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The Effects of Canopy Structure on Photosynthesis in Sphagnum Mosses

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THE EFFECTS OF CANOPY STRUCTURE ON PHOTOSYNTHESIS IN *SPHAGNUM* MOSSES.

By

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ABSTRACT

In open habitats, *Sphagnum* grows with a dense architecture to retain water; mosses adapted to survive in shade persist in looser canopies. It is unknown if there is a physiological advantage of such rough canopies in the shade, but they may have enhanced photosynthesis at low light angles as would occur during spring or fall. It was hypothesized that the rough canopies would have enhanced rates of photosynthesis at lower angles. To test this, a photosynthesis system interfaced with a custom chamber was used to generate light response curves. Preliminary results of the study found no difference in photosynthesis with light normal to the canopy, compared with light at 45° in naturally formed core samples-- a leaf surface would decline with the cosine of the angle. Experimental data using rough and smooth canopies showed no significant difference in photosynthesis between rough and smooth canopies ($p=0.09$) at all angles tested (90°, 45°, and 22.5°). Among angles, photosynthesis significantly decreased with the angle of incident light, but outperformed predicted declines. Other factors that influence light transmission within the canopy independent of roughness may account for these results.

ACKNOWLEDGMENTS

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INTRODUCTION

Non-vascular plants, commonly known as bryophytes (mosses and their relatives), can make up to 50% of atmospheric CO₂ exchange in temperate, boreal, and Arctic ecosystems (Goulden et al. 1997, van Cleve et al. 1983). Yet, these mosses lack adaptations to control water loss and have evolved the ability to remain alive at fluctuating water contents, a condition known as poikilohydry. Their poikilohydric characteristic allows these plants to remain metabolically inactive when water levels are too low, or light intensity is high enough to desiccate the mats of mosses (Niinemets et al. 2009). In addition, due to the plant's minute size and tolerance of low light, mosses often colonize in forest floors and other habitats, which can experience low average light intensities with a high degree of variation in irradiance (Niinemets et al. 2009). For example, Swanson and Flanagan (2001) found that between 15 and 30% of light makes it to the forest floor in boreal forests, a habitat often dominated by mosses. Additionally, much of this light may be scattered or reflected from the forest canopy on its path to the forest floor, and thus strike the mat structures at vastly differing angles. Low ambient light angles are also present in spring and in fall when temperatures and water availability often favors moss growth. Therefore, it is important to understand the light-capturing abilities of mosses during such conditions as they are important carbon sinks in many high-latitude ecosystems. Furthermore, this genus of mosses have an immense ecological effect on the global ecosystem. This genus alone accounts for about one-third of the globe's soil carbon content, by covering 3.5×10^6 ha and showing carbon peat deposits of up to 4600 years of accumulation (Gorham 1991). These minute plants are a desperate subject for further study, as their activity will be of growing importance to global carbon dynamics as climate change exposes more of their northern latitude habitats, and releases methane-releasing microorganisms from newly melting permafrost (Gorham 1991). Atmospheric carbon sequestration from *Sphagnum* may be a paramount concept to fully grasp for efforts of biologists and environmental scientists to shed light on the ramifications of climate change.

Further, the size and physiological characteristics of *Sphagnum* mosses allow small-scale study of these large ecological concepts. The mosses show vertical growth gradient of varying photosynthetic ability and senescence, which produce canopy-wide effects on carbon fixation (Titus et al. 1984). Canopy function can arise from many different levels of interactions: from cell to cell, leaf to leaf, and even throughout branches and individual capitula (Rice et al. 2005). This complex morphology makes *Sphagnum* unique plants in the fact that it presents a means to examine canopy-level interactions across multiple functions. The known factors responsible for influencing these complex interactions include cation-exchange capacity, desiccation tolerance, desiccation resistance, water-holding capacity, drying rates, and photosynthetic response at differing water contents (Andrus 1986). Furthermore, nonvascular plants, which cannot exert control over carbon and water exchange like vascular plants, utilize surface area and capillary action for extracellular water retention and transport (Rice et al. 2011). Because of this extracellular transportation system, the layer of water creates a barrier for gas and light exchange; the degree of impedance is often connected to canopy structure, as well as canopy location relative to the water table (Rice et al. 2011, Titus & Wagner 1984). However, as this water film decreases due to evaporation, the canopy of bryophytes, which exhibit uniform drying and hydrating responses across entire canopies, will reach an optimum photosynthetic rate: below which desiccation and other factors retard photosynthetic output (Rice et al. 2011, Dilks & Proctor 1979).

Additionally, although photosynthesis in bryophytes is limited at very low light intensities, they grow and thrive in low light environments (Glime 2007). This dictates that the plant has become able to produce net carbon gains from photosynthesis in light environments that are inhospitable to other plants (Glime 2007). Many studies have been carried out to identify the suite of traits that make plants so well adapted to shade environments (Smith et al. 2009, Niinemets et al. 2014, Niinemets et al. 2009, Rice et al. 2008). For vascular plants, Smith et al. (2009) stated some attempts to measure photosynthesis, such as total leaf area, can vastly overestimate the total amount of light striking the

photosynthetically active individual leaves, and also overestimates the cosine and reflectance effects of complex structures. These factors must be avoided when developing a new method to measure form's relationship with photosynthetic function; simply using canopy area would not be an acceptable means to scale photosynthesis. Further, foliage structure of bryophytes, when less strongly aggregated and plant density decreases as observed in lower light, seems to provide the plant with increased efficiency of light harvesting (Niinemets et al 2014). The random dispersion of photosynthetic surfaces in bryophytes, as described by Niinemets et al. (2014), has been shown to influence light transmission throughout the canopy, affecting the plant's efficiency. Yet it has also been speculated that dispersion of the leaves has not been a significant determining factor for modeling light climate in the canopy (Niinemets et al. 2014).

Niinemets et al. (2009) showed that only about 40% of light is available further than 2 cm below the surface of the canopy in the moss *Pleurozium schreberi*, a forest moss, and that open habitat wefts support more dense aggregation of stems, causing greater self-shading. Thus, the utilization of light observed in *P. schreberi* will be interesting to consider if tightly packed mats only allow 2 cm of light penetration, for this study, which will vary canopy variation by placing capitulum in a more varied arrangement than previously measured. In a study of *Sphagnum* canopies, Rice et al. (2008) measured relationships between specific factors that contribute to photosynthetic efficiency and the photosynthetic assimilation on the basis of mass and area of the *Sphagnum* species tested. The study found that, even across species of the family *Sphagnum*, water content, carotenoid concentration, plant height, as well as the ratio of mass of the capitulum to the stem, all significantly effected photosynthetic output, standardized by mass or area (Rice et al. 2008), but the depth of light penetration did not have an effect. However, that study only examined light normal to the canopy surface.

By placing the shoots into dense moss structures, like a turf, the ability of *Sphagnum* to collectively retain water content increase and evaporation rates fall (Niinemets et al. 2009, Rice et al. 2001). This increased ability to resist desiccation has led to the mosses to often growing in the form of colonies or aggregates (Niinemets et al. 2009). Therefore it will be of interest to see how these combined traits, as seen in Rice et al. (2008) can interact with the structural information gleaned from Niinemets et al. (2009) and Rice et al. (2001) to affect carbon fixation in *Sphagnum*.

The purpose of this study is to further explain the effect of canopy structure on photosynthesis, and better understand the physiological consequences for canopies' growth in different patterns. The following two experiments were done to determine if canopy structure is a potential source for the enhanced photosynthetic efficiency of *Sphagnum*. By selecting this genus of mosses, it will be possible to construct varying canopy structures, similar to those seen in the wild, as aggregate colonies. A smooth canopy and a highly varied-height, or rough, canopy, can be analyzed as two particularly different growth styles, observed in nature, to look at the effects of these differing canopies on physiological tradeoffs and carbon dynamics.

These carbon dynamics of these differing canopy structures will be the means to examine the physiological tradeoffs. Also characterized as net photosynthetic assimilation, output can be measured by means of an area-dependent measurement. This type of photosynthetic output measurement would focus on differences of surface area, yet canopy roughness does not alter the surface area exposed to light of varying angles, as explained by Solinsky (2013). Additionally, by controlling the amount of surface area exposed, i.e. sample size, across samples, an area-based measurement of photosynthetic output would be obsolete. Therefore, for the purposes of a study pertaining to canopy roughness measurements (L_r), carbon assimilation must be measured on a basis of biomass and time: as the flow

rate together with the CO₂ concentration is the indicator of carbon uptake in the open photosynthetic system used for experiment (Rice et al. 2005).

The structure of the top portion of the canopy is the focus of this study. Much of the lower layers of *Sphagnum* mosses experience significant senescence below this height, greatly lowering the photosynthetic activity of these layers (Niinemets et al. 2009). Moreover, once the canopy has reached a level of light saturation, the photosynthetic tissues throughout the upper canopy are similarly saturated; therefore, if area of light exposure is continuous across samples, a different means of qualifying output must be used (Rice et al. 2011). Using a photosynthetic rate as a function of surface area would be insufficient in this study: as exposed surface area will be held constant across all trials. In this study, it will be necessary to focus squarely on canopy structure with the capitulum of the mosses and the directly subsequent branches of the moss. Therefore, the effects of canopy structure may be an effective means to determine carbon dynamics of mosses, due to its extreme usage of available sunlight.

The results found by Solinsky (2013) will be used to guide the current study. It is possible that there was more information to be gleaned from that form-function study. Solinsky (2013) found that the net photosynthesis of *Sphagnum* canopies did not vary according to the expected decline predicted by Lambert's cosine law. Instead, the photosynthetic output of smooth and rough canopies at lower angles were significantly different from the expected output (Solinsky 2013). Solinsky (2013) only found a significant difference in photosynthesis due to angle between the measured results and the expected results.

The first part of the present study was done to reinforce this established pattern, as well as the observed efficiency as compared to what is expected from the results predicted by the cosine law, as the angle of light exposure decreases from 90° down to 45°.

The second part of the experiment attempted to determine the degree to which the canopy roughness affects photosynthetic output and if differences in roughness explain the increased efficiency of photosynthesis in *Sphagnum* as a whole. By varying the light angle, the magnitude of light exposure on the surface area will decrease: this means less direct vertical light will hit the canopy surface. Instead, the lower angle light will expose lower levels of the canopy to more light than direct vertical light. These light angles will simulate similar light exposure of varying times of day, as well as variation in seasons. From these expected lower light angles, it is expected to see a significant decrease in photosynthetic output: similar to the production drop seen in flat leaf surfaces dictated by Lambert's Cosine law. This law says that radiant intensity of light on a surface is proportional to the cosine of the angle between the light and normal to the surface. Therefore, in this experiment, it is expected that the photosynthetic output will drop drastically as the angle of light also decreases. It is hypothesized that canopy roughness will directly correlate with photosynthetic efficiency in *Sphagnum* mosses, as the canopies become more rough, the rate of carbon fixation at low angles will be closer to maximum output, as modelled by the normal light exposure. It has been well documented that tighter-packed, smooth canopies regularly appear in locations of higher sun exposure, while rough canopies occur in more shady locations with elevated effects of light scattering (Glime 2007, Niinemets et al. 2009). The degree of roughness of the canopies will have to be measured, to be the independent variable of the study. After being constructed by hand, the gradation of variation in the heights of the plants will be measured, using laser-scanning techniques modelled after the procedure developed by Rice et al. (2005).

METHODS

The experiment included two parts. Part 1: Field Canopies involved the measurement of photosynthesis taken at different light intensities and angles for cores extracted with their natural

canopy structure. Part 2: Experimental Canopies employed experimentally manipulated rough and smooth canopies where, photosynthetic output was measured at three different angles of incident light. An IRGA interfaced open system measured photosynthetic output by measuring CO₂ flux in and out of a custom canopy chamber.

Part 1: Field Canopies

Stems of *Sphagnum fallax* were collected on September 29, 2014, from a fen wetland in Rotterdam, NY. Sample cores were created by cutting 6 sections of the top portion of the stems and placing them within 10 cm diameter PVC sections, 5 cm tall. Canopies used between 38 and 55 individual stems (\bar{x} =44 stems, n =6) across an area of 78.5cm², producing an average canopy stem density of 0.57 stems/cm². These sample cores were maintained to keep the natural canopy structure found on site, no further modifications were made to the samples.

Photosynthesis was measured using a custom chamber, connected to a LiCor 6400 Photosynthesis system (LiCor Inc, Lincoln, NB) in open mode. During measurements, chamber conditions were kept at a flow rate of 500 $\mu\text{mol sec}^{-1}$, with a reference carbon dioxide level of 400 ppm. The samples were then exposed to light at a specified angle (90° and 45° relative to the surface of the canopy), as well as varying light intensities for each angle (50, 100, 250, and 500 $\mu\text{mol}_{\text{photons}} \text{m}^{-2} \text{sec}^{-1}$ photosynthetically active radiation, PAR—wavelengths between 400 and 700 nm) to generate light response curves. Illumination was provided by equal amounts of red and blue LEDs in a light panel. All samples were exposed to each level of PAR intensity beginning at a light level order of 250, 50, 100, 250, and then 500 $\mu\text{mol}_{\text{photons}} \text{m}^{-2} \text{s}^{-1}$, at both angles of incidence. Prior to each measurement, samples were massed, placed within the chamber and allowed to acclimate for 20 minutes before recording photosynthetic rate. Following each reading, canopies were removed and returned to their initial weight before the next measurement to maintain the same water content. Light response curves were

generated and the photosynthetic rate at 90° was compared to 45° and to that expected by the cosine law at the different angles.

Part 2: Experimental Canopies

Twelve canopies were constructed of stems of *Sphagnum fallax* samples from a bog near Oneonta, NY in early October 2104. The stems were collected, and placed semi-covered with thin, clear plastic in a temperature and light-controlled growth room. The samples were exposed to 14 hours of sunlight, using timer set to shine white light from 8 am to 10 pm, daily. Samples were also monitored daily and watered on a two-day cycle. The original 12 samples were then deconstructed, mixed together, and re-assembled into 10 experimental trials. The ten new samples were constructed using between 37 and 51 stems ($\bar{x}=42.3$ stems, $n=10$, 8 of which contained between 37 and 43 stems) of *S. fallax* organized into two treatments: rough ($n=5$) and smooth ($n=5$). These canopies were constructed of 4.5 cm stems, in PVC pipe sections, 6 cm in diameter, creating an average stem density of 1.50 stems/cm². For the rough canopies, half of the stems were displaced above their neighbors revealing one cm exposed to light, while the other half were left at 3.5 cm exposed. All stems in the smooth canopies maintained 3.5 cm of stem exposure.

To ensure that the two canopy structures were significantly different, the exact measurement of canopy structure roughness (L_r) was then measured using laser stripe-canopy intersection to calculate the exact values of canopy variance, as outlined in Rice et al. (2005). The point of first contact of the laser stripe was used to calculate the semivariance measurement, varying vertical distance along with horizontal distance along the stripe. Twice the square root of the semivariance produced the L_r . See Rice et al. (2005) for further details on this measurement.

The intensity of light necessary to saturate the sample was determined from Part 1 to produce the most productive and consistent results. Similar system variables, i.e. flow rate, carbon dioxide concentration, and light-producing equipment, as well as the same photosynthetic measurement instrument and housing chamber used in the part 1 were used again for the second half of the study. The 10 samples were exposed to light at angles of 90°, 45°, and 22.5° relative to the canopy surface, in randomly generated order. Each sample's mass was measured before and after each period in the chamber, and was restored to the original water content before each measurement. Photosynthetic output was measured by the difference of carbon flux in and out of the chamber, for each sample at each angle of light, in ppm. Light levels were maintained beyond the saturation point of the canopies, as determined from the natural canopy light response curves (PAR min: 245 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, max: 506.2 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$).

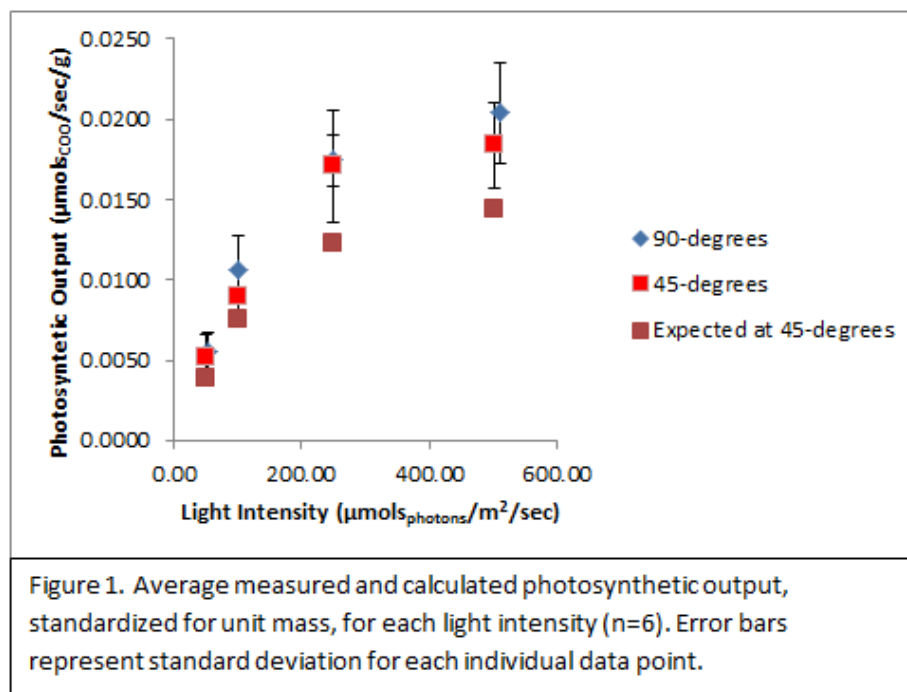
All collected data were organized using Windows Excel. Calibration images and roughness calculation, following the method outlined in Rice et al. (2005) also employed ImageJ (National Institutes of Health, Bethesda, MD), and Vesper v.1.62 (Minasny et al. 1999) software. Repeated ANOVA was used to determine significant relationships between treatment, angle, and any interaction between the two, and was performed using JMP ver. 8 (SAS Institute Inc., Cary, NC).

RESULTS

Field Canopies

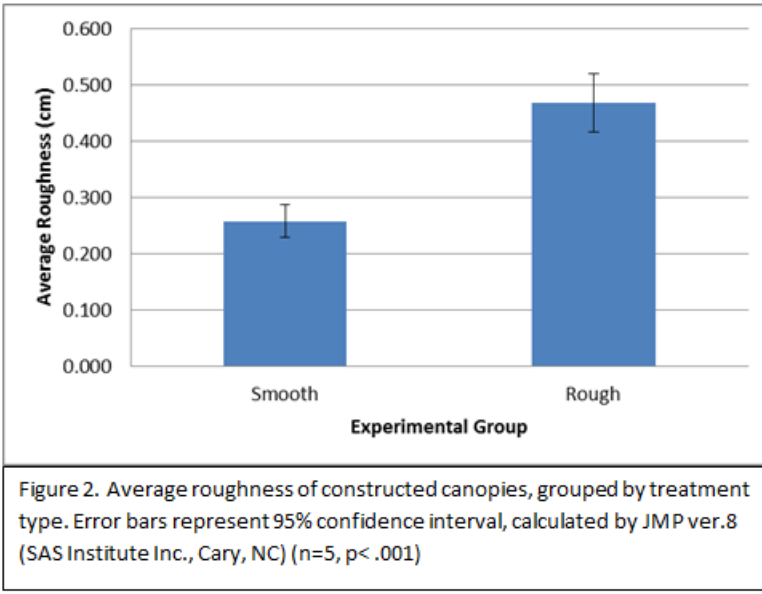
The canopy structure test using field-collected plants was performed to generate baseline information for an experimental study. The dependent variable was the net photosynthesis, measured in $\mu\text{mol CO}_2 \text{g}^{-1} \text{sec}^{-1}$, measured for direct light at a perpendicular angle of incidence relative to the canopy (90°), as well as at an angle of incidence of 45° to the canopy. Expected values for the 45° trial were included, and calculated from the values of the perpendicular trial, through use of the cosine law,

an expected decline of 52%. As the light intensity increased, at both angles, photosynthetic output increased resulting in typical photosynthetic light response curves (Figure 1). The 45-degree treatment included the expected output within the standard error range for lower light intensities (less than 250 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) but did not include the predicted value of Lambert's cosine law using the 90-degree data set at the higher light intensities (250 and 500 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) within the standard error range.

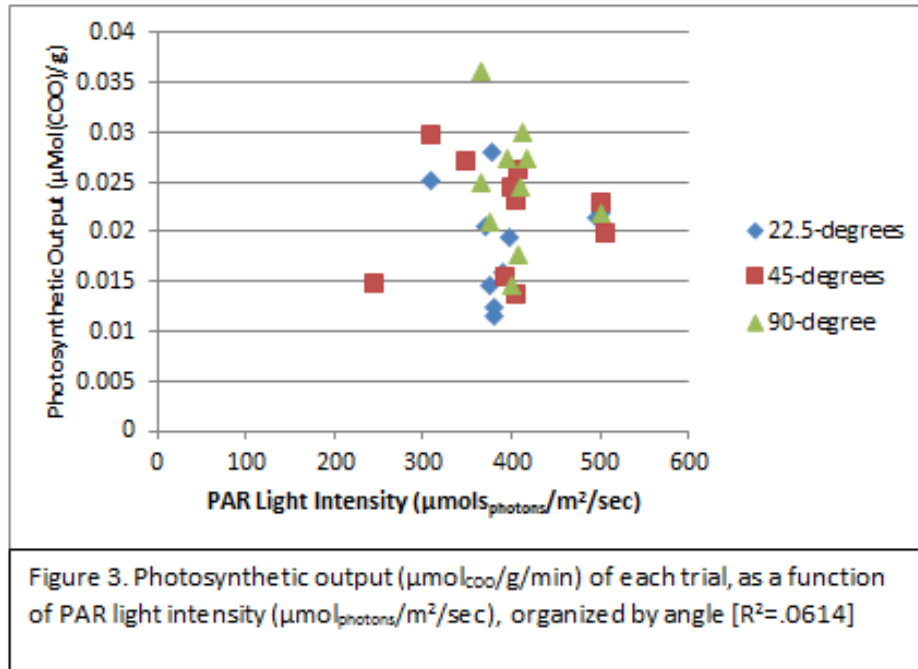


Part 2 Experimental Canopies:

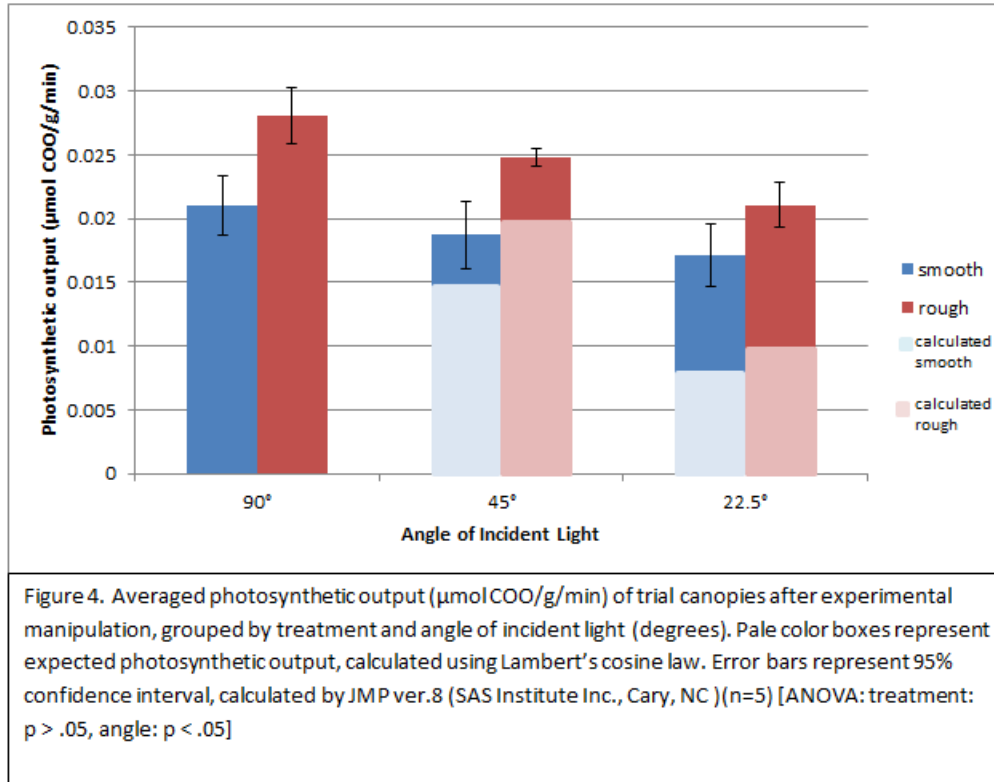
Figure 2 shows the mean L_r for both the constructed smooth and rough canopies, calculated using the square root of twice the semivariance measurement of each canopy, for the smooth treatment was 0.258 cm with a range of 0.079 cm, while the mean for the rough treatment was 0.467 cm, and a range of 0.142 cm. A two-tail t-test indicate that the degree of canopy variation was significant with a p-value less than .05 ($p=0.00004$). Therefore the rough treatment was significantly rougher than the smooth treatment.



Throughout testing of the experimental canopies, light levels were not kept at one specific level for all trials at all angles. Light intensity ranged from 245 $\mu\text{mol Photons m}^{-2} \text{sec}^{-1}$ to 506 $\mu\text{mol Photons m}^{-2} \text{sec}^{-1}$. Graphed against photosynthetic output, measured in $\mu\text{mol CO}_2 \text{g}^{-1} \text{min}^{-1}$, it was determined through regression analysis that in this experiment, no significant relationship between light intensity and photosynthetic output across angles existed, confirming light saturation ($R^2 = .003$). The relationship between photosynthetic output and light intensity was not significant for any of the three angles, ($p > .05$), for each of the three angles tested. Consequently, differences in light intensity were ignored for the comparison of canopy types across the different light levels and canopies were assumed to be light saturated.



The photosynthetic output of each trial and at each of the three angles of light was collected for both experimental treatments. The output for both rough and smooth canopies was significantly different between angle ($p<.05$) with the photosynthetic output decreasing as angle decreased. The difference between canopy structures was not significant ($p>.05$). When comparing the measured photosynthetic rate to the one estimated using Lambert's law of cosin, the rate was much higher than expected (Figure 4). Expected photosynthetic output was calculated using the cosine law and 90° as the maximum output for each treatment. Error bars represent 95% confidence intervals, calculated using JMP ver. 8 (SAS Institute Inc., Cary, NC) as shown in Figure 4 ($n=5$).



DISCUSSION

The analysis of the naturally formed canopies supported and furthered the results exhibited from the past study seen in Solinsky (2013). *Sphagnum* canopies showed improved photosynthetic output relative to the expected decrease as the light angle decreased from 90° to 22.5°, a trend noticed between 90° and 45° in a past study (Solinsky 2013). The naturally formed canopies outperformed the predicted model of Lambert's cosine law. The results from the field canopies showed that while angle decreases, regardless of light intensity, the photosynthetic output of naturally occurring *Sphagnum* canopies perform photosynthesis much more efficiently than expected, with an insignificant difference between canopies exposed to different angle of light at all intensities. Yet these canopies were naturally occurring canopies, which are growth-adapted to their specific degree of variation of canopy heights. This acclimation over a long growing period of spring, summer and some of the fall before the plants' harvest in October could alter the individual plant's localization of photosynthetic pigments. If the plant

had been able to acclimate to a specific canopy orientation, then the plants could concentrate specific compounds to these desired areas of light exposure, to maximize carbon fixation and ensure the plants continuity.

In the experiment using field-collected canopies, many light levels were used to determine where the light saturation occurs and if it changes by angle. This second experiment determined that at this saturation point, the photosynthetic output was similar between treatments. Furthermore, different from the first experiment, the structures of the rough treatment and the smooth treatment varied greatly: a two-way t.test of the L_r measurements of the two populations produced a p-value less than .01. Thus, the differences in structure were great: the rough and smooth canopies both represented a group of individual plants in different orientations, rather than one large surface working together.

The Cosine law is a model for flat surfaces, such as a single broad leaf from a deciduous tree. From the results of both experiments, it was determined there was an increased photosynthetic activity of both smooth and rough canopies to carry out carbon fixation more efficiently than predicted by the cosine law. Other explanations for the measured results are possible. For example, individual capitulum shape, leaf-orientation, or nutrient allocation could contribute to the increased productivity. The complex canopy structure of the naturally formed canopies has inherent roughness, because of the bulbous shape of the individual capitula. This roughness is created by many one-cell thick leaves, which have an extra level of dimensionality compared to flat leaves. Lambert's cosine law would only explain surface exposure of a flat leaf, a 'macrosurface,' which contains variation below the leaves' outer surface, which would experience less light exposure due to the light needing to pass through more plant material to get to the non-surface chlorophyll. Because the individual capitula are made up of a compilation of single cell-thick leaves, this effect could be minimized, thus accounting for the results seen in part 1. Also, by exposing the lower levels of the capitulum to light with a non-perfectly flat

canopy surface, direct light contact to photosynthetic layers just under the capitulum may also account for some of the additional productivity measured. The experimental canopies were then constructed and studied to explore these possibilities.

Some potentialities for the increased photosynthesis come from a suite of specific traits that could arise from the canopy organization as a whole. Some of these include light scattering within the canopy. Moss canopies grow large lateral buds, as well as apical growth (Niinemets et al. 2009). This lateral growth, in particular, could either shade lower levels of the plant from light exposure or help scatter light within the canopy and increase photosynthetic output by maximizing light exposure. In tightly packed smooth mats, these lower levels would not be as impactful as in the looser rough canopies.

Therefore, it was necessary to remove the confounding factor of individual plants acclimating to their natural canopy density, and potentially altering the pigment content of specifically located leaves or structures. The purpose of the second experiment was to isolate the effects of differences in roughness, by controlling other confounding factors, to explain the high levels of photosynthesis at low light angles. The confounding factor of the canopies' ability to acclimate as a collective canopy was removed and specifically structured canopies were formed using a population of similar individual stems for the experiment. In this way, only differences in canopy roughness could be compared.

This was accomplished in part 2 of the study: each canopy was built from randomly selected individual mosses, in a smooth or rough orientation. This process completely negated the potential for the moss canopies to acclimate into one large structure. Thus, the results of the empirical study represent purely the effect of canopy structure on the individual plant's photosynthetic output. The randomly selected stems used for the construction of the experimental canopies controlled for the canopy-wide effects, removing the possibility of confounding effects from the study.

The second set of collected data show a similar result to the first: the treatments both outperform predicted photosynthetic output of Lambert's cosine law. Both rough and smooth canopies significantly outperformed the predicted photosynthetic rate of the cosine of the angle relative to normal to the canopies at both 45° and 22.5° (except for the smooth treatment group at 45°, which included the predicted photosynthetic output from the Cosine Law model within the 95% confidence interval). A repeated measures ANOVA determined that the angles produced significantly different photosynthetic outputs ($p < .05$), while the treatment of structure did not have a significant effect ($p > .05$). The canopy treatments were close to significant, producing a p value of 0.094, indicating that in a more strictly controlled experiment, roughness may play an important role in photosynthetic output. When considered with the result that the smooth treatment at 45° included the model value within the 95% confidence interval, while the rough values were far from the predicted value, it could be further speculated that canopy structure plays a role in photosynthetic productivity.

This study saw the output drop from 90° to 45° by the same amount as seen in Solinsky (2013) rough treatment [$-0.003 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ min}^{-1}$, a 10.7% drop in this study compared with a 12.5% drop in Solinsky (2013)]. The smooth canopy of the latter study dropped $0.006 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ min}^{-1}$ or 22%, while in this study, the smooth canopy only dropped $0.003 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ min}^{-1}$ or 10.7% from the normal light angle. The results of this study mirrored the results of Solinsky (2013), in that the 45° treatment for both the smooth and rough canopies dropped by much less than the predicted drop from the cosine law (a predicted 21% drop at 45°).

In unpublished results obtained from the Rice et al. (2008) study on multi-species comparisons of *Sphagnum* photosynthesis, average roughness was 1.20 cm with a range of 0.67 cm to 1.98 cm for ten different *Sphagnum* species; this roughness explained less than 1% of the variation seen in photosynthesis at the normal light angle. The present experiment focused on the effects of roughness

and lower angled lights in the same species. Yet these data are important to compare to this experiment, (rough group: \bar{x} =0.467 cm, min. = 0.392 cm, max. = 0.534 cm: smooth group \bar{x} = 0.258, min. = 0.211, max. = 0.290). These values are much higher than the current study's values, indicating that the past study's canopies were much more rough. Because of this increased roughness in the past study, these results can be accepted as further evidence that canopy structure, particularly roughness, does not significantly affect photosynthesis.

The results of both experiments put together could explain why the increased photosynthetic efficiency is not just the canopies' increased efficiency of harvesting light energy as the angle decreases: the light saturation point is similar for both angles of exposure. This mirrored efficiency is interesting, because of the lack of naturally occurring high intensity light at low angles. One would expect that at lower angles, the infrequently exposed understory of the canopy would be relied on more for photosynthesis, thus lowering output, as the interior layers are more often senescent, rather than being relied on for performing photosynthesis (Niinemets et al. 2009). This may have been because the surface area exposed at all angles is similar and the photosynthetic quality of the newly exposed internal canopy material is still close enough to the capitulum to contain sufficient photosynthetically active compounds. The lower levels, which are no longer photosynthetically active, may be involved in redirecting light to maintain maximum photosynthetic output, even at lower angles. In the rough canopies, the exposed sections may either be in the important top 2 cm of the moss, which captures up to 60% of the available light (Niinemets et al. 2009), or below and therefore reflect and scatter light back up towards the capitulum. By concentrating photosynthetic compounds in the mid- to upper-canopy, nonvascular bryophytes may be exhibiting a similar suite of adaptations as seen in vascular plants, with additional adaptations unique to non-vascular plants to achieve a similar P_{\max} at high and low light angles. This concept of growth seen similarly in vascular plants, which tend to produce interior leaves

that grow thicker to effectively harvest all of the rarely available light is due to internal shading (Rice et al. 2008). While in the non-vascular plants, it may be internal reflective surfaces.

Nevertheless, this increased productivity of bryophyte canopies may be due less to the shape of the entire canopy structure and more to the three dimensional organization of the curved leaves of the individual mosses. At each angle, the incident light is still hitting a curved surface, which would create even more scattering of light from the individual leaves, which are only one cell thick and surrounded by a water film, and therefore could reflect and scatter light around the rest of the canopy. Internal reflection of the canopy, as an entire structure, could account for the rough canopy's ability to increase photosynthesis throughout the entire exposed understory and canopy. The smooth canopy would not experience as deep of a penetration of light, and therefore less internal reflectance would occur—related to results shown in Rice et al. 2008. This canopy structure must account for increased photosynthesis because only the most efficient structures of the capitulum are exposed to all of the available light.

The internal reflectance, not present in the smooth canopies that attenuate light more quickly, could be a possible explanation for the rough canopies' increased productivity at low angles. This could help the rough canopies match the output of smooth canopies, which are always performing photosynthesis with only the tops of the capitulum: the most specialized structure for photosynthesis where most of the photosynthetically active pigments are concentrated (Niinemets et al. 2009). It is possible that the exposed understory of the rough canopy's possess a suite of characteristics which increase productivity of the lower levels of the canopy, to account for the lack of difference of output between canopy structures. By utilizing special traits of the exposed understory, the rough canopies may be able to perform photosynthesis more effectively to match the optimum output of the smooth canopy: which only employs the capitulum for photosynthesis.

A major concept that was absent from this experiment was the idea of the individual plants adjusting their physiology as an entire unit. This concept is a difficult variable to control in an experimental set-up. Instead, the physiological trade-off of canopy structure was evaluated, due to the simplicity of the means to do so. However, because the results did not support the hypothesis that photosynthetic output would be affected by canopy structure, in a quantitative manner, other biological factors must be at play in the plant systems, to augment the plants' efficiencies against that of a flat leaf, just not in the form of canopy structure. From this study, it was determined that the difference of photosynthetic rates was not significant between rough and smooth canopies, yet somehow the rough canopy, which exhibited less photosynthetically-optimal exposed surface area, performed similarly to the smooth canopies: which only had the capitulum exposed. Some type of biological factor must account for this additional efficiency of the rough structures.

Nevertheless, as an experiment on the whole, one change could have been made to ensure more validity and consistency in the results: using uniform light intensity across all angles of the empirical trial. This inconsistency may have been significant enough to obscure any subtlety in the physiological trade-off of the canopy structures. In addition, using the exact same number of stems and capitulum would help in increasing the experiments' consistency: yet what was carried out may have been precise enough. If able to, repeating and improving on this suite of experiments may shed more light on the minute differences between smooth and rough canopies.

Even though there were imperfections in the execution of the testing, the results were consistent and plentiful enough to conclude that there must be some type of physiological trade-off to canopy structure. Past studies have expressed that different canopy structures tend to be located in different light conditions, yet, it is possible these varying structures have been adopted by the *Sphagnum* family to serve a different purpose than photosynthetic output directly. It is possible that

these structures have more of an effect on water retention: a topic not covered by this study. Water retention effects carbon fixation, due to bryophytes' inability to conduct substantial volumes of water internally, and instead forms a barrier to gas diffusion through capillary action. Additionally, the differing canopy structures may play a role in the fixation of carbon when exposed to diffuse light. Furthermore, the individual orientation and make-up of the leaves on each capitula and plant could also play a role in the unexpectedly effective carbon fixation of rough canopies. Further studies could look into these topics as potential physiological benefits coming from rough canopy structure.

As for this study, no significantly differing results came from the different structures of canopy, with regard to how the angle of light affects the carbon fixation of *Sphagnum* mosses. While the difference between treatments was not significant: both canopy structures resulted in significantly greater light absorbance than predicted by Lambert's cosine law. Yet, the results still are encouraging of further study of the family, as a whole. Because peat mosses are such an abundant and metabolically active carbon sink found worldwide: found in Australia, as well as Scandinavia and even further north (Gorham 1991). Further study into the carbon-cycling role these abundant organisms should increase as a whole, due to the current hot button topic of climate change in popular culture (Gorham 1991).

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