

Coccolith Conundrum: How shape affects sinking and light acquisition

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Biomechanics Summer B 2012

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key words: Coccolithophore, coccolith, morphology, sinking velocity, light acquisition

Abstract

I use three simple models to assess the degree to which thickness of the upper element of a coccolith and the height of the connecting stalk influence a coccolithophore's sinking rate, and ability to acquire light. One generates different coccolith profiles by varying how the same amount of mass is distributed among three stacked cylinders, representative of a coccolith. Another examines the sinking velocity of the coccolithophore as a function of the height of the stalk. Stalk height has a significant effect on the sinking velocity, as it can extend the radius of the coccolithophore and increase drag. The third model, looks at how transmission of light through a coccolith affects the irradiance at the cell surface. The thickness of the top element of the coccolith has a small effect on the transmission of light to the cell surface. Calcite is pretty translucent, especially when considering the thickness of the structure is ~50 nanometers thick. These models are then cross tested to see what is the effect of upper coccolith element thickness on sinking rate and what is the effect of stalk height on transmission. Physics-based models are a good first step in exploring the relative importance of different morphological features.

Introduction

Coccolithophores are microscopic brown algae with calcareous plates and also one of the major groups of primary producers in Earth's oceans. Fossil coccoliths, the calcareous extra-cellular platelets for which the group is known, date back to late Triassic (some 235 Mya) (Erba, 2006) though the group may have earlier origins of non-mineralizing forms (hence absent from the sedimentary record). Since the Mesozoic, coccolithophores have diversified greatly and are frequently used to delimit biostratigraphic intervals. Despite capitalizing on the distinct

morphology and the relatively high preservation potential of coccoliths since the 19th century, we have only recently begun to understand the group's biology and their evolutionary patterns.

Overall cell size correlates with a phytoplankter's ability to take up nutrients, across multiple clades, and the relationship between cell-size and biomass can be used to classify different nutrient regimes (Cullen et al. 2002). Smaller cells are associated with low nutrients and turbulence, whereas larger cells with high biomass are associated with high turbulence and nutrients environments. The mean size of coccolithophores decreases through the Neogene, but species richness of modern genera is inversely proportional with cell size and there is a high degree of specialization across multiple extant lineages (Aubry 2009). The drivers acting on the traits of an individual coccolith, i.e. height, thickness, or degree of ornamentation, are less clear. The proposed functions for the plates range from deterring predators, to increasing drag, to creating a boundary of chemically regulated water outside the cell's surface.

In this study I examine simple physics-based models to assess the degree to which thickness of the upper element of a coccolith and the height of the connecting stalk influence a coccolithophore's sinking rate, and ability to acquire light for photosynthesis. I link together three simple models: one characterizing the shape of the side profile of an individual coccolith, another characterizing the transmission of light to the cell's surface, and a third characterizing the sinking rate of a coccolithophore as a function of overall radius. Although incomplete and simplified, as most models are, the resulting relationships can help evaluate the importance of certain features to the state of the organism and broaden our understanding of its function.

Methods

Morphological Model: redistribution of mass relationship

Many coccoliths are composed of alternating calcite units repeating over and over to form different morphologies. These are the V-unit, in which the c-axis of the crystal is oriented vertically, and the interlocking R-unit, which is oriented the c-axis radially (fig. 1a). This VR model has been identified across many families from different geologic periods and the mechanism behind it is thought to be phylogenetically conserved (Young et al 1999). It is possible that the different coccolith shapes are modifications of the same basal plan, since they have the same structural elements. With this in mind, I model coccolith shape as a function the [re]distribution of mass to the different sections of the structure (see fig. 1b for explanation of terms). I start with the relationship between mass (m) and volume (v), density (ρ).

$$\rho = mv$$

I assume the general shape of a coccolith is described by three stacked solid cylinders. Although the solid cylinders model is not perfectly accurate, it yields profiles resembling those observed in different coccolithophore taxa and it is easy to model the overall volume as the sum of the individual cylinders.

$$V_{total} = V1 + V2 + V3$$

Since I assume the same amount of mass is being redistributed among the three cylinders, I can have the radius or height of one of these cylinders, this case the top cylinder, with volume V_3 , vary as a function of the radius or height of the another cylinder, in this case the middle cylinder (stalk height).

$$V_3 = \frac{m}{\rho} - V_1 - V_2$$

$$V_{cylinder} = h \pi r^2$$

$$L_3 = \frac{\frac{m}{\rho} - V_1 - V_2}{\pi r_3^2} \quad \text{Or} \quad r_3 = \sqrt{\frac{\frac{m}{\rho} - V_1 - V_2}{L_3 \pi}}$$

In this model L_3 and r_3 refer to the thickness and the radius of the top cylinder, respectively, representing the upper element of the coccolith. V_1 refers to the volume of the basal cylinder, representing the lower element of the coccolith, V_2 refers to the volume of the middle cylinder, representing the stalk, ρ is the density of calcite ($3.18 \cdot 10^{-6}$ g/ms) and m is the mass of the coccolith ($1.8 \cdot 10^{-25}$ g).

I first examine how the stalk height, l_2 , changes as I vary the thickness of the top cylinder, l_3 , from $9 \cdot 10^{-8}$ m to $2.5 \cdot 10^{-6}$ m, with all other parameters held constant. The two have a linear relationship, where stalk length decreases as thickness increases (fig. 2). Next, I examine how the stalk height changes as I vary the radius of the top cylinder, r_3 , from $5 \cdot 10^{-8}$ m to $2 \cdot 10^{-6}$ m. This yields an exponential curve, in which stalk height decreases with increasing disc radius (fig. 3).

Sinking Rate Model: How does the height of a coccolith affect the sinking rate of the whole coccolithophore?

Since coccolithophores are microscopic in size (1-10 microns in diameter) they exist in a low Reynolds environment in which viscous forces dominate. This does not mean there are no

inertial forces present. The cells are still susceptible to sinking, which can place a cell out of the photic zone. George Stokes modeled the drag acting on a small at low reynolds numbers as

$$D = 6 \pi \mu r u$$

where D is the drag force, μ is the viscosity of the fluid, r is the radius of the sphere, and u is the velocity it is traveling at. When the sphere reaches a steady stream flow, the magnitude of the drag force will match that of gravity, which is acting in the opposite direction. I substituted the drag force for the force of gravity (mass (g)* gravitational acceleration(m/s²)) and solved for the sinking velocity.

$$u = \frac{m g}{\mu \pi 6 r}$$

I use this relationship to model the effect of stalk height on the sinking velocity of the organism. As the stalk height increases, so too does the effective radius of the organism, which results in a reduction of the sinking velocity (fig. 4). I vary r from 0.5 microns to 10 microns, a range observed in extant coccolithophores and see an exponential decline in u with increasing r .

Transmission Model: How does the thickness of a coccolith affect light transmission?

Coccolithophores are photosynthetic and depend on light to generate energy and building material. Acquiring enough light is critical and can be limited by the properties of mineralized structures. Calcite, a stable form of CaCO₃ with variable crystal habits, is very translucent, but not perfectly so. As you increase the thickness of the material, you increase the amount of matter

that can interact with light thus increasing the quantity that is absorbed. But would absorption be significantly affected by the thickness of the upper element at these small scales? For this model, I start with by modeling irradiance to the cell surface, I_{cs} , as a function of the total light coming in, I_0 , multiplied by the transmissivity of the upper element, t_3 , and of the base, t_1 .

$$I_{cs} = I_0 * t_1 * t_2$$

In order to relate irradiance to a morphological feature of the coccolith, I relate thickness of a coccolith element, l_n , to the amount of light absorbed. By changing the absorption of the structural element, A and keeping the amount of light reflected (a surface property of the material), R , constant, I can generate values of transmissivity that can be substituted back into the above model as a function of the thickness of the upper coccolith element.

$$t_n = 1 - A_n - R$$

$$A_n = 3 * 10^6 * l_n$$

$$t_n = 1 - R - (3 * 10^6 * l_n)$$

$$I_{cs} = I_0 * t_1 * (1 - R - (3 * 10^6 * l_n))$$

I vary thickness from $8 * 10^{-11}$ m to $1 * 10^{-9}$ m and see linear decline in irradiance as thickness increases (fig. 5). It is worth noting that this model operates using a ray/pencil model of light to characterize behavior. At these small scales, the thickness of the material with which light is interacting is in the same order of magnitude or smaller than the wavelengths of visible light, which ranges from 380nm to 750nm, and even some ranges in the ultraviolet end. It may

be more appropriate to model the behavior of light as a particle, but the physics required is beyond the scope of this project.

Results

With the models relating sinking rate and irradiance to coccolith morphology set up, I test the effect of upper disc thickness and radius on the sinking velocity of the coccolithophore and the affect of stalk height on irradiance to the cell surface. In the modified sinking model, stalk height varies as a function of disc radius (fig. 6). As radius increases, the stalk height decreases, and there is an exponential increase in the sinking velocity. There was no notable change in sinking velocity as I varied disc thickness since a change in thickness has a small effect on the stalk height (different orders of magnitude). In the modified Irradiance model (fig. 7), the thickness of the upper coccolith element changes as a function of varying stalk height. As stalk height increases, disc thickness decreases which reduces absorption and increases irradiance to the cell surface. From this, it appears that selection on disc radius would change the rate of change (slope) of stalk height/ coccolithophore radius to a greater extent than selection on thickness. On the other hand, selection on stalk height would change the disc thickness and hence irradiance to the cell surface. The relationship between irradiance and stalk height graphs in a linear fashion, where irradiance decreases as stalk height increases.

Discussion

With these simple models I demonstrate that, due to the material properties of calcite and the miniscule size of the platelets, the thickness of an individual coccolith minimally affects the transmission of light to the cell surface. I also demonstrate that the height of the stalk, as a

response to changing the radius of the upper coccolith element, has an exponential effect on the sinking velocity of a coccolithophore. Needless to say, these models make many assumptions about the platelets and exclude other important factors that could be driving the diversity of shape (both coccolith profile and ultrastructure).

One important morphological factor excluded in this study is a coccolith's ability to scatter and redirect light. The scatter from detached coccoliths en masse results in the blue-green coloration, visible from space, that's associated with blooms. Saruwatari and colleagues (2006) show that the orientation of the c-axis in the R and V units affects the direction of entering light beams and their projections, resulting in crystallographic chiral aspects. Another major assumption I make is that coccolithophores have one type of coccolith morphology and that they are spherical in shape. Elongated body forms do exist, and many groups employ a polymorphic coccosphere, allowing them to have specialized plates.

It is still possible to draw conclusions from the models. If selection is acting on stalk height to increase the a coccolithophore's resistance to sinking, it would lead the thickness or the radius of the upper coccolith element to decrease, if we believe the redistribution of mass relationship operating in the morphological model. This could prove beneficial to the cell if it was light limited, but also potentially detrimental since calcite transmits ultraviolet radiation, which can cause damage to the cell. If selection is acting to increase upper coccolith element thickness and driving down the stalk height, the coccolithophore would sink faster meaning it would not stay in the water column as long. It is important to bear in mind that while coccolith thickness is minimally important to a coccolithophore's ability to acquire light, since calcite is very translucent, it can be important to other aspects of the organism's biology, such as resistance

to dissolution in high pH environments(Irie et al, 2010). Models are a good way to begin to consider the potential importance of different morphological features, though their predictive power increases when they are supported by other independent models, observations in the field, and laboratory experiments.

Acknowledgements

I thank Patrick Martone, Moose O'Donnell and especially Emily Carrington, for their valuable insight throughout all stages of the project. I also thank Danny Grunbaum and Robin Kodner for help brainstorming in the early stages of the project. I extend my gratitude to the members of the summer 2012 Biomechanics course at Friday Harbor Labs, and our wonderful TA Matt George, for their support and inspiration. Funding for this project came from the National Science Foundation, NSF award EF-1041213 to Emily Carrington, and the people and facilities at Friday Harbor Laboratories.

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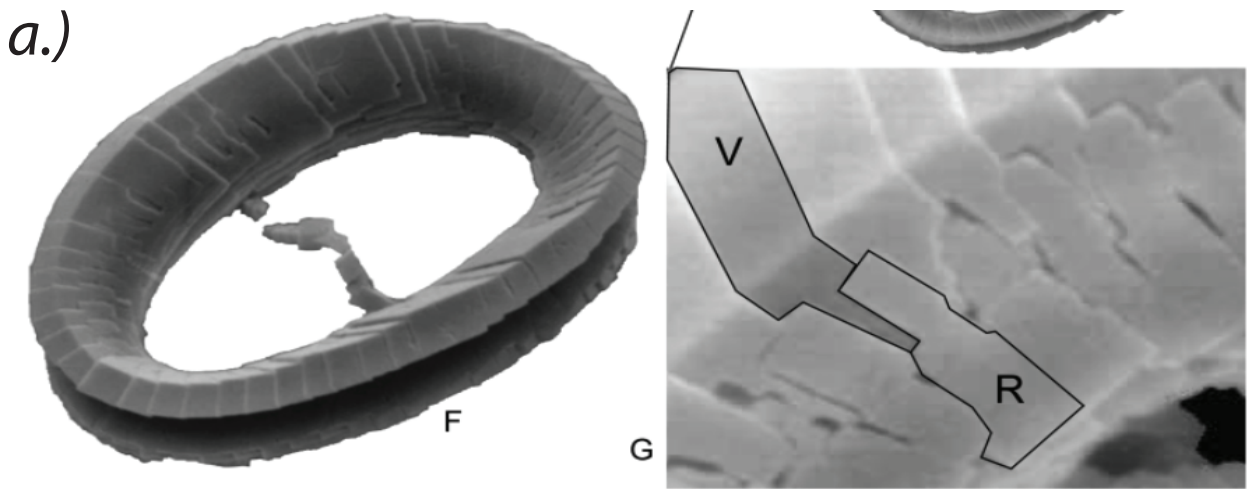
Allan R. Robinson, James J. McCarthy, and Brian J. Rothschild ISBN0-471-18901-4 ©
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b.) *green= Upper coccolith element/ disc*
red= Middle coccolith element/ stalk
blue= Lower coccolith element/ base

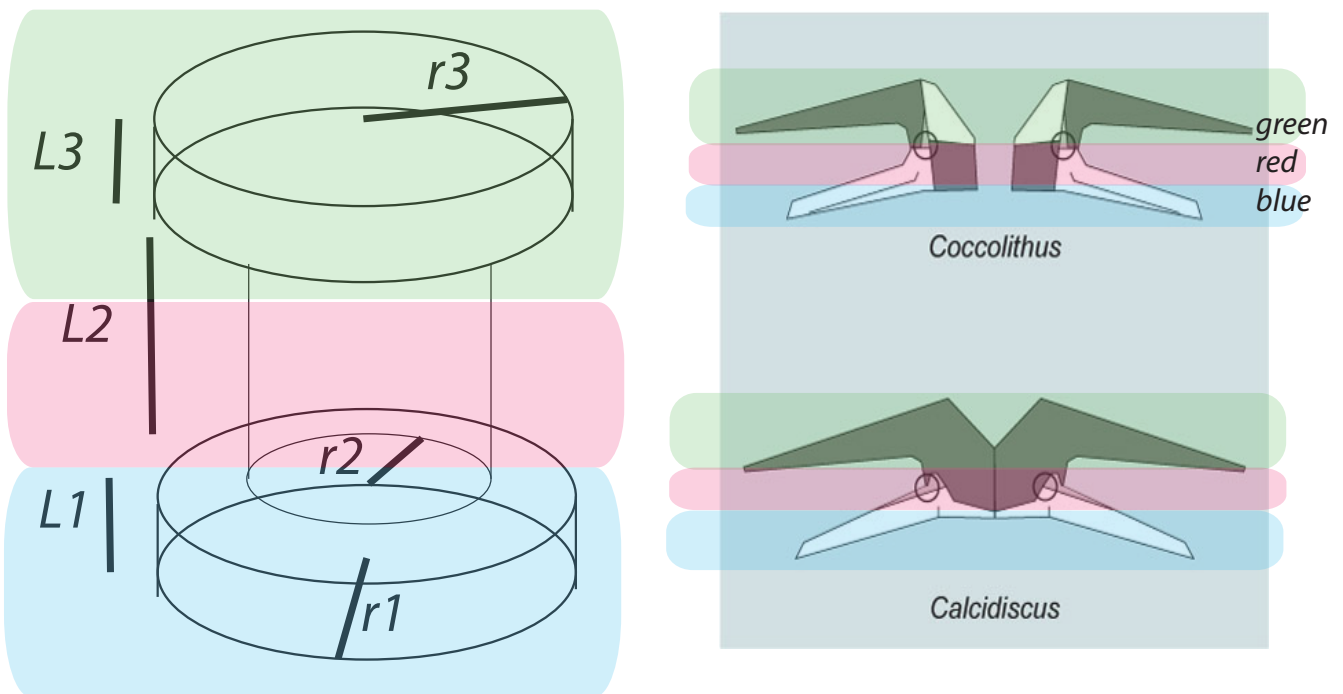


Figure.1a.) Scanning electron micrograph of a *Coccolithus pelagicus* coccolith, from Young & Henriksen (2003). Close up highlights individual V and R crystal units. b.), Schematic diagrams of three cylinder model and profile cross section of coccolith. Lengths and radii are indicated on each cylinder. The structures are divided into three parts: *green= Upper coccolith element/ disc*, *red= Middle coccolith element/ stalk*, *blue= Lower coccolith element/ base*.

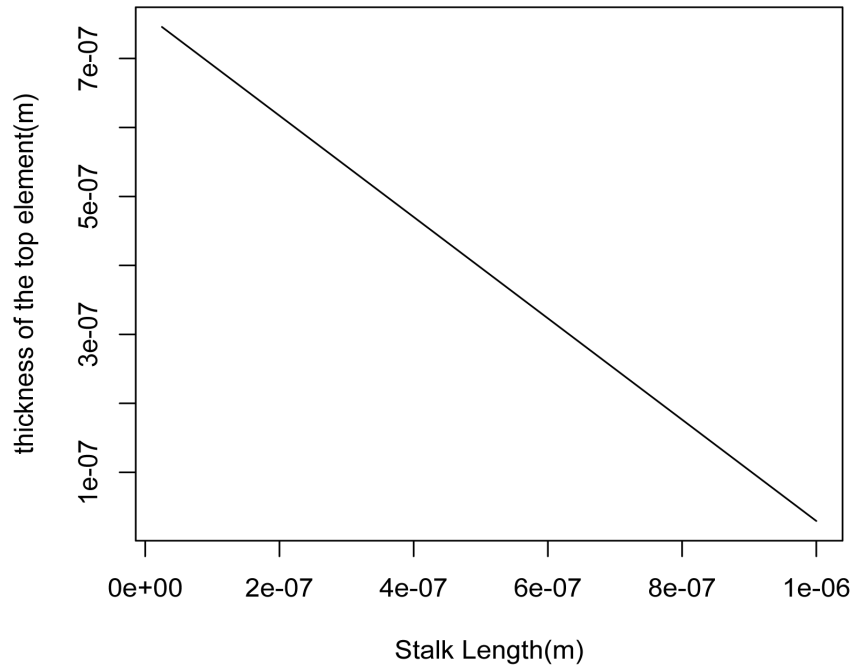


Figure 2. Morphological mass redistribution. Thickness of the top coccolith element plotted against stalk length, which varies from $9 \cdot 10^{-8}$ to $2.5 \cdot 10^{-6}$ m. All other dimensions held constant.

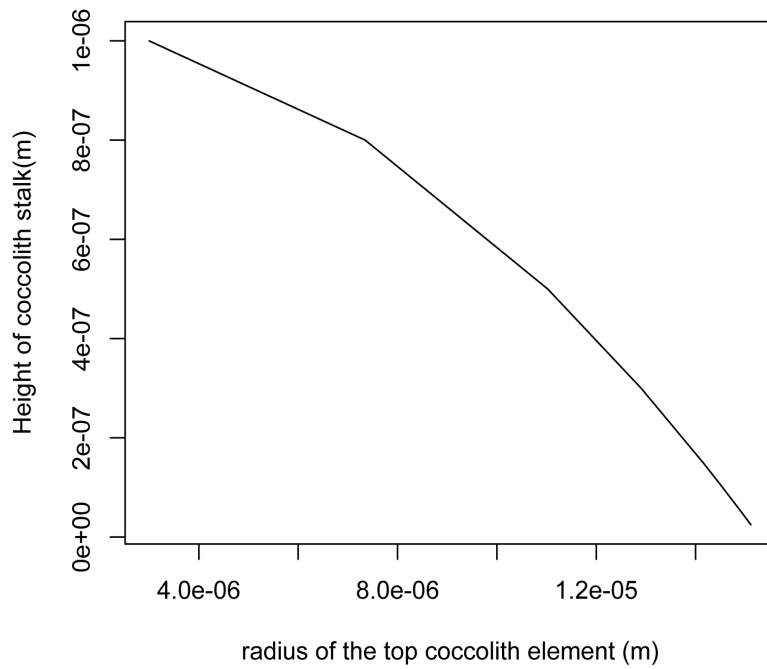


Figure 3. Morphological mass redistribution. Stalk length plotted against radius of the top coccolith element, which varies from $5 \cdot 10^{-8}$ to $2 \cdot 10^{-6}$ m. All other dimensions held constant.

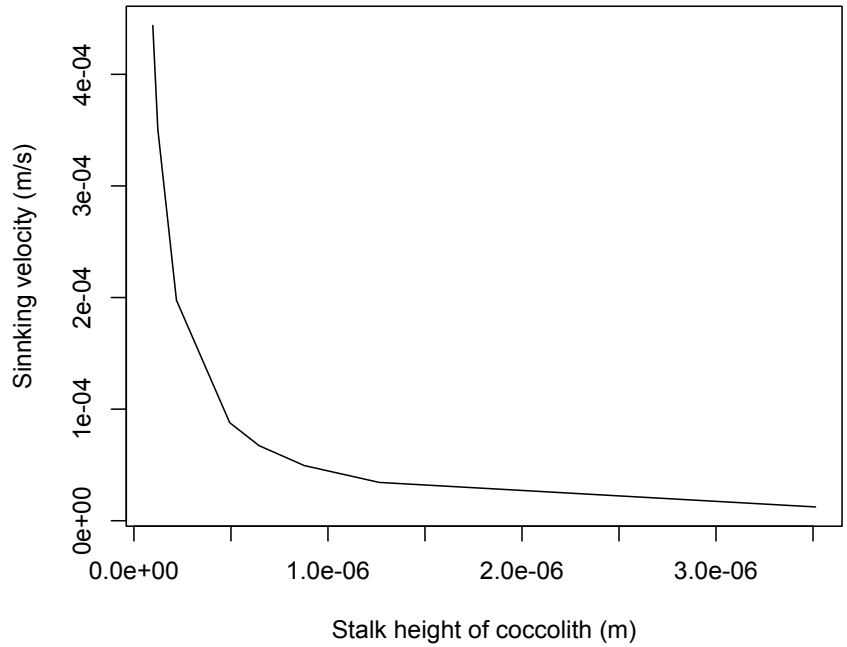


Figure 4. Sinking velocity (m/s) plotted as a function of stalk height (m). Mass = 3×10^{-11} g. Radius varies from 5×10^{-7} m to 1×10^{-5} m. Dynamic viscosity = 1.88 g/ms.

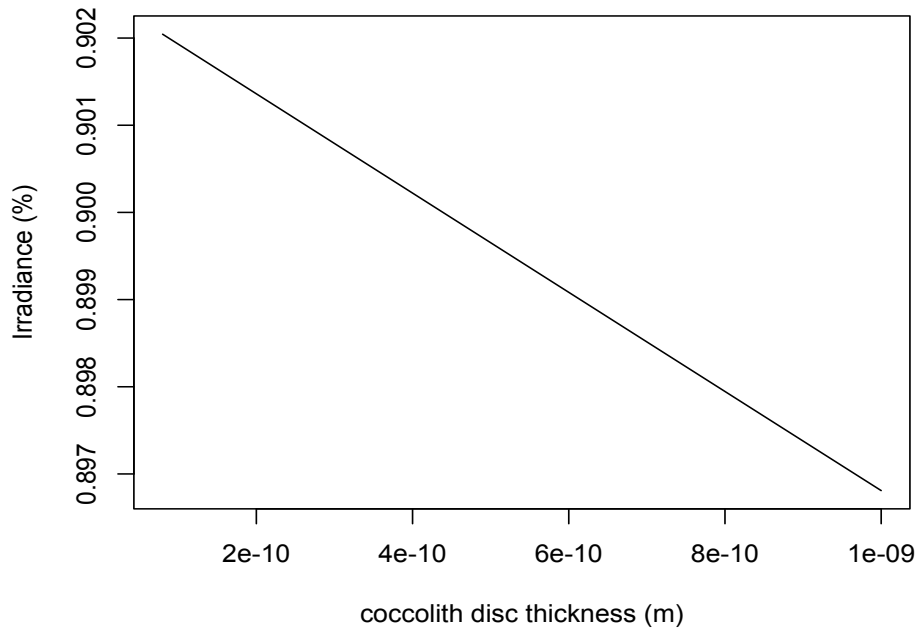


Figure 5. Percent of incoming light that makes it through the coccolith plotted against the thickness of the upper coccolith element (meters). Total transmission is the amount of light coming through minus the light that is absorbed and the light that is reflected.

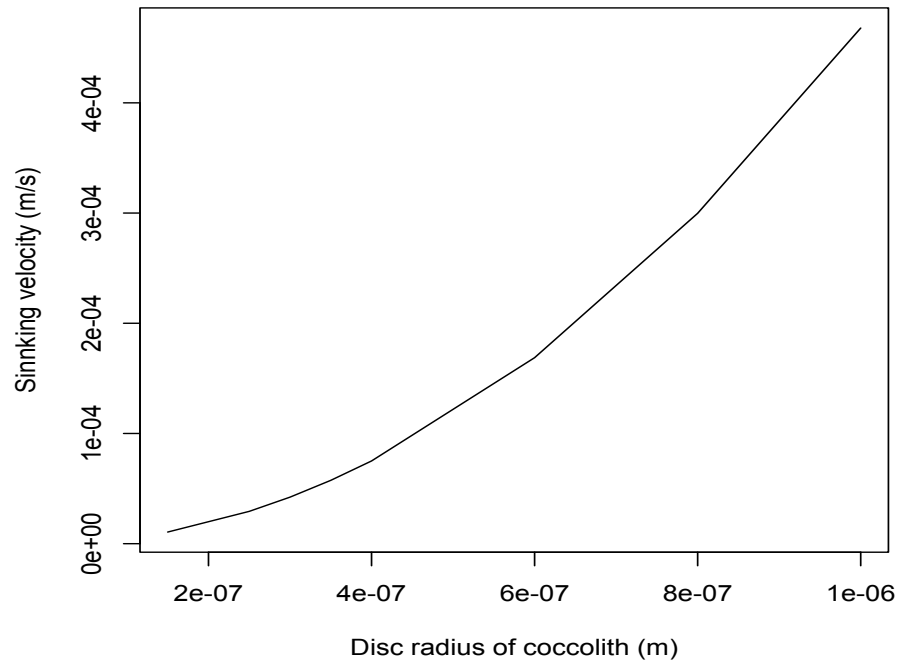


Figure 6. Sinking velocity (m/s) as a function of changing disc radius (m). Using the morphological model, stalk height values were determined from disc radii, which vary from $1.5 \cdot 10^{-7}$ to $1 \cdot 10^{-6}$ m. Derived stalk heights were then used in the sinking model.

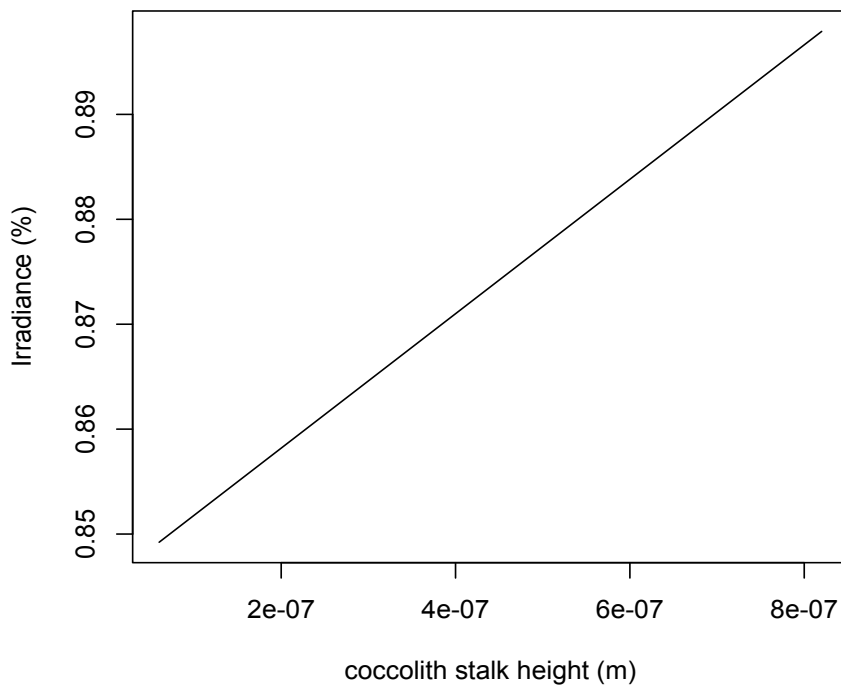


Figure 7. Irradiance to the cell surface (%) as a function of changing disc stalk height (m). Using the morphological model, disc thickness values were determined from stalk height, which varies from $6 \cdot 10^{-8}$ m to $2 \cdot 10^{-7}$ m. Derived thickness were then used in the previous irradiance model.