Investigation 2 – Causes and consequences of carbon dynamics in biological systems:  
Scaling from molecules to ecosystems

Tasks

• Evaluate the effect of variation in leaf photosynthesis (and its controls) on plant growth rate.

• Design and carry out investigations of the effects of photosynthetic performance and growth rate on performance in interspecific competition.

• Design and carry out investigations of biomass production and energy flow in periodically disturbed tallgrass prairie communities.

Conceptual lessons

• Plant growth is an integrative process that depends on the uptake and allocation of carbon and energy as well as on plant morphology and environmental circumstances.

• Plant growth and allocation (and the controls of these processes) have consequences for the performance of individuals and populations in interspecific competition.

• The input and subsequent dynamics of energy and materials in ecosystems arise from the scaling up of photosynthesis and respiration through individual, population, and community levels, and they are affected by environmental conditions, including disturbance.

Background

Energy, materials, and life. All organisms must acquire energy and materials to sustain themselves. With rare exceptions, the energy for life on earth comes ultimately from the sun, as light energy is converted to chemical energy and reducing power in the process of photosynthesis. Respiration releases the energy in products of photosynthesis and returns carbon dioxide to the atmosphere.

Last semester, in Biology 251, you examined biochemical, cellular, physiological, and environmental sources of variation in photosynthesis and respiration in seed plants, one of the major groups of photosynthetic organisms (also known as autotrophs [self-feeders] or producers) (Fig. 1). This semester you will apply what you learned about that variation in two new contexts. First, you will develop and test hypotheses about the effect of variation in leaf-level photosynthesis and respiration (and other factors) on variation in individual plant growth rate and competitive ability (Fig. 2). Second, you will scale up your study of energy and growth, by investigating the role of disturbance and other conditions on the energy flow and biomass production in multi-species communities in tallgrass prairie (Fig. 3).
Part 1: Plant growth rate and allocation exercise

*RGR*. Plant biologists most commonly estimate plant growth as mass increase (rather than, say, height increase), because it is the accumulation of living matter (and the energy it contains) that enables individuals to devote resources to functions such as resource acquisition, maintenance, defense, and reproduction. Symbolizing mass as $M$, one can estimate the rate of mass increase in an absolute sense, $dM/dt$, or in a size-specific, relative sense, $(dM/dt)(1/M)$. The latter measurement, *relative growth rate* (RGR), adjusts for the tendency of larger plants to grow faster in absolute terms simply because they are bigger to start with. Thus, RGR is appropriate for comparing growth rate between taxa, genotypes, or experimental treatments in which general size might be variable.

Whether one wants to estimate absolute growth rate or RGR, the basic experimental design is the same. The usual protocol consists of cultivating a set of plants in controlled conditions, and then periodically harvesting, drying, and weighing subsets of those plants. Relative growth rate for a given time interval is then calculated as:

$$\frac{[\text{Mass at time } t+1 - \text{Mass at time } t]}{\text{Mass at time } t \cdot \text{time interval}}$$

This estimate applies not to individual plants but to a set of plants treated in some common fashion, as it is impossible to harvest and weigh the same plant twice.

*The determinants of RGR.* Because photosynthesis adds mass increase while respiration takes it away, it is reasonable to expect that rates of leaf photosynthesis and respiration affect RGR. These factors might not, however, be the only ones that matter. For example, suppose one plant species allocates almost all its resources to roots rather than leaves, while another allocates most of its resources to leaves. The leafy species might grow faster, even if its per-mass photosynthetic rate is lower, simply because it has more tissue that can acquire carbon and energy (i.e., leaves). Of course, the outcome might not be so easy to predict. The leafy species has traded off some ability to acquire water and soil nutrients. If those resources limit growth more strongly than light limits growth, then the rooty species might actually be the faster grower. Thus it may be valuable to characterize a species’ allocation when you estimate its RGR. Root-shoot ratio (root mass over shoot mass) and root fraction (root mass over total mass) are suitable allocation measures; the latter is preferable because fractions tend to be better “behaved” (in a statistical sense) than do ratios.

*Class exercise.* Just as sections of Bio 251 estimated rates of leaf photosynthesis and respiration for each study species, sections of Bio 252 will estimate each species’ RGR and allocation. Each research group will be responsible for providing the rest of the class with estimates of RGR and root fraction for a single species. Take over the experiments that your instructors have already begun. This week take a random sample of $N/2$ of the individuals, harvest entire plants, clean them carefully, separate them into roots and shoots, and record wet weight’s of each, put them into envelopes in an oven, and dry them, and weigh them after 48 h for dry weight. Next week, repeat these steps for the remainder of the plants in your experiment. Estimate root fraction as the mean value of week 1 root mass, divided by week 1 shoot mass. Estimate RGR as above.
Investigation 2 – Causes and consequences of carbon dynamics in biological systems: Scaling from molecules to ecosystems

Fig. 1. Bio 251 investigations. Some controls of variation in carbon and energy dynamics at the leaf level.

![Diagram](image1)

A. Leaf photosynthesis and respiration (& their environmental responses), Allocation of resources to different tissues & functions, Nutrient and water relations, Environment

B. Growth rate & its controls

Growth rate

Competitive performance

Fig. 2. Bio 252 investigations: Some controls of variation in individual growth rate (A) and competitive ability (B).

![Diagram](image2)

Productivity of individual species, community composition, environmental conditions (including history of disturbances such as fire)

Dynamics of biomass and energy in ecosystems

Fig. 3. Bio 252 investigations: Some controls of ecosystem energy flow and material cycling.

Investigation 2 – Causes and consequences of carbon dynamics in biological systems:
Part 2: Interspecific competition projects

*Interspecific competition in plants.* Most plants occur in communities that consist of several (sometimes hundreds of) coexisting species. How so many plant species coexist when all plants have the same basic resource requirements (space, light, soil nutrients, and water) is not fully understood (We encourage you to search the literature for the latest and best ideas.) One way to develop understanding of plant diversity is to investigate mechanisms and consequences of interspecific competition in plants. What happens when two plant species compete for the same resources? Is it possible to predict the outcome of competition under a given set of environmental conditions by knowing certain characteristics of the study species (e.g., photosynthetic rates or RGR)?

*Designing competition experiments.* You should ask yourself some questions before you begin.

- The first set of questions your group must answer concern what you want to learn.
  
  a) Which species will you study, and why? Select study organisms for which there is a sound rationale for studying interspecific competition. Consider ecological, physiological, and perhaps even economic interests. Why would someone want to know how those species perform in competition? What do you know about the species’ photosynthesis, respiration, RGR, and allocation? Can knowing these features help predict the outcome of competition?

  (b) More specifically, what do you want to know about those species? You may want to know which species “wins” in mixtures of two species, or you may want to quantify how one species affects the performance of the other, or, who knows? Maybe you want to know something else!

2. The second set of questions to address concern how to perform the comparison. Evaluating relative long-term competitive ability may require field experiments that take several years. Evaluating short-term competitive ability (which should have consequences for long-term performance) is simpler, at least in principle. At a minimum, to estimate competitive ability, you need to compare the performance of each species in and out of competition with the other. While you ponder possible designs for your competition experiments, make sure that your design

- gives a clear answer,
- has sufficient replication for statistical power, and
- is straightforward to analyze.
(a) How will you mix the two species in your experiment?

There are four basic ways to create mixtures of two species for the purpose of investigating competition.

- **Pairwise experiments** do not vary density, though they may vary other factors, such as resource levels.

- **Additive series** experiments vary the density of one species but not the other. The simplest form would be to set up one treatment as a species grown alone (at a set density, perhaps just a single plant per replicate), while the other treatment is identical except that the other species is added (at a set density, perhaps just a single plant per replicate).

- **Replacement series** experiments vary the density of each species, while keeping total density constant. These are the designs you’re most likely to see in an introductory textbook. (This does not mean that they are always the best design!)

- **Response surface experiments** vary both the density of each species and the total density of the mixture in each replicate.

(b) Which, if any, of these experimental designs could tell you what you want to know?

(c) What is the appropriate statistical analysis for each kind of experiment? Which are the easiest designs to analyze, and how easy would it be to interpret the analysis?
Experiment planning form  

Group___________________________  Instructor check? ____

- What is your central scientific question?

- If a hypothesis is appropriate for this study, state and justify your hypothesis.

- What results are possible, and what would results do you predict?

- Describe briefly the study design and methods you will use, including experimental and/or observational features, sample sizes, number of replicates, etc.
• What data will you record?

• When and how often will you record data?

• How will you display the results of your study?

• If you plan to use one or more graphs, draw prototypes of them, including a sample figure caption and labeled axes. Be sure the graph presents analyzed data – not raw data. Include error bars if necessary.

• Do the results obtained from your data and reported in the tables and graphs relate directly to your question and, if applicable, your hypothesis?
### Schedule

<table>
<thead>
<tr>
<th>Week</th>
<th>Objectives</th>
<th>Outcomes</th>
</tr>
</thead>
</table>
| 4-5   | 1. Take Bio 251 findings and make predictions about variation in growth rate and performance in competition, based on interspecific variation in chlorophyll, photosynthesis, respiration, environmental responses, or other features.  
     | 2. Each group is responsible for estimating RGR in one species and making the data available to all.                                                                                                         | 1. Develop technical and conceptual expertise.                                                 |
|       | 3. Individual groups design and begin interspecific competition experiments.                                                                                                                                 | 2. Estimate RGR for each species, and analyze contributions to RGR of physiological traits characterized in 251 |
| 5-13  | 1. Care for, collect data on, harvest, and analyze competition experiments.                                                                                                                                   |                                                                                               |
| 14    | 1. Turn in scientific articles about competition experiments.                                                                                                                                                  | 1. Experience the intense satisfaction of a job well done.                                     |
|       | 2. Estimate standing crops, soil organic matter, soil respiration, etc. in CERA experiments                                                                                                                   | 3. Compose and turn in science journalism articles about system carbon dynamics in tallgrass prairie. |

*Detailed description of these investigations will be distributed when their time nears.*