test (either independent samples or a paired t-test) on a TI-83 type calculator, first create 2 "lists" for your data (e.g. maple photosynthetic rates in List 1 and cherry photosynthetic rates in List 2) using the STAT menu (STAT, EDIT, create lists). Then return to the STAT menu and select TESTS. The examples given in this activity correspond to test choice 4: 2 Sample TTest. On the 2 Sample TTest screen, highlight inputs as follows: Inpt = Data; List1: L_1 (or other location), List2: L_2 (or other location), Freq1 =1, Freq2 =1. The next line asks for your working hypothesis

(mean 1 not equal to mean 2, or mean 1 < mean 2, or mean 1 > mean 2).   Notice that, as discussed above, your conclusion will depend on whether your working hypothesis was non-directional (mean 1 not equal to mean 2) or directional. Select the appropriate working hypothesis, and lastly, select Pooled = Yes. Then highlight Calculate and press Enter to see the results. The calculator will report the t-statistic , the P-value that corresponds to this test statistic for your sample sizes, etc., the degrees of freedom, the means and sample sizes for each sample group, and the standard deviations for each sample (shown as S_{x1} and S_{x2}). The null hypothesis, H_o, is rejected if $P > 0.05$. Graphing calculators offer an instructive way to learn the importance of specifying a one- or two-tailed t-test because you can easily return to the menu and answer questions such as: "What outcome would I have had if I had specified a non-directional hypothesis rather than a directional one?"

Acknowledgments

Appendix A

Instructor's Notes for Setting up the Li-Cor 6400 Portable Photosynthesis System for this Lab

1. Before you leave campus, make sure you take the ceptometers, walkie talkies, and other supplies. Also take extra AA batteries - these can be used for the ceptometers and be sure that you have the tripod, sensor head, cable / hose assembly, extra batteries, CO_2 cylinders, and o-rings for the LiCor 6400.
2. Also bring jars of extra desiccant (drierite), and CO_2 scrubber compound (calcium chloride). If either of these need to be replaced, do it before you leave.
3. As soon as you arrive at the first field site, connect the cable/hose assembly to the LI-6400 and   sensor head, attach the sensor head to the tripod, and turn the machine on.
4. Make sure that the red cap is off the air intake port (near the ON switch).
5. When the Open 3.2 screen comes up, press f4 to get the New Measurements menu.
6. Open the leaf chamber and listen to make sure that the leaf fan is running (it will hiss).
7. Put in a new CO_2 cylinder if the machine has been sitting overnight. One cylinder should work fine for several hours at least, but if the machine sits overnight, the cylinder will need to be changed. Even if the machine is turned off, the gas leaks out of the system.
8. If you take out a cylinder that still has gas in it, release the pressure slowly or the o-ring will   freeze and need to be replaced.
9. To replace the cylinder, put a new cylinder into the housing and screw the housing onto the base until you feel some resistance. Then, tighten the housing the rest of the way quickly to puncture the cylinder without venting the gas to the outside.
10. Set the flow rate to 400 μmol$\cdot$ s^{-1}
11. Adjust the leaf chamber tension (use the knurled knob) so that the foam gaskets are compressed   a bit when the chamber is closed, and then leave the chamber closed.
12. Set CO_2 mixer to maintain a reference concentration of 400 μmol$\cdot$ mol$^{-1}\cdot$ s^{-1}, and set the soda   lime to full scrub.
13. Set the desiccant to full bypass.
14. Exhale around the leaf chamber. If there are no leaks the sample chamber CO_2 concentration shouldn't increase by more than about 1 μmol$\cdot$ mol$^{-1} \cdot$ s^{-1}
15. Match the IRGA's:
    a) enter match mode by pressing f5 on level 1 of the function keys
    b) after the readings are fairly stable, the display will give you the option to MATCH IRGAs (f5) or EXIT (f1). When the readings are pretty stable, press f5.
    c) After matching, press f1 to exit match mode.
    d) You're now ready to clamp onto your first leaf.
16. After you're done making measurements:
    a) Make sure that the soda lime and desiccant knobs are set halfway between bypass and full scrub.
    b) Make sure that the leaf chamber lid tension is adjusted (use the knurled knob) so that the foam gaskets are not compressed when the chamber lid is closed.
17. When your lab is finished**:**
    a) Set up the ceptometers to charge (if you're using rechargables).
    b) Put fresh batteries in the LI-6400, and plug the ones you used into the charger.
    c) Clean up the machines and cases if any leaves, sand, etc. got on them.

Appendix B

Sample Class Data Sets and Student Worksheets

Sample data sets. Compiled class data are posted 2-3 years at a time at K. Greg Murray's course website for Biology 280: Ecology and Evolutionary Biology (URL below). This collection includes instructions for downloading data sets as well as for importing text files into either SYSTAT or Microsoft Excel data tables. *(http://www.hope.edu/academic/biology/classdata/bio280/280home.htm)*

Sample Student Worksheet for Photosynthetic Strategies and their Consequences for Community Succession.
   Part 1. Light environments in gap vs. understory patches
   a. Statement of hypotheses.
   1) Null hypothesis to be tested: *Any difference between mean PAR in gap and understory sites is small enough to be due to sampling error alone*
   2) Alternative hypothesis to be tested: *Mean PAR is higher in gap sites than in understory sites.*

   b. Means and standard errors for % incident PAR in gap and understory patches.

	Mean % PAR	Standard Error
Gap sites	*41.05 (n=12)*	*12.744*
Understory sites	*0.91 (n=12)*	*0.145*

   c. Results of t-test

Value of t computed from data	*3.149*
Degrees of freedom for test	*22*
Critical value of t from table	*1.717 (for 1-tailed)*

   d. Summary statement for statistical results, and biological conclusion.
   Since 3.149>1.717, I reject the null hypothesis and accept the alternative hypothesis, and conclude with 95% confidence that mean PAR is higher in gaps than in forest understory.

   e. Attach a copy of your bar graph of mean PAR (± S.E.) in gap vs. understory patches.
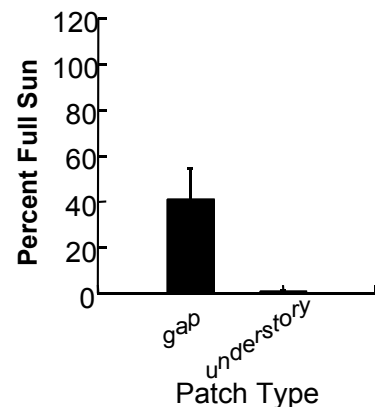
Part 2: Seedling/sapling growth responses in gap vs. understory patches
A.   Growth rates of pioneer vs. primary forest species in gap conditions
      a.   Statement of hypotheses.
      1) Null hypothesis to be tested: *Any difference between mean annual growth increment of cherry and maple seedlings/saplings under gap conditions is small enough to be due to sampling error alone.*

      2) Alternative hypothesis to be tested: *Mean annual growth increment of cherry seedlings/saplings is greater than that of maple seedlings/saplings under gap conditions.*
   b. Means and standard errors for previous season's shoot growth of pioneer and primary forest species in gap patches.

	Mean shoot growth (mm)	Standard Error
Pioneer species *(Cherry)*	*154.80 (n=59)*	*14.252*
Primary forest species *(Maple)*	*84.58 (n=60)*	*7.237*

   c. results of t-test

Value of t computed from data	*4.415*
Degrees of freedom for test	*117*
Critical value of t from table	*approx. 1.658 (for 1-tailed)*

d. Summary statement for statistical results, and biological conclusion. *Since 4.415>1.658, I reject the null hypothesis and accept the alternative hypothesis, and conclude with 95% confidence that mean annual growth increment is higher in cherries than in maples under gap conditions.*

e. Attach a copy of your bar graph of mean (± S.E.) shoot growth of pioneer vs. primary forest species in gap conditions.
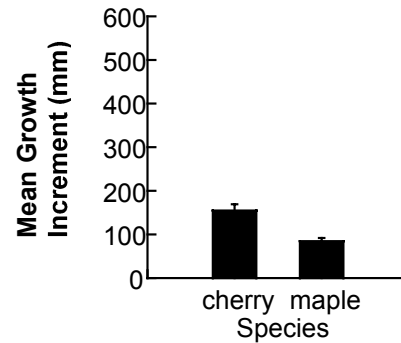
B. Growth rates of pioneer vs. primary forest species in understory conditions

a. Statement of hypotheses.

 1) Null hypothesis to be tested: *Any difference between mean annual growth increment of cherry and maple seedlings/saplings in understory conditions is small enough to be due to sampling error alone.*

 2) Alternative hypothesis to be tested: *Mean annual growth increment of maple seedlings/saplings is greater than that of cherry seedlings/saplings in understory conditions.*

b. Means and standard errors for previous season's growth of pioneer and primary forest species in understory patches.
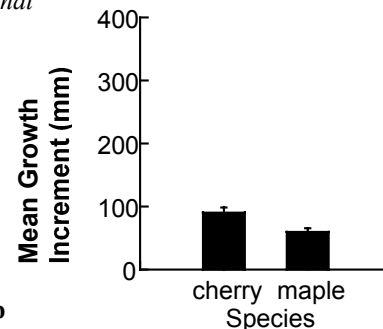
	Mean shoot growth (mm)	Standard Error
Pioneer species *(Cherry)*	*90.27 (n=60)*	*8.100*
Primary forest species *(Maple)*	*59.70 (n=60)*	*5.675*

c. results of t-test

Value of t computed from data	*3.091*
Degrees of freedom for test	*118*
Critical value of t from table	*approx. 1.658 (for 1-tailed)*

d. Summary statement for statistical results, and biological conclusion. *Despite the fact that 3.091>1.658, the mean annual growth increment of cherry seedlings/saplings was higher than that of maples (i.e. the opposite of that specified by our alternative hypothesis), so that I must accept the null hypothesis that the difference observed in means is small enough to have resulted from sampling error alone. This case illustrates an interesting consequence of specifying a directional alternative hypothesis (which also allows us to do the more powerful one-tailed statistical test). We specified the directional alternative hypothesis because our working hypothesis was directional, and this was in turn based on our biological intuition (as it should be), rather than on anything having to do with statistics. In a case like this, we can't simply go back and change our alternative hypothesis and conclude that cherries have higher annual growth increments than maples in the understory, since doing so would be testing an hypothesis with the same observation that prompted us to generate it in the first place – a terrible scientific practice, but one that is too frequently committed. Instead, the correct course of action would be to revise our working hypothesis (and, hence, our alternative hypothesis), and test it with a different set of data.*

e. Attach a copy of your bar graph of mean (± S.E.) shoot growth of pioneer vs. primary forest species in understory conditions.

Part 3: Photosynthetic responses of pioneer vs. primary forest trees in gap and understory light environments

A. Photosynthetic rates of sun-adapted pioneer vs. primary forest species in gap conditions

a. Statement of hypotheses.

1) Null hypothesis to be tested: *Any difference between mean photosynthetic rate of sun-adapted cherry and maple seedlings/saplings under gap light conditions is small enough to be due to sampling error alone.*

2) Alternative hypothesis to be tested: *Mean photosynthetic rate of sun-adapted cherry seedlings/saplings is higher than that of maple seedlings/saplings under gap light conditions.*

b. Means and standard errors for net photosynthetic rate (in $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) of pioneer and primary forest species under gap light conditions.

	Mean net photosynthetic rate	Standard Error
Pioneer species *(Cherry)*	*8.92 (n=12)*	*1.447*
Primary forest species *(Maple)*	*3.73 (n=12)*	*0.354*

c. results of t-test

Value of t computed from data	*3.480*
Degrees of freedom for test	*22*
Critical value of t from table	*approx. 1.717(for 1-tailed)*

d. Summary statement statistical results, and biological conclusion. *Since 3.480>1.717, I reject the null hypothesis and accept the alternative hypothesis, concluding that mean photosynthetic rate in sun-adapted cherries is higher than that of sun-adapted maples under light conditions typical of treefall gaps.*
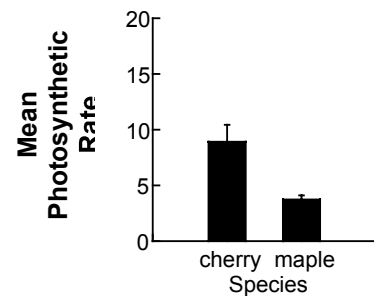
e. Attach a copy of your bar graph of mean (± S.E.) photosynthetic rate of pioneer vs. primary forest species in gap light conditions.

B. Photosynthetic rates of shade-adapted pioneer vs. primary forest species in understory light conditions

a. Statement of hypotheses.

1) Null hypothesis to be tested: *Any difference between mean photosynthetic rate of shade-adapted cherry and maple seedlings/saplings under understory light conditions is small enough to be due to sampling error alone.*

2) Alternative hypothesis to be tested: *Mean photosynthetic rate of understory-adapted maple seedlings/saplings is higher than that of cherry seedlings/saplings in understory light conditions.*

b. Means and standard errors for net photosynthetic rate (in $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) of pioneer and primary forest species in understory light conditions.

	Mean net photosynthetic rate	Standard Error
Pioneer species *(Cherry)*	*0.77 (n=12)*	*0.207*
Primary forest species *(Maple)*	*0.61 (n=12)*	*0.182*

c. results of t-test

Value of t computed from data	*0.565*
Degrees of freedom for test	*22*
Critical value of t from table	*approx. 1.717 (for 1-tailed)*

d. Summary statement for statistical results, and biological conclusion. *Since 0.565<1.717, I accept the null hypothesis and conclude that the difference in mean photosynthetic rate between shade-adapted cherries and maples in understory light conditions could have resulted from sampling error alone.*
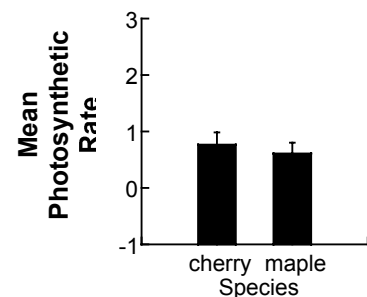
e. Attach a copy of your bar graph of mean (± S.E) photosynthetic rate of pioneer vs. primary forest species in understory light conditions.

Address the following questions, based upon the data you analyzed:

I. How did light levels differ between the two patch types (gap vs. forest understory)?

   Light levels differed in the way that we predicted: gaps had much higher light intensity than did understory patches. This finding is consistent with that from many other temperate and tropical forests as well; estimates of 1-2% of incident light reaching the forest floor are fairly typical.   Interestingly, light level (hence, percent incident sunlight) was highly variable among different treefall gaps, probably because we combined measurements made in the morning (when no gaps received direct-beam sunlight) with those made in the afternoon (when many did). Nevertheless, the data show that treefall gaps have a demonstrable effect on light intensity at the forest floor. Taking all measurements at noon, or even integrating a larger number of measurements from many locations within each gap would likely yield a more realistic (and less variable!) estimate of the light intensity in gaps.

II. Do the results from our experiments on photosynthetic rate support our predictions - i.e., that pioneer species are better adapted to conditions typical of gaps while primary forest species are better adapted to those in shaded forest understory?

   Here the results provide mixed support for our hypothesis. On the one hand, sun-adapted cherries had significantly higher photosynthetic rates under gap light conditions (PAR = 1000), as we had predicted. Thus cherries appear to be better able to translate gap conditions into higher photosynthetic rates than are maples, at least when grown in conditions simulating those occurring in gaps. On the other hand, there was no significant difference between photosynthetic rates of shade-adapted maples and cherries in understory light conditions (PAR = 16). On this basis we might conclude that maples and cherries are about equally well-adapted to conditions in the understory (both had low but positive photosynthetic rates). Perhaps a good next step would be to increase our sample size of PAR measurements in gap and understory sites to get a better representation of light levels to which plants at the forest are actually acclimated, and then to measure photosynthetic rates at those same light intensities.

III. Do the results from our measurements of annual growth increment support these same predictions? If not, can you suggest possible explanations?

   Here again, the results support some of our predictions and not others. Cherries did grow more than maples during the current growing season in gaps, as we predicted. However, the same thing occurred in the forest understory, in contrast to our prediction that maples would grow faster there. The latter result is not consistent with our finding of no difference between shade-adapted cherry and maple photosynthetic rates in understory light conditions. As discussed above, we would have to collect more data to really determine whether cherries grow more rapidly than maples in the understory, but the data we collected certainly suggest so.

IV. Speculate on the likely effects, at the community level (i.e., species composition) of an increased disturbance rate in this forest, such that the proportion of land area in gaps increased and that beneath intact tree canopy decreased (say, via increased storm or fire frequency or intensity due to climate change or land management practices)?

   Based upon data presented here, increased disturbance in this forest would likely lead to increased recruitment of pioneer species like Black Cherry, since the higher light levels would allow them to grow more rapidly than primary forest species. Even though the cherries we sampled grew more than maples even in the understory, the difference in growth increment between the species was greater in gaps. If the increased disturbance rate was consistent over time, we might expect to see increased representation of pioneers in the forest canopy, relative to primary forest species like the maples.

V. Similarly, speculate on the likely effects of a decreased disturbance rate.

   Data presented here do not suggest an unambiguous effect of a decreased disturbance rate. The data on growth rates in the understory suggest that we might expect an increased density of cherries, just as for an increased disturbance rate. On the other hand, our finding of roughly equivalent photosynthetic rates in cherries and maples in understory conditions suggests that neither species should have an advantage under low light conditions. The prediction of increased cherry density even with decreasing disturbance rate makes little biological sense in light of other researchers' work on the responses of these plants to light. The inconsistencies between this part of our study and those of other scientists, as well as between different parts our own study, suggest caution in interpretation. At the very least, we should increase our sample sizes and measure photosynthetic rates at the light levels actually experienced by plants in the understory.