Chapter 12. Competition.

Today's activities:

1. Collect data on survival, size, and mass of plants
2. Plan data entry
3. Discuss our findings
4. Discuss expectations for lab report

What you should get out of today's class:

You should get a feeling for how to think and work through a controlled experiment, with treatments, controls, and replicates. You should understand the concept of competition in the sense of what happens to individuals and in the sense of how it can contribute to the development of community structure. You should also be getting comfortable with how to bring real data and models together to produce deep insights into how nature works.

Handouts:

1. Imhoff, M. L., L. Bounoua, T., Ricketts, C., Loucks, R., Harriss, R., and W. T. Lawrence. 2004. Global patterns in human consumption of net primary production. *Nature* 429:870-873.

Introduction

The theory of natural selection assumes that living organisms compete for limited resources. Those individuals with phenotypes that allow them to more efficiently gather those limited resources and turn them into viable offspring are favored over time and are selected for. In the case of plants, competition between neighbors for sunlight, water, and nutrients influence patterns of growth and reproduction (Harper 1977). In other words, nearby competitors of the same or other species reduce the amount of resources available to an individual, which may then suffer reductions in growth, reproduction, germination, and survival. In addition, competition may affect how plants allocate resources to aboveground or belowground growth and reproductive structures (such as flowers) (Harper 1961).

Plants have developed mechanisms to deal with competition. Competition for light results from shading by the leaves and stems of neighboring plants. To compensate for the reduced light availability caused by their neighbors, plants may change leaf morphology to capture more of the available sunlight (recall our *t*-test on shade versus sun leaves in **Chapter 2: Introduction to Ecological Methods**). Competition for water and nutrients occurs belowground. Plants have evolved root structures to access water in different parts of the soil column (such as on the surface or deeper down), allowing some plants to grow a little closer together without experiencing quite as much competition. And some plants, such as creosote bush (*Larrea tridentata*), may even excrete chemicals into the soil that inhibit the growth of nearby plants (known as *allelopathy*), effectively reducing the competition experienced by the allelopathic plant (Mahall and Callaway 1992).

Competition also contributes to the development of plant communities. Have you ever noticed that mature forests tend to have widely spaced trees, whereas younger forests tend to have trees spaced more closely together? When a forest begins to regrow after a disturbance, many seeds may germinate, and many small young trees will begin to grow. As the trees get larger however, their demand for nutrients increases, causing increased competition among the trees. Ultimately, many of the young trees die out, leaving a maturing forest with more widely spaced trees. This decreasing density of stems as the stems get larger is called *self-thinning*.

As you may have guessed, the negative relationship between the number of plants and the size of the plants follows a power law. We can write:

$$M = kD^{\Theta} \qquad \text{equation 10.1}$$

where M is plant mass, D is plant density, Θ is the exponent characterizing the relationship, and k is the prefactor (see **Sidebar: Anatomy of a Power Law**, page 17).[3] Original estimates of Θ were -3/2, fitting a simple geometric model of plant growth (Yoda et al. 1963). The geometric model is based on the idea that plants fill a three-dimensional space but cover ground in only two dimensions (thus 3 over 2). Recent evaluations of the rule suggest a value of Θ = -4/3, which can be accounted for by a fractal model of plant allometry (Weller 1987, Niklas 1994, Enquist et al. 1998). An allometric relation, again, is one where traits of various organisms can be linked to body mass via a power law (see **Chapter 3: Allometry**). In this case, the fractal branching of a plant's roots and stems determines how much space is required by a plant of a given body size, which in turn determines how many individuals can fit in an area. Try to imagine how a tree's branches and roots fan out and begin to intermingle with the branches and roots of neighboring trees. Branching structure determines how much space a plant needs. The exponent is -4/3 because the plant is operating in three dimensions plus time (four dimensions) to move resources through the branching network, but they do it through space (thus 4 over 3).

In this exercise, we will perform a controlled greenhouse experiment with cultivated radish to measure competition in plants and test the theory that plant mass scales with density to the -4/3 power. We will plant seeds at a variety of densities, watch them grow, and measure the relationship between size and density at the end of the experiment. Because competition impacts survivorship, growth, and reproduction, we also will examine the effects of density on survivorship and on the tendency to store energy in tubers (the radish itself).

Hypotheses

1. There will be lower survivorship as densities increase,
2. The plants will grow larger at lower densities, creating a negative relationship between plant mass and density,
3. The mass of the plants will scale to density to the -4/3 power,
4. The plants will be less likely to store energy in tubers at higher densities.

Materials

- 36 10-cm plastic pots
- 36 plastic markers
- 2 plastic starter trays
- Newspaper
- Sand and potting soil thoroughly mixed at a 1:1 ratio

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3 Notice that instead of having the plant density depend on body mass, as allometry typically does, we have the mass depend on density. This approach is simply a convention that has differed over the years between plant and animal biologists. The same relationship can be had if the variables were switched, but the exponent would be the negative inverse of the original. Instead of the predicted -4/3, for example, we would predict ¾ for density scaled to mass.

- ~850 radish seeds
- Rulers
- Electronic balance

Planting Methods

1. Set up the pots in the trays. We will decide on replicates and treatments in class, but we often have 4-8 replicates of four density treatment (2 and 10 or 25 and 50 plants). Each class section will set up the same number of replicates. We will distribute all the pots among about four trays on our lab bench in the teaching greenhouse.

2. Tear (~15 cm by ~15 cm) squares of newspaper and crimp into the bottom of each pot.

3. Mix the potting soil.

4. Fill each pot with an equal amount of soil. The easiest way to do this is to fill the pots up to about 1.5 cm from the top of the pot, or to the point where the pot gets a little wider, if it does, or to a lip in the pot, if there is one. Try not to let the soil quantity vary from pot to pot.

5. Label pot stakes with the treatment and the replicate (eg, 10 a = 10 plants and replicate a). Insert the pot stakes randomly into the pots. You do not need to conduct a computerized randomization of the replicate and treatment layout, just blindly put the stakes into the pots, and then have several students rearrange the pots over and over until you are comfortable that any unintended bias is removed. You may decide on another approach to randomization as well.

6. Lay the correct number of seeds out for each pot. Add extra seeds to make sure that if not all seeds germinate that we will still have the correct number of plants (we will decide as a class how many extra to add). After germination, we will randomly prune the seedlings down to the correct treatment level.

7. Push the seeds no more than ¼ inch into the soil and cover with a small amount of soil.

8. Lightly spray the top of the soil with water and fill the tray up to about 1 inch deep with water.

9. Sign up to water the plants, and note your watering days on your calendar. On every other day we will rotate the flats so that they all get equal exposure to the light during the course of the experiment.

10. We will thin the pots after about two weeks.

Measurement Methods

1. We will do all of the measurements on the day the competition lab is scheduled. Bring all of the plant trays into the lab.

2. When we get started, always take care to note which treatment and replicate you have.

3. Count the number of surviving stems in each pot. You may have to decide what constitutes surviving because some plants will be yellowing and not dead yet. Assume that the original number of plants in a pot can be determined by the total number of living and dead shoots.

4. Measure the height of the plants from the soil surface to the extent of the tallest leaf. Grab the tallest leaf of all of the plants and estimate the highest extent for the plants as a group, and take your measurement there.

5. Dig up the plant and shake the soil loose from the roots. Determine the mass of the plant by weighing it on the electronic balance. Cut off the radish itself and weigh that. Now we have the whole plant mass, the aboveground mass, and the belowground mass.

6. If the plants have sent up inflorescences (flowering stalks), we will want to quantify the number, height, and perhaps number of flowers, too.

Analysis Methods

1. Enter measurements into a spreadsheet, pool among sections, and distributet to whole class.

2. Evaluate the effect of density on the mass of the plants
   - 2.1. Calculate the mean above-ground, below-ground, and total mass of the plants for each pot. Do this for separately for plants that flowered and for plants that flowered. That is, for each pot, there are going to be two sets of averages. (This is already done for you).
   - 2.2. Take the log (base 10) of the masses and the density. (You must modify the spreadsheet and do this yourself).
   - 2.3. Plot all three types of log mass (whole plant, above ground, and below ground) against log density. There should be two plots one for plants that flowered and one for plants that did not. Add the linear regression trendlines and their equations to the graph. Plot the R^2 value and the fitted regression trendlines on the plot. Note: you can move the legends around so that they are more legible and easier to connect to the correct trendline. Make sure that the legend clearly states which set of data are plotted with each color or symbol.
   - 2.4. Using the coefficients from the regression equation above, produce the power laws that relate each type of plant mass to density. You might consider putting all of the power laws in a table in the lab report.

3. Evaluate the scaling relation between flowering and density
   - 3.1. Do the same type of plot as in 3 above. This time however, plot the log(density) on the x-axis and the log(average # of flowers) on the y-axis. Fit a linear trendline and add R^2 and equation to the graph. Make sure to use only the set of data for plants that flowered.

Results and Discussion

What did we learn? Did the plants get smaller as density increased? ________. Can you list the resources for which the plants competed that would cause this pattern? __________________ ____________________________. Were there any results, perhaps a particular treatment, that came out other than expected? Was there a lot of within-treatment variation? What would cause the variation?

Did we find the expected power law between size and density? _________. What was the scaling exponent? _________. Was this close enough to -4/3 to believe that is really what we found? _______________. If not, why do you think it wasn't? Did the experiment give an adequate test of the theory?

Literature Cited

Enquist, B. J., J. H. Brown, and G. B. West. 1998. Allometric scaling of plant energetics and population density. *Nature* 395:163-165.

Harper, J. L. 1961. Approaches to the study of plant competition. Pp 1-39 *in* Mechanisms in Biological Competition (F.L. Milthorpe, ed.), Symposium No. 15, Society for Experimental Biology. Cambridge University Press, Cambridge.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London.

Mahall, B. E., and R. M. Callaway. 1992. Root communication mechanisms and intracommunity distributions of two Mojave desert shrubs. *Ecology* 73:2145-2151.

Niklas, K. J. 1994. Plant Allometry: The Scaling of Form and Process. University of Chicago Press, Chicago.

Weller, D. E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. *Ecological Monographs* 57:23-43.

Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology Osaka City University* 14:107-129.

Homework # 12 – Lab Report 3 (30 points)

Assignment

You will write up a lab report covering this chapter's questions and analyses. The report is due on November 20st (Tuesday section) and 21nd (Wednesday section). Write a short but complete report that tells what your question was, how you answered it, and what the answer was.

What needs to be in the report:

1. *Introduction*. Introduce the topic of intraspecific competition and how it influences access to resources and growth. In your own words describe the theory relating plant size to density. Describe how your study relates to that theory. What specific questions are you asking? Generally, how are you going to answer them? Specify what needs to be shown to support or refute your hypothesis. Strategically, you want to pose a compelling question that is answerable by the results, thereby creating a meaningful storyline for the reader to follow.

2. *Methods*. Describe what you did in just enough detail to allow someone else to repeat your study.

3. *Results*. Without any discussion our interpretation, describe what you found. You must include the figures discussed in 2 and 3 of the analytical methods above. The graphs must be produced in a spreadsheet program. Each graph must have clearly labeled x- and y-axes and a figure legend (below the figure) that orients the reader to the result. In the text, describe the results in words. For example, you could say, Survival of plants declined with increasing density of plants (Figure 1), or Plants were taller in the low-density treatments (Figure 2). Say what you found as simply and directly as possible. As an author, your task is to guide the reader's attention to the key information. Some specific style requirements are 1) use the past tense, as you have already conducted the study, and 2) do not add additional tables of data or printouts of your spreadsheet.

4. *Discussion*. What is/are the answer/s to your question? Is it what you expected? If not, why not? Were the methods insufficient? Were there enough data? How does this study relate to the major studies? Was there something we did that limits what we can say from our results? Do you have alternative interpretations that are consistent with your results?

5. *Literature cited*. Properly list the references cited in your text. The list should definitely include Enquist et al. (1998). It should also include at least two other peer-reviewed journal articles that you have found. Format references like the **Literature Cited** of this chapter.

Grading key to the lab report on competition and mass-density scaling

Use this key to help you include the necessary components of the paper (30 points total).

Introduction (6 points)

- General opening to paper..1
- Defined competition..1
- Described theory of size-density scaling (i.e., the power law that relates them)..1
- Stated hypothesis/question..1
- Errors and readability..2

Methods (8 points)

- Explained our experimental setup..2
- Explained our efforts at reducing bias and confounding variables..1
- Explained how we determined flowering, density, and mass..1
- Explained how we determined the power law in our study..2
- Errors and readability..2

Results (9 points)

- All three figures included with legends..3
- Presented relationship between density and flowering..1
- Presented relationship between density and mass..2
- Errors and readability..2

Discussion (7 points)

- Discussed relationship between density and flowering..1
- Discussed relationship between density and mass 2
- Two additional references.. 2
- Critique of methods..1
- Errors and readability..2