Fire-enhanced competition between grass tufts: a mathematical model

Math 23, Spring 2014

Due Date: May 28, 2014

1 Introduction

Your paper will be based on two biology papers on grasses, which are posted on the website. In the introduction to your paper, you will summarize what these papers did and how they relate to the investigation below. You will explain what Van Auken and Bush were testing and how your model will simulate (some of) their tests. In short, what is that article about and why do we want to simulate these results?

In the remainder of this paper, each group will do the basic model analysis and tune the models to a "control" experiment, which is a best match to the data for the grass in the Wallace article. Each group will also be assigned a pair of experiments from the Van Auken-Bush article to simulate for their own unique contribution.

In addition, you will introduce the role of fire in changing how the two species compete with each other. This question is a specialty of Paul Gagnon, ecologist at Murray State University in Murray, Kentucky (http://www.murraystate.edu/paulgagnon), and of interest to his colleague, mathematical biologist Maeve McCarthy. Because of their interest, we will ask you for an electronic copy of your final paper along with a paper copy.

2 Description of the Models

I explain here how I put these models together. Please put this in your own words and, preferably, written better than what you read below.

Before we put grasses in competition, we need to think about how a single tuft of grass grows. Plants grow upward and outward. Therefore, I suggest we model growth of the tuft as a cylinder, as in Figure 1 (see Appendix). We have two differential equations, one describing height of the tuft, H, and one describing surface area occupied, S, which I shall assume is roughly a disk. This disk shaped cross section is measured as the area of the "crown area", which is the growing mass just at the surface of the soil.

Biomass, that is, the total mass of the plant (as measured in the Van Auken-Bush paper) is then proportional to the volume of the cylinder, HS. Carrying capacity limits biomass. I will also assume that horizontal growth is not only limited by biomass, but is proportional to the area of the disk. This simple proportionality reflects the way growth rates are measured in the Wallace paper you received. In Figure 1, you see that height includes both above and below ground height. The ratio of these is measured by something called “root to shoot ratio”, which you will see in the Van Auken-Bush paper. Note that the height reported in the Wallace paper is only above ground, and you need the root to shoot ratio to determine what the full height ought to be.

I did not assume the area of the disk had a natural limit. I put the usual logistic limit on growth of both H and S in terms of biomass. I also limited the height with a second logistic factor depending on height alone, reflecting the fact that these plants never exceed a certain height. I assumed that the natural growth in height is proportional to the height itself. This simplifying assumption is justified by the Wallace paper.

2.1 Growth of a single tuft of grass

Growth is controlled in two ways: by limiting the vertical growth rate by using a logistic limit on H, and a logistic limit on growth in terms of biomass for both H and S. Again, the basic growth rate is a simple proportionality, reflecting the way data on growth rates are given in Figure 1 of the Wallace paper.

$$H' = aH\left(1 - \frac{H}{m}\right)\left(1 - \frac{HS}{k}\right) \tag{2.1}$$

$$S' = bS\left(1 - \frac{HS}{k}\right) \tag{2.2}$$

To enter this into the Big Green Ordinary Differential Equation Machine (BGODEM) with parameter values $a = 0.9$, $b = 0.8$, $m = 2$, and $k = 10$, and initial conditions $H(0) = 0.1$ and $S(0) = 0.1$:

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H=.1, H'=a*H*(1-H/m)*(1-H*S/k)
S=.1, S'=b*S*(1-H*S/k)
a=.9, a'=0
b=.8, b'=0
m=2, m'=0
k=10, k'=0
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Put this equation into BGODEM or Matlab and explore it a bit. Will this model produce plants of different heights depending on initial conditions?

2.2 Multiple Tufts

Consider two separate tufts instead of one big tuft. They must share resources, so the logistic cap reflects the biomass of both of them for crown area, whereas the height does not have such an added constraint. However, according to biologist Paul Gagnon, crowded grasses should grow taller than uncrowded ones. Does the model reflect that? How would you interpret this height limitation in the context of competition?

In the following model, H and S are the height and crown area of the first tuft and G and R are the height and crown area of the second tuft.

$$H' = aH\left(1 - \frac{H}{m}\right)\left(1 - \frac{HS}{k}\right) \tag{2.3}$$

$$S' = bS\left(1 - \frac{HS}{k} - \frac{GR}{k}\right) \tag{2.4}$$

$$G' = aG\left(1 - \frac{G}{m}\right)\left(1 - \frac{GR}{k}\right) \tag{2.5}$$

$$R' = bR\left(1 - \frac{GR}{k} - \frac{HS}{k}\right) \tag{2.6}$$

In the language of BGODEM:

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H=.1, H'=a1*H*(1-H/m)*(1- H*S/k)
S=.1, S'=b1*S*(1-H*S/k-G*R/k)
G=.1, G'=a2*G*(1-G/m)*(1-G*R/k)
R=.1, R'=b2*R*(1-G*R/k-H*S/k)
a1=.9, a1'=0
b1=.8, b1'=0
a2=.9, a2'=0
b2=.8, b2'=0
m=2, m'=0
k=10, k'=0
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2.3 Competition

To model competition between two types of grasses, we will assume that this competition constrains the growth of the neighbor's cross sectional area rather than height. There are two kinds of constraints—spatial and direct interference. We will model spatial competition by including both species in the carrying capacity. This is a sort of "fair fight" for space to grow. The second constraint (the terms $-fSHGR$ and $-gSHGR$) measures added competition. What would it mean if $a_1 \neq a_2$, $b_1 \neq b_2$, and $f = g = 0$? What would that say about the nature of the competition between the two? Why would we take $f = g = 0$ as the natural situation if the two plants were the same species? Why might it be desirable to measure f and g for a pair of species?

$$H' = a_1 H\left(1 - \frac{H}{m_1}\right)\left(1 - \frac{HS}{k}\right) \tag{2.7}$$

$$S' = b_1 S\left(1 - \frac{HS}{k} - \frac{GR}{k}\right) - fSHGR \tag{2.8}$$

$$G' = a_2 G\left(1 - \frac{G}{m_2}\right)\left(1 - \frac{GR}{k}\right) \tag{2.9}$$

$$R' = b_2 R\left(1 - \frac{GR}{k} - \frac{HS}{k}\right) - gSHGR \tag{2.10}$$

2.4 Constants

Growth constants a_1, b_1 for *S. scoparium* are given as relative rates in Figure 1 of the Wallace paper. We take the data from June/July because it is similar to the conditions in the Van Auken-Bush article, giving a relative rate of around 0.75 for crown area and 0.9 for height. Maximum aboveground height for *S. scoparium* is given by Wikipedia as 100 cm. To get belowground height, use the root-shoot ratio in Figure 2 of the Van Auken-Bush paper for the control experiment, which we are going to take to be the case when pH is 7 and there is no added nitrogen or phosphorus (-N, -P, pH 7). The maximum height, m, is the sum of the aboveground and belowground heights. Both authors use months as their time unit, and so will we. The carrying capacity, k is arbitrary because it depends how much total land area is being consider. You should take k to be equal to 10.

For *P. plicatulum* we have to work harder. You will scale a_1 and b_1 to get a_2 and b_2. You will find "tuned control constants" in Section 4.1. Find the constant ρ which you must scale by to get the data in the Van Auken-Bush paper for the control to agree as close as possible with your model. The above ground terminal height of *P. plicatulum* is also 100 cm (according to Wikipedia), but the root-shoot ratio is different, so you have to figure out what the terminal height will be. We will assume that $k = 10$ for this species also.

These will be your default constants for the control trials of the two species.

3 Model Analysis

You will analyze three models:

1. the model given by equations 2.1 and 2.2 for a single tuft of grass,
2. the model given by equations 2.3–2.6 for multiple tufts of the same grass (which is a special case of the next model),
3. the model given by equations 2.7–2.10 for two tufts of competing grasses.

Your analysis must include:

1. a full list of critical with parameters given symbolically,
2. the Jacobian for each model,
3. eigenvalues of the Jacobian for the 2-dimensional model (number 1 above) in terms of the parameters (symbolically),
4. the characteristic polynomial satisfied by the eigenvalues of the Jacobian of the 4-dimensional models (2 & 3 above),
5. the actual eigenvalues of the 4-dimensional models (if you can figure them out),
6. discussion of stability of equilibrium states, including algebraic criteria for stability deduced from the formula for eigenvalues.

4 Methods

Here you summarize how you went about tuning the models below. Tables of parameters calculated can go here, as well as the data you are using. The mark of a good methods section is that another person can reproduce your results, so include such things as initial conditions and label all figures in your paper carefully with a legend containing relevant parameters and initial conditions, or other information as necessary.

4.1 Tuning the model to experiments on two grass species

We will model these grasses based on the Van Auken-Bush paper. For example, the table below gives a small fraction of data from Figure 1 of that paper. Notice that we have added the aboveground and belowground dry weight. In addition to the control whose constants were discussed above, variations in added phosphorus, added nitrogen, and pH were tested in that paper. You will simulate one of these tests. For example, in the data table below, there was no added phosphorus or nitrogen, but the pH was lowered to 5.6. This is unlikely to affect the carrying capacity or maximum height, but it will certainly affect the growth rates. From here, I am referring to **control** as the situation discussed in Section 2.4, and your particular extra data (as assigned by the instructor) will be the **experiments**.

trial	initial dry weight	dry weight at 4.5 months	root-shoot ratio
P. plicatulum, -N, -P, pH 5.6, single plant	0.39 +/- .03 g	1.9 g	0.8
S. scoparium, -N, -P, pH 5.6, single plant	0.27 +/- 0.05 g	2.9 g	0.8

Your job is to estimate new constants for your experiments (both *P. plicatulum* and *S. scoparium*). What are the equilibrium values for your model? How do these compare to the control?

In summary, for this part of the project you will do the following.

1. Figure out initial conditions to simulate the trials in Van Auken (both species, one for the control and one for the experiment).
2. Using the constants you derived in section 2.4, run the control for the same time as the experiments were run. If biomass doesn't match up, tune the constants up or down accordingly. We'll call these new constants "tuned control constants" for each of the two species. **Added on 4/29:** Find a_2 and b_2 by scaling a_1 and b_2 by some constant. Choose this constant so that the model most closely fits the data for *P. plicatulum*.
3. Now using the initial conditions for the experiment, tune the growth rates to get the right final biomass at the right time.
4. What are equilibrium values with these parameters?
5. Given the root-shoot ratios described in Figure 2 of the Van Auken-Bush paper, indicate final above and below ground biomasses and heights.
6. Give a clear description of all four trials—the two controls and the two experiments.
7. Give a description of your method for finding the best constants to represent each of the four.
8. Give a table displaying the results of all four runs, which constants gave the best match, final values (height, area, biomass), error with data if you were not able to match it exactly, and the data itself (estimated from Figure 1 in Van Auken and Bush).

4.2 Modeling competition between these two species

The authors then compared two plants of the same species versus one of each species grown together in the same pot. They measured "absolute competition intensity" as monoculture dry mass per plant minus mixture dry mass per plant (at the end of the time period). In other words, final dry mass of *P. plicatulum* grown in a pot with two *P. plicatulum* versus grown in a pot with one of each species. You can find these measurements in Figure 3 of the Van Auken-Bush paper. The table below gives one example. It shows that when the two species were grown together at soil pH 5.6 with no added nitrogen or phosphorus, *P. plicatulum* had a final dry weight of 0.2 g less than it did when grown with another plant of the same species, while *S. scoparium* was 0.5 g heavier in dry weight than when it was grown with another plant of the same species.

trial	abs.competition intensity
P. plicatulum, -N, -P, pH 5.6, mixed	-0.2
S. scoparium, -N, -P, pH 5.6, mixed	+0.5

Now you have models for two sets of growing conditions for two species. You also have models of what happens when two identical plants are grown in a single pot. To measure competition, you have one plant of each species grown together in the same pot. The competition equations above have two parameters (f, g) that can be chosen to attempt to create this effect. In short, for this section you will do the following.

1. For each of three growing conditions, set up a competition model for the two species using the parameters you derived in the last part for that particular set of growing conditions.

2. Figure out what the initial conditions should be.

3. Assume all constants are the same as before for each species, leaving only f and g to adjust.

4. Run the models with $f = g = 0$.

5. Compute absolute competition intensity from your model for when $f = g = 0$ and compare with the data from the paper.

6. Adjust f and g upwards in an orderly way and compute absolute competition intensity.

7. Which f and g best match the data in the Van Auken-Bush paper?

8. Report results in an orderly way (tables, figures).

4.3 The role of fire

Here is a simple question your model might be able to answer. Suppose you have the competition situations you have modeled for just two plants, one of each species or two of the same, in each of two habitats (control and experiment). Let them grow for 12 months. Now we assume a fire passes through that destroys only the shoots, but leaves crown and roots intact. Thanks to different root-shoot ratios, the two species now have different biomasses. Now run the system another 12 months (or 24, or 36). Let a fire pass through again, reducing plants to just their crown and roots. Do this five times.

To do this part well you have to set up an orderly experiment. For this part, you should answer the following questions.

1. What is the medium-run impact of fire on the system?

2. How do the results change in control versus experimental habitats?

3. How do the results change for frequent versus infrequent fires?

5 Results

Here you report via figures, tables, and prose what you found out in your investigations in the last few parts. It is important to be thorough, but you can't include all of your computer runs. Therefore, you may have to figure out elegant ways of displaying the results of your runs that condense a lot information into a few graphics. If you don't use Matlab, Excel can be helpful here.

6 Discussion

In this section, you have to think about what your simulations mean in comparison with what Van Auken and Bush think their experiments might mean. Here, you revisit questions in light of your results, such as:

1. Why do we want to simulate these results?
2. What do the results say about the nature of the competition between the two species?
3. How is competition affected by changes in N, P, and pH (as appropriate for your study)?
4. What is the overall effect of periodic fire?
5. What interactions are there between fire and properties of habitat such as N, P, and pH?
6. Any other observations you can make based on your research.

7 Bibliography

Cite your sources. Use any recognized system, but please be consistent. Cite your software. Acknowledge any help received from others.

8 Appendix

Use an appendix to include in any Matlab (or other software) code that you used to generate data or figures.

Below, find numerical data corresponding to the data from Figures 1-3 of the Van Auken-Bush paper.

	Above Ground Dry Mass			Below Ground Dry Mass		
Type	pH 5.6	pH 7.0	pH 8.2	pH 5.6	pH 7.0	pH 8.2
P. plicatulum -N, -P	1.0	0.8	0.7	0.9	0.2	0.2
P. plicatulum -N, +P	2.0	1.7	1.9	1.7	1.0	0.3
P. plicatulum +N, -P	1.5	1.0	0.9	0.4	0.3	0.2
P. plicatulum +N, +P	6.1	3.1	2.1	2.5	1.2	0.7
S. scoparium -N, -P	1.6	1.8	2.0	1.3	1.2	1.0
S. scoparium -N, +P	2.2	2.4	2.0	2.2	2.4	1.4
S. scoparium +N, -P	1.3	2.0	1.0	0.2	0.2	0.1
S. scoparium +N, +P	3.4	4.2	2.8	0.4	0.2	0.2

Table 1: Summary of the data from Figure 1.

	Root-shoot Ratio		
Type	pH 5.6	pH 7.0	pH 8.2
P. plicatulum -N, -P	0.8	0.3	0.2
P. plicatulum -N, +P	0.9	0.6	0.3
P. plicatulum +N, -P	0.3	0.5	0.3
P. plicatulum +N, +P	0.5	0.4	0.3
S. scoparium -N, -P	0.8	0.6	0.4
S. scoparium -N, +P	1.0	1.0	0.7
S. scoparium +N, -P	0.3	0.2	0.2
S. scoparium +N, +P	0.2	0.1	0.2

Table 2: Summary of the data from Figure 2.

	Above Ground Absolute Difference			Below Ground Absolute Difference		
Type	pH 5.6	pH 7.0	pH 8.2	pH 5.6	pH 7.0	pH 8.2
P. plicatulum -N, -P	-0.2	0.1	-0.1	-0.1	0.0	0.0
P. plicatulum -N, +P	0.1	0.1	0.2	0.1	0.1	0.1
P. plicatulum +N, -P	0.0	0.1	0.0	0.0	0.1	0.0
P. plicatulum +N, +P	-3.8	-0.2	0.8	-1.6	-0.1	0.2
S. scoparium -N, -P	0.5	0.5	0.8	0.4	0.3	0.3
S. scoparium -N, +P	0.5	0.7	0.9	0.5	0.7	0.6
S. scoparium +N, -P	- 0.2	-0.1	-1.8	-0.1	0.0	-0.2
S. scoparium +N, +P	1.1	0.9	0.3	0.1	0.0	0.0

Table 3: Summary of the data from Figure 3.

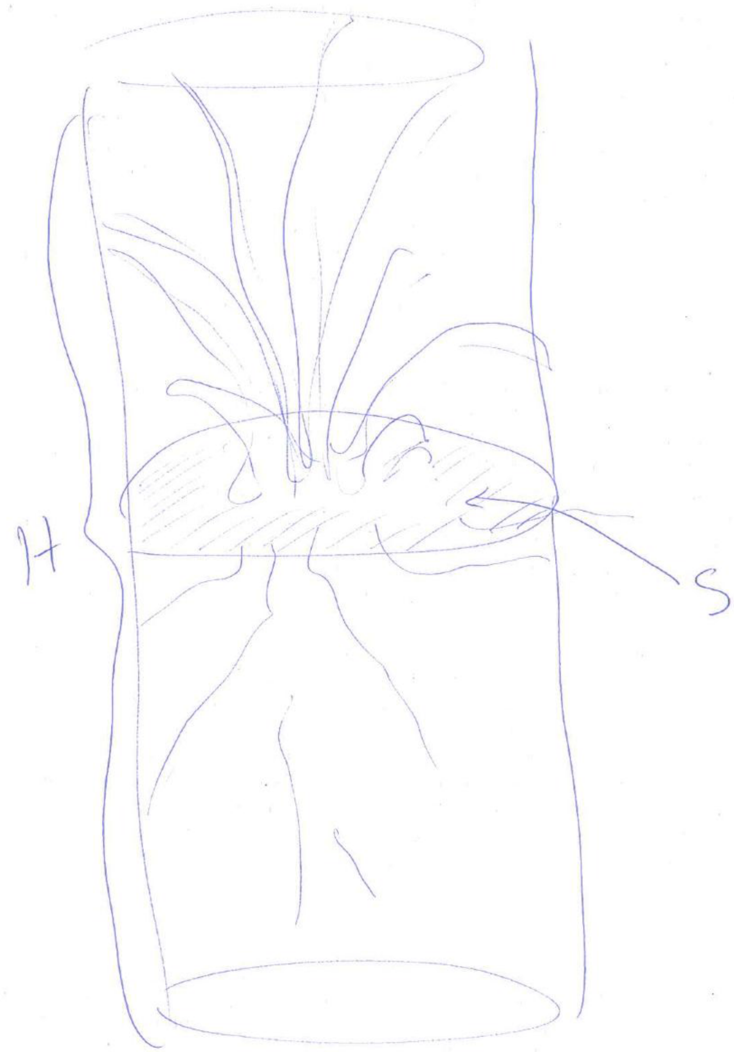

Figure 1: A grass tuft, reimagined as a cylinder.