Species Interactions in Goldenrod Communities
What can we learn from studying ecological interactions
between organisms of different species?

[Most of the ideas and resources for this lab came from educational materials developed by C.F. Sacchi (Teaching Issues and Experiments in Ecology 2006), W.G. Abrahamson & P. Heinrich (Solidago & Eurosta website 2005) and C.J. Yahnke (American Biology Teacher 2006).]

OVERVIEW
In this three-week lab, students examine hypotheses about the interactions between herbivores and plants or herbivores and their predators in goldenrod communities. This lab involves the study of the relationship between tall goldenrod and gall-forming herbivorous insects and their insect and bird predators. Students, working in groups of four, may address a variety of questions: do plants with particular attributes differ in susceptibility to attack by herbivores, do herbivores act as parasites, commensals, or possibly mutualists when they feed on plants by having a negative, neutral, or positive effect on plant reproduction, and do predators choose galls with particular characteristics (as well as many others). In this lab, students will discuss the nature of the interaction of herbivores with plants or predators with herbivores, collect original data, analyze data, examine primary sources from the research literature to address the hypothesis they tested, and draw conclusions and communicate their findings in group presentations.

PART 1: Week of Sept. 10: Introduction to study system and developing hypotheses and research methods (in lab room)
PART 2: Week Of Sept. 17: Data collection in field (different sections will be going to different field sites – your GSI will let you know)
PART 3: Week of Sept. 24: Data analyses and presentation preparation (in computer lab in SLC)
Group Presentations given in following week (week of Sept. 24) at beginning of class during first Evolution lab

BEFORE COMING TO LAB:
1. Read this entire lab handout.
2. Complete the Reading Assignment for this lab (below).
3. Answer the Pre-Lab Questions.
4. Bring the following with you to lab:
   A copy of this lab handout.
   A copy of the three papers from the reading assignment
   A pen and notebook or loose-leaf paper.

Download the following papers from the CTools course site and read the “Introduction” section of each paper.
Be ready to discuss these questions in lab.
1) What is herbivory? Name three types of herbivores and the plant tissues that they feed on. Are all plants and plant tissues equally available as sources for nutrition for herbivores?
2) What are the predictions made by the Plant Vigor and Plant Stress hypotheses? How can you test each of these hypotheses?
3) What are the predictions made by the Herbivore Impact, Herbivore Tolerance and Overcompensation hypotheses? How can you test each of these hypotheses?
4) What is natural selection? List the possible ways that species interactions can influence the traits of plants, herbivores and predators in the goldenrod community.
5) How can gallfly predators affect gall size? What size gall do you expect to find in communities with lots of downy woodpeckers? What would the optimal gall size be in areas where Eurytoma wasps are abundant?

PART 1: Week of Sept. 10
Introduction & Hypothesis Design

Species Interactions in Goldenrod Communities
What can we learn from studying ecological interactions between organisms of different species?

Ecology is the sub-discipline of biology that concentrates on the relationships between organisms and their environments. It seeks to explain the factors that determine the range of environments that organisms occupy and how abundant organisms are within those ranges. It also emphasizes functional interactions between co-occurring organisms. When organisms live together, they inevitably interact in many ways. Over time, these species interactions shape the traits that organisms display. This lab is designed to allow you to explore species interactions using the scientific process. You will develop a hypothesis, design an observational field study, analyze your results, and present your research findings to the class.

As primary producers, plants form the foundation of terrestrial trophic pyramids in terrestrial ecosystems providing a source of nutrition, first, for primary consumers. These primary consumers (called herbivores) include invertebrates, primarily insects as well as some vertebrates, including mammalian herbivores such as white tailed deer and rabbits. The question of whether all plants provide food that is equally accessible to herbivores could be studied in light of the observation that plants produce a variety of secondary chemical compounds that cause plants to differ in their palatability to herbivores.

Many plants also have also evolved physical defensive traits, aside from chemical compounds, that allow them to escape from herbivory. Such traits include spines and thorns, hairs on leaves, and tough tissues that include highly indigestible compounds such as lignin. With both chemical and physical defenses, plants can differ in their suitability as food for herbivores. Herbivores in turn have diversified to feed on plants and the different tissues produced by plants. Free-feeding insects live and feed on the exterior surface of plants. Endophytic insects, which are not free-feeders, are confined to, and develop within, a particular plant structure; such species include gall-forming insects and leaf miners. Gall-forming insects lay their eggs in plant tissue and
induce the plant to produce a conspicuous protective structure, the gall, within which the juvenile insect feeds and develops.

The diversity of herbivores, their feeding habits, the tissues that they feed on, and other elements of their biology result from the complex interactions between plants and the herbivores, as well as the enemies of the herbivores. Within a population of a given plant species there is variation in attack by herbivorous insects which has led to a variety of hypotheses to explain why some plants are more readily attacked by herbivores while other individuals in the same population experience lower levels of, or even escape, herbivore attack.

Goldenrod and Gall-Forming Insects
The tall goldenrod, *Solidago altissima* (Asteraceae), is a widely distributed fall-flowering species found in successional fields, prairies, or woodland edges throughout eastern and central North America. The plant flowers in late summer into fall and produces many small seeds in each inflorescence that are evident on plants in early to late fall.

Stems of tall goldenrod are attacked by three different species of gall-forming insects. The gall forming insects and the names for the gall they form are: 1) *Eurosta solidaginis* (Diptera: Tephritidae) that forms the goldenrod ball gall (see figure 1), 2) *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechiidae) that forms the goldenrod spindle gall (see figure 2) and 3) *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae) that forms the apical rosette gall (also called the bunch gall, see figure 3). Following oviposition by the female insect in late spring, the galls begin to develop and become evident in early to mid-summer. Much is known about the biology of the goldenrod ball gallfly, *Eurosta solidaginis*, (you will watch a video of this species in lab) but the other two species of gall-forming insects are less well studied. In the Ann Arbor area, both ball galls and rosette galls are present on tall goldenrod (see Table 1 for key to *Solidago* goldenrod species and figures 1 and 3 for pictures of the galls).

Conceptual Background
Gall-forming herbivores may improve their offspring's growth and potential for reproductive success by choosing to oviposit (lay eggs) on individual plants of high nutritional quality. One hypothesis, the *Plant Stress Hypothesis*, proposed the idea that plants that were physiologically stressed as a result of lack of water would provide the best food for herbivores because these plants produced tissue that contained higher nutrient content, particularly nitrogenous compounds in the form of free amino acids (White 1993). This hypothesis suggested that plants exposed to drought might be more susceptible to herbivore attack; further, this susceptibility to herbivore attack might account for observed outbreaks of herbivorous insects often following periods of drought.

A second hypothesis, the *Plant Vigor Hypothesis*, proposed that herbivores should prefer healthy, vigorously growing plants that provide abundant nutrition to allow insects to feed and grow more rapidly (Price 1991). Plants growing in environments that provide abundant water and mineral nutrients and that provide access to appropriate levels of sunlight may grow more rapidly than plants that are deficient in any of these resources making such plants high in nutritional quality. There have been studies that have supported both hypotheses; some have shown that water-stressed plants are attacked most heavily by herbivores offering support for the
Plant Stress Hypothesis (White 1984). Other studies have shown that plants of great vigor may support the highest survival and most vigorous growth of herbivores, lending support for the Plant Vigor Hypothesis (Craig et al. 1986). Price (1991) suggested that the Plant Stress and Plant Vigor Hypotheses should not be seen as strict alternatives that would lead to one hypothesis winning out over the other, but rather as ends of a continuum to account for the diversity of responses of herbivores to plants found in diverse natural systems.

In traditional theories about the evolution of plant defenses in response to herbivores, a central assumption was that herbivores would reduce the fitness, the reproductive success, of plants they feed on (Strong et al. 1984). The Negative Impact Hypothesis states that herbivores will lead to reduced reproductive success of plants that are fed on by insects. In recent years, researchers have suggested the Plant Tolerance Hypothesis, the idea that plants faced with herbivory may have evolved the ability to tolerate the loss of tissue that is either consumed by herbivores or allocated to galls. With tolerance, plants fed upon by herbivores will produce a similar number of seeds compared with plants that have not been attacked by herbivores (Strauss and Zangerl 2002). Finally, a third hypothesis about plant response to herbivores has been advanced. The Overcompensation Hypothesis proposes that plants attacked by herbivores are able to produce more flowers, fruits, and seeds than plants that have not been attacked by herbivores (Paige and Whitham 1987). The reproductive response of tolerant plants or of those that overcompensate may result from increased photosynthesis in plants attacked by herbivores, reallocation of stored resources, or increased growth rate (Fornoni et al. 2003).

Herbivore-plant interactions also influence the herbivore’s biology. In goldenrod communities, the probability that a gallfly larva will survive is greatly influenced by the size of the gall that a larva induces in the host plant. But what size gall is the best? As it turns out, this depends on several different factors. In places where the Eurytoma gigantea wasp (a very effective predator of gall fly larvae) is abundant, there is strong selection for large galls. This is because large galls have walls that are too thick for the wasp’s ovipositor to penetrate, protecting the gall fly larva. In this case, flies that produce large galls may have high fitness, while those that produce small galls may have low fitness. In areas where downy woodpeckers and chickadees are abundant the story is different. Downy woodpeckers and chickadees are also very efficient predators of the gall fly larvae and preferentially choose large galls over small galls. It's assumed that they choose large galls because those galls are likely to contain larger larva, making a better meal for the effort. So, in areas with lots of bird predators, flies that produce large galls may have low fitness and flies which produce small galls may have high fitness. Finally, in the case where both Eurytoma gigantea wasps and downy woodpeckers and chickadees are common the two competing selection pressures produce a net selection for intermediate (medium) sized galls. Other factors that have been shown to affect gall size are the ability of the flies to produce large or small galls and the effect of the plant’s genotype on gall size.
**Possible Ecological Questions That Can Be Addressed in the Goldenrod System**

Usually in this class, we will expect you to develop your own research questions, but we suggest some possibilities in this first lab since you are all new to the scientific process.

1. Does host plant vigor or physiological condition (as measured by plant size) influence the oviposition (egg-laying) decision of a gall-forming herbivorous insect?
2. What are the effects of these oviposition decisions and gall formation on subsequent host plant growth and reproduction?
3. Why might the physiological condition (as measured by plant size) of a host plant matter to an herbivore?
4. Do different predators (wasps or birds) of the gallfly select particular gall characteristics?
5. Do females of different species of gall-forming herbivorous insects select host plants with similar characteristics?
6. Do females of gall-forming herbivorous insects select stems in dense host plant stands or do they prefer isolated stands of their host plant?

**Additional Useful References:**

A. You will be assigned to lab groups (3 - 4 students per group) to compare your responses to the pre-lab questions.
   • Develop a group consensus to the pre-lab questions
   • Whole class discussion of pre-lab questions
B. What questions about ecological interactions in the goldenrod community does your group find most compelling?
C. What can you measure in the field to test your ideas?
   • What are some characteristics of the goldenrod plants or the herbivore galls or the predators that you can measure easily in the field? Keep in mind that some questions may be more appropriate in fall or winter seasons – see figure 4 for life cycle of one common gall-forming insect.
   • What constraints are we faced with in this laboratory? Remember, due to time constraints (only 3 hours for data collection) and because we don’t want to negatively impact the natural area we are studying, this field study will be **observational**, not experimental. We will not manipulate or kill plants, herbivores or predators. We will measure characteristics on one or more of these species but leave the community as intact as possible once we have completed our measurements and observations.
D. Designing your observational field study.
   • Decide what questions about species interactions you would like to explore in the goldenrod community and construct your hypothesis and the methods to test it.
   • Using the Field Study Design Work Sheet as a guide, design your observational field study.
Species Interactions in Goldenrod Communities

Field Study Design Work Sheet:
Lab Group: ______
Student Names: ___________________________  ___________________________
____________________________________  __________________________________

1) Describe the rationale for your observational field study. In a short paragraph (4-5 sentences) describe the question about species interactions that you will test. Explain what you are planning to test and why you have selected the specific methods you plan to use.

2) State the specific hypothesis that will be tested. Write a concise statement in 1 or 2 sentences describing a tentative explanation for the scientific problem about species interactions that you are planning to test. Remember that your observational study should be designed to either support or discredit this hypothesis.

3) Design the methods you will use to collect your field observational data. Be as detailed as possible and have backup plans in case your original methods don’t work well in the field. You will only have a limited time (less than 3 hours) in the field so you will need to know exactly how you are going to collect your data before you go out there.

On the day your lab section is scheduled to go into the field, each lab room will have access to the following supplies: tape measures, meter sticks, rulers, dial calipers. You must remember to bring some paper and a clipboard as well as a pen or pencil, water and wear appropriate field clothing.

In your lab group, develop one copy of the Field Study Design Worksheet to turn in to your GSI for review before you leave lab.
PART 2: Week of Sept. 17

Data Collection
A. Record data on your observational field study.
B. You may want to search for peer-reviewed literature on the internet for the introduction of your presentation. Useful sites include:
   - Google Scholar - http://scholar.google.com/
   - Web of Knowledge - http://portal.isiknowledge.com/
C. Assign members of your group to develop rough drafts for the Introduction and Methods sections of the presentation your lab group will present at the completion of this laboratory unit.

PART 3: Week of Sept. 24

Data Analysis & Presentation Preparation
A. Prepare graphs for your data using Microsoft Excel.
B. Analyze your data following the guidelines laid out in lecture.
   What conclusions can you make based on your findings? Do your findings support or refute your lab group’s hypothesis?
C. Begin preparing the Results and Discussion sections of your presentation.
D. Develop Presentation.
   Each lab group will prepare a presentation. The presentation should include a Title, Introduction, Materials and Methods, Results, Discussion, and Future Directions sections. The presentation must include figures and graphs that include descriptive legends. It should also cite all references used in preparing the talk.
E. Reflection: On an index card, list three skills/abilities that you were able to practice during this lab that you think you might use in the future.
Figures 1: ball gall, Fig. 2 elliptical gall, Fig.3 rosette gall. from Abrahamson & Heinrich *Solidago Eurosta* Gall Homepage [http://www.facstaff.bucknell.edu/abrahmsn/solidago/plantid.html](http://www.facstaff.bucknell.edu/abrahmsn/solidago/plantid.html)
Table 1. Some Notes on Recognition of the Members of the *Solidago* Polyploid Complex
from Abrahamson & Heinrich *Solidago Eurosta* Gall Homepage
http://www.facstaff.bucknell.edu/abrahmsn/solidago/plantid.html

<table>
<thead>
<tr>
<th>Species Name</th>
<th><em>Solidago gigantea</em> (tetraploid &amp; diploid)</th>
<th><em>Solidago canadensis</em> (diploid)</th>
<th><em>Solidago altissima</em> (hexaploid)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Name</td>
<td>Late Goldenrod</td>
<td>Canadian Goldenrod</td>
<td>Tall Goldenrod</td>
</tr>
<tr>
<td>Habitat</td>
<td>Wet spots in open fields, meadows, ditches. Occasionally under shade of deciduous woods.</td>
<td>Generally found in open areas, but avoids the very dry portions of fields, where <em>S. altissima</em> tends to predominate.</td>
<td>Most cosmopolitan of the three ploids in habitat preference, can grow side-by-side with other two but usually found by itself in very dry habitats (hillsides, roadbanks, backlogs, etc).</td>
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<tr>
<td>Stem</td>
<td>Totally glabrous (smooth) from ground level up to inflorescence. Often with a waxy whitish bloom that gives the stem a pale blue or purple cast. Distinctive.</td>
<td>Has villous (woolly, long-haired) pubescence from inflorescence 1/2 to most of the way to the ground, often tapering off sharply on the bottom few inches.</td>
<td>Entire stem is pubescent (hairy), usually with very short, almost granular-gritty hairs. Some forms, however, show a long, woolly pubescence similar to <em>S. canadensis</em>. Separate using leaf characteristics.</td>
</tr>
<tr>
<td>Leaves</td>
<td>Very sharply serrate (with small toothed edge), always totally glabrous above. Usually smooth below, although some plants show pubescence on major leaf veins.</td>
<td>Sharply serrate to dentate (deeply cut, sawtooth teeth), smooth or slightly scabrous (course) above, with pubescence on underside but confined almost entirely to the three major leaf veins. Leaves can be very broad on some plants.</td>
<td>Shallowly serrate to subentire (almost no teeth); almost always smoother edged than leaves of <em>S. canadensis</em>, but highly variable. Usually very scabrous above and with pubescence over entire underside, not just on veins. Leaves tend to be more lanceolate (narrow) than <em>S. canadensis</em>.</td>
</tr>
<tr>
<td><strong>Flowers</strong></td>
<td>Not needed to identify this distinctive species. Bloom starts in very early July-early August.</td>
<td>Involucral bracts usually 2-3 mm high, ray flowers about 2.5 mm long. Bloom starts in late July.</td>
<td>Involucres tend to be large (&gt; 3 mm), as do ray flowers. Inflorescences can sometimes be enormous. Bloom commences later, usually August.</td>
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<tr>
<td><strong>Remarks</strong></td>
<td>Easiest ploid to identify. In southern PA, it seems to be totally free of ball galls, but is a common host to the elliptical gall and occasional rosette galls in northern PA. In New England and the upper midwest ball galls are common. In Ann Arbor area, few galls of any species were found. Not a rare goldenrod species, but never as plentiful as <em>S. altissima</em>.</td>
<td>Like <em>S. gigantea</em>, seems to be free from all but the occasional ball gall. Often tricky to separate from <em>S. altissima</em>. This species often looks darker green than <em>S. altissima</em>. Not common, doesn't seem to occur in huge unbroken clones like <em>S. altissima</em>. More common in northern New England.</td>
<td>Any plant in central PA with a ball gall is liable to be this species. Also host to elliptical, rosette, and various leaf galls. Can grow in amazingly barren ground, i.e., railroad embankments. Abundant. In Ann Arbor area, host to both ball galls and rosette galls.</td>
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Late Wasp
Egg Laying
Early Wasp
Spring
Emergence
Summer
Winter
Bird Attack
Fall
Flower Beetle
Late Wasp
Fig. 4 Ball Gall Fly Life Cycle & Predators