Bam 1-008 Mathematical modelling of canopy development in bambara groundnut

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We are interested in developing a mathematical model that can accurately describe the growth of the canopy of a single plant, specifically the Bambara Groundnut and how canopy interactions between plants can affect their individual growth. We will go on to use this to examine the effect that individual plants have on each other when they are directly competing for light and resources. The growth process of a plant begins with shoots and roots developing from the seed. If we assume the plant receives all of the nutrients and energy it needs; the shoots will develop and strengthen to become a trunk or stem, with more shoots growing from the stem/trunk. After time we may see leaves begin to develop at the end of new shoots. As this happens the plant will develop a canopy. After time the canopy will fill out until it becomes fully closed, i.e. if we were to look down on the plant we will not be able to see past the canopy to the ground underneath. To simplify our model we are going to initially assume that the canopy is fully closed for the entire growth process, and later develop the model to incorporate gaps in the canopy and also radiation penetrating through the canopy. Figure 1 illustrates this basic plant model. We are interested in including direct competition for light between two adjacent plants. There are three scenarios that we might expect to see: the two plants grow equally, Plant 1 overtakes plant 2 or Plant 2 overtakes plant 1. Scenario three is illustrated in Figure 1. As we are assuming that the canopies are fully

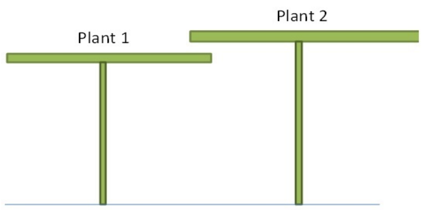


Figure 1: Two Competing Plants

closed, they can therefore be modelled as circular flat plates. The overlap between the two plants will decrease the amount of radiation reaching the shorter plant. Measure canopy (c) as the total above ground biomass of the plant, including all stems and leaves. As we are interested in the spatial overlap of each plant we must find a way to convert the above ground biomass into a plant area. Primarily we are interested in the growth during the vegetative stage. Cornelissen (2005) tells us that during the vegetative stage, the above ground biomass can be divided amongst the leaves, stems and petioles. Hence $c = W_l + W_s$, where W_l is the leaf weight and W_s is the shoot weight, which is made up of the stems and petioles. In order to convert these weights into an area we need a conversion parameter. The Specific Leaf Area (ϕ) is the conversion of leaf mass to leaf area. ϕ will vary between plant species and even within species.

Hence the leaf weight can be taken to be

$$W_1 = \frac{A}{\phi}. \tag{1}$$

where A is the total leaf area of the plant. We also have the weight of the shoots given as

$$W_s = W_l * \gamma \tag{2}$$

where W_l is the leaf weight given in equation (1), W_s is the weight of the stems and petioles and γ is the partitioning coefficient between leaf weight and shoot weight. Bamgro uses a value of 0.2 for the partitioning coefficient during the vegetative stage, which means that the shoot weight is approximately 20% of the total leaf weight. Combining equations (1) and (2) and rearranging gives

$$A = \frac{\phi c}{1+\gamma}. \tag{3}$$

As we are assuming that the canopies grow as fully closed circular flat plates. As these canopies absorb solar radiation in order to grow, any overlap between two adjacent plants will intercept the radiation, which affects the growth rate of the shorter plant and therefore its canopy size. This means we need to find an effective means of measuring the geometrical overlap between two plants so that we can accurately adjust the incoming solar radiation to an individual plant. With these basic assumptions in place as to how our plant will grow and interact we now formulate the respective governing equations for our model.

$$\frac{dh_1}{dt} = \bar{\alpha}_1 h_1 \left(1 - \frac{h_1}{k_{11}}\right) - d_{11} h_1 \tag{4}$$

where $\bar{\alpha}_1 h_1 \left(1 - \frac{h_1}{k_{11}}\right)$ assumes the height grows logistically at a rate α and carrying capacity k_{11}. This will give a growth rate of approximately α_1 until the plant reaches height k_{11} at which point the plant will stop growing upwards. The term $d_{11}h_1$ gives the rate of decay/degradation of the height of the plant, we would expect this to be very small. The growth of the plant canopy is described by

$$\frac{dc_1}{dt} = k_i P k_{c1} c_{k1} \left(1 - e^{-kLAI}\right)\left(1 - \frac{O.H}{A_1}\right)\left(1 - \frac{c_1}{k_{12}}\right) A_1 - d_{12} c_1. \tag{5}$$

The term $k_i P k_{c1} c_{k1} \left(1 - e^{-kLAI}\right)\left(1 - \frac{O.H}{A_1}\right) A$ gives the growth rate of the logistic function for canopy, which means that the canopy will grow at this rate until it reaches carrying capacity k_{12}. k_i is the maximum input radiation from the sun and depends on the number of daylight hours, P is the photosynthetically active radiation, i.e. the proportion of radiation that is photosynthetically active and is assumed to be constant. $\left(1 - \frac{O.H}{LA_1}\right)$ is a term to include the extinction of incoming radiation caused by overlap from the other plant. O is the overlap area mentioned previously. H is a Heaviside function which only switches on when the plant is overlapped by the other plant, i.e. when the dominant plant is taller and therefore shadowing the dwarf plant. A is the area of the plant given in equation (3). k_c is the proportion of energy the plant uses to make the canopy and c_k is the increase in biomass per unit energy. Both k_c and c_k vary slightly between plants. k is known as the light extinction coefficient, this is typically taken to be 0.6 for all landraces of the Bambara Groundnut.

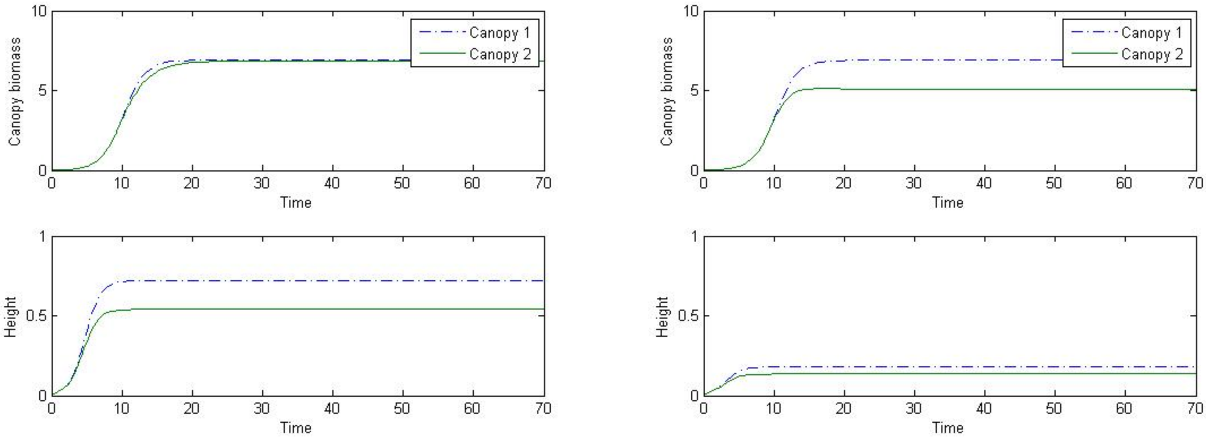
Similarly for the second plant

$$\begin{aligned}
\frac{dh_1}{dt} &= \bar{\alpha}_2 h_2 \left(1 - \frac{h_2}{k_{21}}\right) - d_{21} h_2 \\
\frac{dc_1}{dt} &= kiPk_{c2}c_{k2}\left(1 - e^{-kLAI}\right)\left(1 - \frac{OH}{A_2}\right)\left(1 - \frac{c_2}{k_{22}}\right) A_2 - d_{22} c_2,
\end{aligned}$$

where LAI is a dimensionless variable known as the leaf area index which is the leaf area per unit ground area. One of the initial assumptions of this model is that the canopies grow as a perfect circles and so the leaf area is equal to the ground cover. This would give a LAI of 1. This assumption will lead to overestimating the geometrical overlap, however for now we will make the assumption to simplify the model.

The results for this model can be found in figure 2(a). Note: the only difference between the two adjacent plants is the carrying capacity of the height between plant 1 and 2.

From figure 2(a) we can see that the growth rate for the two plants is the same until the point at which the plants start overlapping. At this point the growth rate for the shorter plant is reduced by the present overlap



(a) Basic Model

(b) Incorporating a carrying capacity that is a function of the overlap.

Figure 2: Results for the updated four equation model for canopy and height growth.

and so it takes longer to reach it's full size.

If one plant overshadows the other we would expect it to not only reduce the growth rate but also to stunt the overall growth of the smaller plant. To do this we will make the carrying capacity a function of the overlap and therefore change the final canopy size of the shorter plant.

If we choose the carrying capacity for the canopies to be

$$k12 = \frac{1 \pm \gamma}{\phi}\left(\frac{\phi K max}{1+\gamma} - O\right)$$
$$k22 = \frac{1 \pm \gamma}{\phi}\left(\frac{\phi K max}{1+\gamma} - O\right)$$

where the overlap only turns on when the plant is taller and so overlapping the other. The results with the updated carrying capacity can be found in Figure 2(b). Figure 2(b) clearly shows that the shorter plant has a smaller canopy mass. We now want to consider how the carrying capacity for the heights of the plant will be affected by competition from the other plant. We also want to extend the model to consider how canopy interactions between a larger number of competing plants affects the size of each individual plant (height and canopy) and the total yield of all plants (assumed here to be the total biomass of all plants. To do this we will have to examine the geometrical overlap of multiple overlapping plants and how that effects the growth. So far we have only examined the effect of light limiting growth; later models will include descriptions of water and nutrient limiting growth.