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The effect of canopy organization on the photosynthesis of Sphagnum

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THE EFFECT OF CANOPY ORGANIZATION ON THE PHOTOSYNTHESIS OF *SPHAGNUM*

By

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ABSTRACT

SOLINSKY, BRIAN The effect of canopy organization on the photosynthesis of *Sphagnum*

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With climate change becoming a greater problem the ability of plants to photosynthesize and sequester carbon becomes more important for us to understand. *Sphagnum* moss stores more than a third of the world's soil carbon. Much is understood about the physiology of *Sphagnum*, but what is generally not understood is the effect of variation in canopy organization in *Sphagnum*: why are they both rough and smooth? This study examined whether different canopy structures influenced how the canopy uses different angles of light for photosynthesis. The first step was modeling photosynthesis in two simulated structures (rough and smooth) as the angle of light changes. Following Lambert's cosine law, relative photosynthesis was determined by integrating light absorbance and intensity of light the plant receives. The model showed both structures decrease in relative photosynthesis as the angle of light decreases following the same path. The second part was to test empirically using rough and smooth samples made from *Sphagnum fallax.* Photosynthesis was measured using the Licor 6400. Five samples, both rough and smooth, were made and each was tested 4 times, first at 90 degrees and then 45 degrees. The samples followed the model with no significant differences in net photosynthesis between the rough and smooth samples at either angle. When compared to the model, the rough, but not the smooth, showed significantly greater rates of

photosynthesis at low light angles. Further study is needed to understand if there is a reason for the two canopy structures of *Sphagnum* in relation to photosynthesis.

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TABLE OF CONTENTS:

LIST OF FIGURES

Introduction

Plants are very important to our planet; one reason for that is their ability to sequester carbon dioxide through photosynthesis. The reason atmospheric carbon dioxide is so important is because it acts as a green house gas, which helps keep the earth warm; however if too much is produced and put in to the air the earth gets too warm. This is a problem that we are having now and is referred to as global warming. To help reduce atmospheric carbon dioxide, plants come in handy because of their ability to take it in through photosynthesis. For a plant to photosynthesize at optimal efficiency it must use sunlight, carbon dioxide, and water as effectively as possible. Smith and Hughes (2009) examined how leaves and branches have adapted to work at optimal efficiency within many different types of environments. Plants have evolved traits that allow them to survive in extreme conditions: from incredibly dry and sun saturated deserts to very wet and cloud covered forests. The plants can do this because the leaves and root systems have evolved to work best in these diverse environments: using water, capturing sunlight, and taking in carbon dioxide in different ways to meet its needs.

Leaves of plants have become exceptionally adapted to optimize their use of sunlight (Smith and Hughes 2009). The leaves often position themselves in a way so that they can capture as much sunlight as possible, or find ways to self-shade when they are at risk of drying out. Different leaves have adapted ways of limiting the amount of sunlight that they take in even when they are fully exposed, for instance having different structures on the leaf surface such as trichomes, commonly referred to as leaf hair. That adaptation allows the plant as a whole to use sunlight in the best way possible. For example, Thérézien et al. (2007) examined the shading phenomena in pine trees and found that self-shading and other properties of the pine needle clusters allowed the needles to capture and use sunlight efficiently when exposed to high light.

On the other end of the spectrum, some plants use their leaves to capture more light at low light intensities. Usually these plants are found in dense forests and have a flat structure that allows the leaves to capture more light at different angles and even allows the plant to better use diffuse light. Some trees such as oak trees have shading of internal leaves, but because of transmittance and diffuse light getting through, even those leaves can optimally photosynthesize. They have adapted to using these lower levels of light as efficiently as a leaf in the sun uses direct sunlight (Stenberg et al, 2001).

Another way leaves change structurally to use light as best as possible is having different thicknesses of the leaves depending on the level of light. In a study done by Abrams and Kubiske (1990) they found that leaves on hardwood trees found in Wisconsin varied in thickness based on light levels. The leaves found in direct sunlight at the top of the tree or on the outer edges of branches were thicker and the leaves on the interior that were shaded were thinner. This variation is important because it shows that leaves and plants can structurally change to optimally handle light levels.

Bryophytes, and specifically those of the genus *Sphagnum,* are important ecosystem engineers because of their ability to dominate carbon, water and nutrient dynamics in wetland systems; they also store and sequester carbon in these systems (Glime 2007). They can do this for many reasons; one is because they can tolerate very stressful low nutrient environments where other species cannot survive and where decomposition is slow. The adaptations that *Sphagnum* has acquired allow it to store immense amounts of carbon once fixed; the fixation of carbon dioxide is a main step in photosynthesis that *Sphagnum* has slightly altered. Most studies of bryophytes, specifically *Sphagnum,* go into detail looking at this storing of carbon because it is so important and gloss over the more intricate details that may be at play for why *Sphagnum* works the way it does. A lot of these studies take more of an overarching approach and that is why what they do on a global scale is clearly understood (Rice 2006).

Sphagnum acts similarly to vascular plants when it comes to photosynthesis, using the same biochemical process as C3 plants (Rice et al, 2008). However, the capability of some *Sphagnum* to store a lot of water or handle very dry conditions without dying makes it different from vascular plants. Their ability to store carbon dioxide makes them important to understand; we need to know exactly how they work to better understand the role they play in carbon cycling. A key part of that is to understand the adaptations that *Sphagnum* has to optimize its ability to capture light for photosynthesis. Although there is a lot known about how variation in tissue qualities affects rates of photosynthesis, little is known about the role of canopy organization in light capture.

Sphagnum canopies can differ in their organization and be characterized generally as rough or smooth. Rough *Sphagnum,* a layered plant structure with branches similar to a bush*,* has it's leaves set up in layers that keep some partially shaded and others fully exposed to the sun, and is usually found within a forest or area that is shaded from the sun. The smooth version of the plant is typically found in open patches and form fields. They take over their local ecosystem and usually cover the entire ground making them very exposed to the sun. This difference is known to have consequences for water retention; the rough canopies have higher rates of water loss than the smooth canopies (Rice et al 2001). However, the reason for the different versions of the *Sphagnum* as it pertains to light acquisition is relatively unknown, but, plants usually adapt to take advantage of their environment. Even different subspecies of *Sphagnum* may have adapted to have the rough and smooth version.

This study will investigate the consequences of the rough and smooth canopy organization as they relate to photosynthetic properties. Specifically, this study will examine light use efficiency of the rough and smooth *Sphagnum* by studying rates of carbon dioxide uptake. These will be investigated across different isolation angles and compared to a model. The first reason for studying angled light is studies of vascular plants show certain plants adapt to better handle reflected light. The reflectance of the leaves at different angles may be a factor in *Sphagnum,* but has not been studied (Niinemets and Tobias 2013). The angle of light could also be a factor for two more reasons: different levels of light capture at changing angles of the sun due to rough or smoothness, or surface area of the leaves that are able to use the light for photosynthesis. A leaf generally has a rough surface to allow it to capture more or less sunlight. Internal reflectance may also be a factor for rough *Sphagnum* light absorption, increasing photosynthetic rate and carbon dioxide uptake. If the structures do show a difference it will support that physiological consequences have caused the different canopy organizations. Then it will be important to understand the mechanisms that account for any difference.

The first step in our process will be to model how the two canopy structures will use the light. Initially before modeling the thought was that the rough would be better adapted to lower solar angles of light because it has changing surface areas that can catch the light with different intensities. However, after some diagramming before modeling it appeared that the changing surface areas and intensities of the rough balance out to remain the same as the smooth. Thus the hypothesis for the model is that the rough and smooth will have the same relative photosynthesis and both will decrease in relative photosynthesis as the angle of light decreases. Then the empirical testing will be run and the expectation is that the results of the test will follow the model. Therefore, if the model is correct, the rough and the smooth will follow the same downward trend in relative photosynthesis as the angle of light decreases. However, a biological factor we did not take into account in the model could be at play and cause our model to be off, such as; certain leaf surfaces may not be able to absorb as much light, which would cause the photosynthetic rate of the rough plant to go down. If the model is followed that means the variations of canopy structure in *Sphagnum* are not because of changing angles of light and that the factors deciding photosynthetic rate are the ones in our model. If the model is not followed by one canopy structure or by both then some factor not taken into account in the model is attributing to that difference and it will be important for a future study to find out what that is.

Methods

The study used two approaches to try and understand if the light use is a factor in the existence of the different canopy structures. The first looked at the expected photosynthetic rate of the two different types of *Sphagnum* through simulation modeling. This model established expectations about how light absorption and, thus, photosynthesis, should vary with the canopy structure and light angle. The second part empirically tested the photosynthetic rates looking at light angle and its relationship to photosynthetic rate and then comparing this to the model. For the empirical testing a photosynthetic chamber was constructed that was able to hold both rough and smooth *Sphagnum* samples. The chamber was constructed in a way that allowed the angle of light to be manipulated around it. The same species of *Sphagnum* was used for both the rough and smooth and the same surface area was exposed to the light.

How the model works is based on a smooth sample being flat and fully exposed to light, while the rough sample has some parts of the plant up and other parts down causing some shading. A depiction of how this works can be seen in figure 1: it shows that at different angles of light the intensity of the light changes and in the case of the rough samples the surface area exposed to the light changes. The intensity of the light changes according to Lambert's cosine law (Jones 1992), where the intensity is directly proportional to the cosine of the angle between where the light is coming from and its surface to the normal.

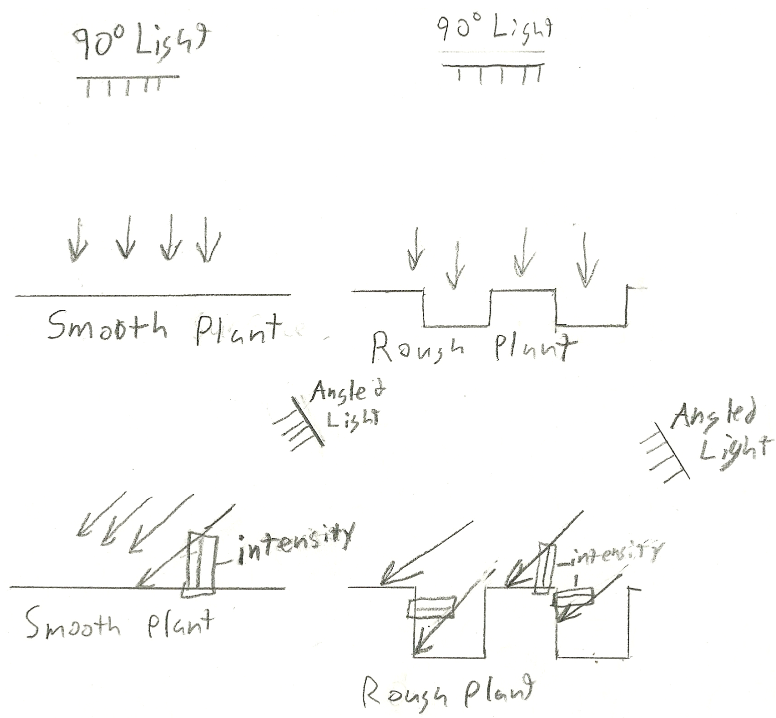

Figure 1 Original idea for how to make the model. All of the plants have the same surface area exposed however how the plant intercepts the light changes.

The model specifies a smooth plant to be a flat surface that always has the same leaf area exposed (E_s) no matter what the angle of the sun is. What does change for the smooth *Sphagnum* is the light intensity (I_s) and that is a function of the sine, $I_s=\sin(\theta)$. For the smooth plant as the angle of the sun goes down the light absorbed (A_s) will change along with the changing I_s ($A_s=I_s$). This formula is based on Lambert's cosine law (Jones 1992). To set up the model for the rough plant it was split into three parts a top, bottom, and vertical. At 90 degrees (light source directly overhead) only the top and bottom leaf areas will be exposed, so in theory at this angle the rough and smooth should intercept and absorb the same amount of light. However, as the angle of the sun goes down, the bottom and vertical will have changing exposure to the sunlight.

As the angle of the sun changes the exposed leaf surface will change and the intensity will change as well. The top rough intensity (I_{tr}) will work the same as the smooth $I_{tr}=\sin(\theta)$ as well as the absorption (A_{tr}) $A_{tr}=I_{tr}$. For the bottom the leaf area exposed (E_{br}) changes as a function of $1-\cot(\theta)=E_{br}$ until 45 degrees when it goes to zero because at that point the bottom will be completely shaded. The intensity of the bottom (I_{br}) remains a function of the sine, $I_{br}=\sin(\theta)$ and the overall light absorbed (A_{br}) by the bottom is the intensity multiplied by the exposure $A_{br}=I_{br}*E_{br}$. The vertical exposure (E_{vr}) at 90 degrees is zero however after that until 45 degrees the E_{vr} is 1. After 45 degrees E_{vr} changes following this equation $E_{vr}=\tan(\theta)$. The intensity of the vertical (I_{vr}) is the cosine of the angle $I_{vr}=\cos(\theta)$. Then the actual light absorbed (A_{vr}) is these two parts multiplied together, $A_{vr}=I_{vr}*E_{vr}$. To make an equivalence 6 parts of smooth were taken to be six times the intensity $A_s=6*I_s$. While the rough was 3 times the summation of the top, bottom, and vertical $A_r=3*(A_{tr}+A_{br}+A_{vr})$, multiplied by 3 because one top and bottom is equivalent in distance to 2 tops.

For the empirical testing, samples of *Sphagnum fallax* were obtained at a fen located in the Woodlawn Preserve in Schenectady, NY. The *Sphagnum* was then made into smooth samples for testing. Individual stems were placed through a mesh and the capitula formed a dense smooth layer. 89 stems were placed in the mesh with an area of 78.54cm^2 giving a surface density of roughly 1.13 stems/cm^2. Five samples of this nature were made, all containing roughly the same biomass and exposed surface area. The samples were then tested using the Licor 6400 photosynthesis machine that was connected to the chamber that had been made for us. All the samples were weighed before and after testing. The chamber was kept at a flow rate of 700μmol s^{-1} and a reference carbon dioxide of 400ppm. The light for the first three samples was placed 90 degrees overhead, 20 inches from the plants, with an intensity of 500μmol quanta m^{-2} s^{-1} . Each sample was left in the chamber for 10 minutes and then a reading was taken of the delta CO_2, the relative humidity, the pressure, and the temperature of the plant. After the first three samples were run at 90 degrees the light angle was moved to 45 degrees for the last two samples. All the light parameters were kept constant with adjustments made to the light to make to make sure the intensity remained at 500μmol quanta m^{-2} s^{-1}. After the last two samples were tested at 45 degrees the first three samples were tested at 45 degrees. Then the last two samples were tested at 90 degrees. The reason three of the samples were tested at 90 degrees first and two at 45 degrees first was to check if there was a bias based on order.

After testing all the smooth samples at both angles, the samples were converted into rough samples. This was done by pulling stems further through the mesh thus moving some capitula lower down and keeping some higher up. The rough samples had about half the capitula up and half the capitula down in an attempt to simulate a rough *Sphagnum* canopy structure. To test the photosynthesis of the rough samples we used the exact same method as we did for the smooth samples. After all of the samples were run they were dried out in an oven for 24 hours and then a dry weight was taken.

To work through the data everything was put into excel. The delta CO_2 was converted to relative change in CO_2 so that it could be compared to a model. To see if the results were significant for the change in CO_2 a t-test was run. To more critically understand the differences and similarities of the smooth and rough canopy structures net photosynthesis was also calculated for all samples. The net photosynthesis incorporates the flow rate and the dry weight of the samples. The equation is: net photosynthesis (μmol CO_2 g dry $wt^{-1}s^{-1}$) =(flow*delta CO_2)/dry weight. To understand the relationships of the two variables, canopy structure and angle, an analysis of variance (ANOVA) test was run. A two-factor ANOVA with repeated measures on both factors was used and implemented using Vassar stats (www.vassarstats.edu).

Results

The results of the model in Figure 2 show that the rough and smooth *Sphagnum* should not show a difference in relative photosynthesis; as the angle of the sun changes the intensity and surface area exposed change at equivalent rates and the absorbance remains the same.

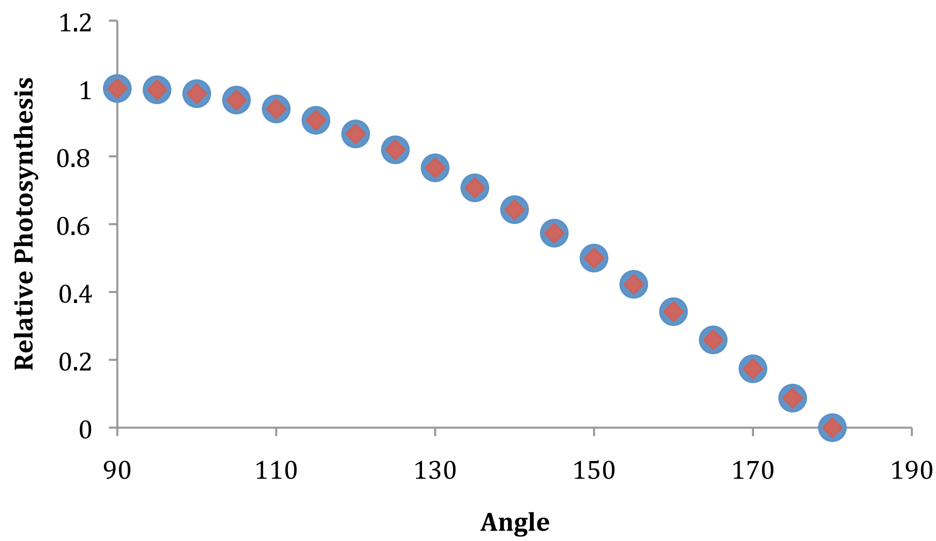

Figure 2̅ The relative photosynthesis versus the angle. The smooth is depicted as blue circles and the rough is the red diamonds. The relationship they have with the relative photosynthesis angle is identical. Both show a decrease in absorbance as the angle of light goes down. The angle 180^o is the same as zero.

For the empirical testing the results are split into two parts; one compares the relative photosynthesis to the model and the other compares the net photosynthesis of each sample type with all of the other sample types. The results show that the smooth *Sphagnum* closely resembled the model at 45 degrees with the model fitting into the 95 percent confidence interval. The rough *Sphagnum* however did not have the model within its 95 percent confidence interval. The models relative photosynthesis at 45 degrees is 0.707μmol CO_2/g/s, the smooth is 0.768μmol CO_2/g/s with a 95 percent confidence interval of plus and minus 0.061μmol CO_2/g/s, and the rough is 0.846μmol CO_2/g/s with a 95 percent confidence interval of plus or minus 0.074μmol CO_2/g/s. These confidence intervals place the model just within the smooth samples range. Even though the rough does not have the model within its 95 percent confidence interval it does have the smooth within it. A t-test was run to see if the rough and smooth were significantly different at 45 degrees and the p-value was 0.186 meaning that the difference is not significant because the p-value is greater than 0.05. Figure 3 shows how the different samples and the model are related.

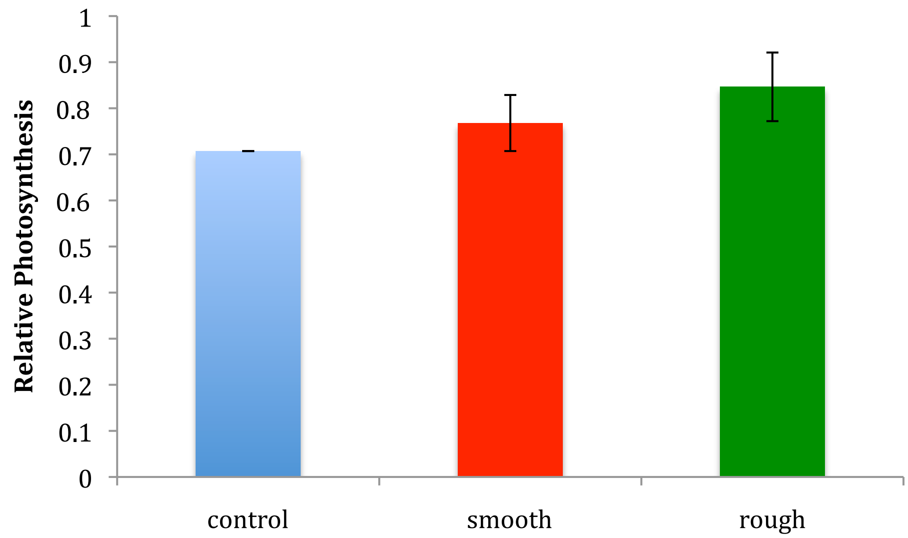

Figure 3 shows the model in blue, the smooth in red, and the rough in green all at 45 degrees. The model represents both the smooth and rough because they are the same. The smooth is the mean of the smooth samples and the error bars are at a 95% confidence interval and contain the model. The rough is a mean of the rough samples and the error bars are at a 95 % confidence interval and do not contain the model. The smooth and rough do not differ significantly.

When the net photosynthesis was used for the ANOVA it showed that at 90 degrees and 45 degrees there is a significant difference in the net photosynthesis with a p-value of 0.0007 which is less 0.05. The difference between the net photosynthesis between the smooth and rough samples at 90 degrees was not significant with a p-value of 0.169. The difference between the net photosynthesis between the rough and smooth samples was not significant with a p-value of 0.157. Figure 4 shows that for both the smooth and the rough the net photosynthesis changes with the angles but does not significantly change with the canopy structure. At a 95 percent confidence interval the only factor that does not overlap is between the changing angles.

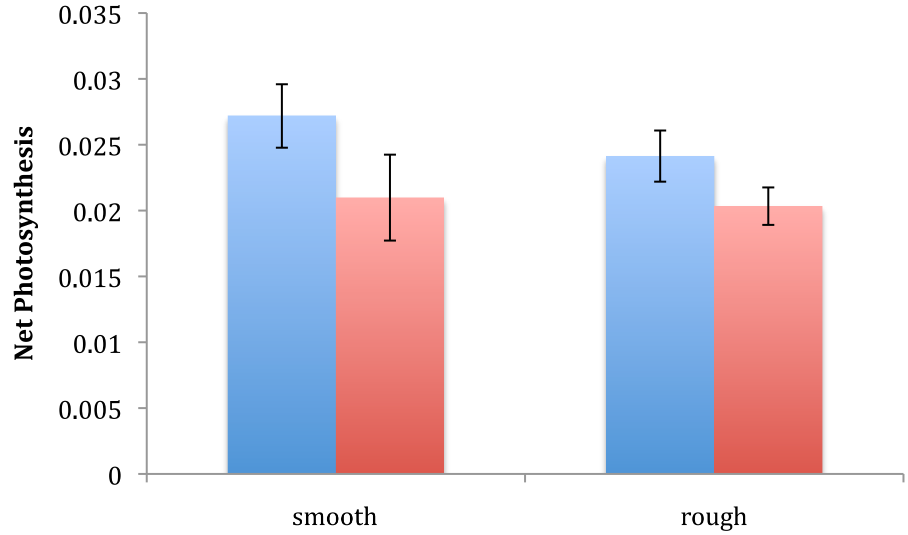

Figure 4 The net photosynthesis (μmol CO_2 g dry $wt^{-1}s^{-1}$) of smooth and rough canopy structures at 90 and 45 degrees. The blue represents the net photosynthesis at a 90 degree angle and the red represents it at a 45 degree angle. The only significant difference is between the net photosynthesis at the different angles with a p-value less than 0.05. The difference between the smooth and rough is not significant at either angle. This information was found using a two-factor ANOVA with repeated measures on both factors.

Discussion

The model supports our first hypothesis in that it shows that the rough and smooth canopy structures should not show any difference in photosynthetic rates at any angle. However, the photosynthetic rate should decrease as the angle of light decreases from 90 degrees down to zero. The model worked out this way because no matter the angle of light the rough structures surface area exposed along with its intensity always remains the same as the smooth structure even though different surfaces are using the light at different angles, based on Lambert's cosine law.

After the model was made and support was found for our first hypothesis the empirical testing was done and for the most part support was found for our second hypothesis that the smooth and rough structures would follow the model. When looking at the relative photosynthesis just using the delta CO_2 a difference could be seen between the photosynthetic rates at the two angles. However, no significant difference existed between the smooth and rough *Sphagnum* at 45 degrees. A t-test showed that the rough and smooth canopy structures did not significantly differ with a p-value greater than 0.05. The mean relative photosynthesis of the rough sample at 45 degrees did not contain the model within its 95 percent confidence interval demonstrating that it may be significantly different from the model. However, because it did contain the smooth within its confidence interval and the smooth contained the model within its 95 percent confidence interval, the difference of the rough from the model is likely insignificant. Demonstrating that *Sphagnum* followed the light angle hypothesis.

More support was found for a significant difference between photosynthesis at 90 degrees and 45 degrees by looking at net photosynthesis. An ANOVA test showed that the difference between net photosynthesis at the two angles was significantly different with a p-value less than 0.05. This means that more support was found for the model that as the angle decreases photosynthesis decrease. The ANOVA also found support for the model because it showed that there was not a significant difference between the rough and smooth samples at 90 degrees and no difference was seen at 45 degrees with both having p-values greater than 0.05. The ANOVA showed a significant difference in one of two main factors, the angle and that is the main factor a difference was expected for.

A main purpose of this study was to see if the reason why *Sphagnum* has two forms, a rough and smooth, is because of physiological consequences that cause differences in canopy organization in an effort to optimize photosynthetic abilities. Since support was found for the model that means other biological factors that could have been at play likely do not have an effect on the absorbance of light and photosynthetic rates. Because, if biological factors did play a part then a difference would have been seen; as mentioned in the introduction this was a possibility because plants adapt to optimize efficiency in the environment they live in.

Although the findings of this study did not show a significant difference between photosynthetic rates of rough and smooth *Sphagnum* structures that does not mean they do not exist. Even though the difference between the smooth and rough canopies was not significant they still exhibited a difference with a small p-value of 0.186 at 45 degrees for relative photosynthesis. This difference although not significant means that some other factor may be at play in the rough canopy structure for photosynthesis. The other result that makes future study important is the rough canopy differed significantly from the model with the model falling outside of its 95 percent confidence interval. This means the rough canopy likely has some other factors at play that were not included in the model that attributes to its photosynthetic abilities.

Reasons why our study did not show these differences to be significant could be because it was very limited in sample size with only 5 samples for smooth and rough, a larger sample size would be more likely to show a significant difference because the possibility of chance occurrences is lowered. A lack of significant difference may have also been because of a fairly rudimentary way of making the rough samples from the smooth ones, the samples were not consistent. If the rough samples were more uniform it also may have cut down on chance occurrences and could have been more likely to show significant differences.

Even with the possible flaws in our testing, and that differences did exist but were not significant, it does not change that no clear answer has appeared to the question, does canopy structure change for photosynthetic purposes? One possible study to see if photosynthesis is one of the reasons for the two structures could come from looking at diffuse light. Rough plants are normally found in areas of diffuse light while smooth plants are normally found in direct light (Niinemets and Tobias 2013). For that reason it is expected that the rough plant will be better adapted for diffuse light because it normally lives under conditions of diffuse light while the smooth plant does not. If in a future study this turns out to be the case then diffuse light could be one of the main reasons for the rough form of *Sphagnum*. It is logical to expect that the two types of Sphagnum will show a difference of some sort because plants do not change structures just to look different. Plants adapt so that they can thrive in new environments just as animals do. Even though this study did not lead to further understanding of why the two structures of *Sphagnum* exist it did show another way that *Sphagnum* behaves like a vascular plant by following Lambert's cosine law.

With support found that *Sphagnum* works similarly to vascular plants it is important that shading and diffuse light be looked at more closely. In the study by Thérézien et al. (2007) it was shown that vascular trees had changing forms of pine clusters based on light level. Therefore, if *Sphagnum* is behaving like a vascular plant the rough structure may have come about because it can more efficiently use lower levels of light compared with the smooth counterpart. The results of this study and the Thérézien et al. (2007) study are also similar in that light angle did not appear to be a factor in the structural formation of the plants for photosynthetic proposes. This also shows that *Sphagnum* structural differences may be closely related to light levels due to shading rather than the angle of light. Another reason it will be important to look at diffuse light is leaf structures in vascular plants usually change because of shading or diffusing more so than for light angles. Hardwood leaves have changes in thickness levels because of internal shading not because of changing light angles. The thick and thin leaves could both handle changing light levels quite similarly (Abrams and Kubiske 1990).

Although no significant statistical difference was found when looking at how the angle of light affects the two forms of *Sphagnum,* now having better understanding of how this moss works is important because as a whole mosses are not studied enough even though they are abundant worldwide (Waite and Sack 2009). In the study by Waite and Sack they found that mosses that had diverged structurally continued to show analogous traits, which, is quite similar to the results of this study. It appeared that although ecological conditions had forced slight changes in the structures but when put in the same conditions the mosses show the same traits. In our study, although, two structural forms of *Sphagnum* were used they showed a similar trait in photosynthetic rates.

Conclusion

Support was found that the photosynthetic rates of *Sphagnum* at different angles can be successfully modeled for both rough and smooth canopy structures. The models for the structures are the same with relative photosynthesis decreasing as the angle of light decreases. The reason the two models are the same is because even though the surface exposed to the angled light changes on the rough and does not change on the smooth, the overall surface area and the intensity of the light on that surface area remains the same on the rough and the smooth with the changing angles. When the model was empirically tested using rough and smooth samples with matching surface areas it was found that they generally followed this model. Therefore the results showed: the rough and smooth samples did not show a significant difference in net photosynthesis; there was a significant difference between the net photosynthesis at different angles; and there was no significant difference between the relative photosynthesis of the model and at least one of the samples. The smooth did not significantly differ from the model but the rough did meaning some factor not included in the model could be at play in the photosynthesis of the rough plant. However, this result is not completely significant because the confidence interval of the rough does over lap with the smooth, which overlaps with the model.

What this means for our question is, the angle of light may be a factor for why the two different forms of *Sphagnum* exist but significant differences were not found in this study. Support was found that points to the rough canopy structure having a photosynthetic advantage over the smooth at 45 degrees but not a significant advantage. It is possible that the angle of light could be a factor and that for this study not enough samples were used. This result may also mean that the reason for the different structures in accordance with photosynthesis lies more in diffuse light. In addition it could mean that the different canopy structures do not have any relationship to optimizing photosynthesis. However, this seems unlikely because plants do not usually change structures without any regard for photosynthesis. While this study only served to eliminate another reason for why *Sphagnum* has two different canopy structures for photosynthesis it is still important to look into other factors that may be the cause. The more we can understand about *Sphagnum* the better because it is incredibly important for carbon cycling. With our global climate rapidly changing due to carbon cycling it is crucial to know as much as possible about this Bryophyte that has the ability to store and sequester carbon.

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