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Carbon Fluxes in Mosses in Alpine Ecosystems

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Abbrevations

A: Photosynthesic rate per µmol kg^{-1} s^{-1}.

A_{gross}: Gross photosynthesic assimilation rate per µmol kg^{-1} s^{-1}.

A_{net}: Net photosynthesic assimilation rate per µmol kg^{-1} s^{-1}. $A_{gross} – R = A_{net}$.

R: Respiration rate per µmol kg^{-1} s^{-1}.

PARi: Photosynthetically active radiation intensity.

RWC: Relative water content.

Abstract

Background and aims – Alpines areas expected to see an increase in temperature as a response to climate change and bryophytes are decreasing in coverage compared to vascular plants. Thus it is of interest to see if the photosynthesic activity of mosses are affected by the increase in temperature and if not, it might be that the cause of decrease in bryophyte coverage is a result of competition from shrub plants.

Methods – Samples of six different species (*Aulacomnium palustre*, *Dicranum* sp., *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune* and *Sphagnum* sp.) were used in gas exchange measurements at four different temperatures (13, 16, 19 and 22°C). Samples of the six species were also collected and used for measuring of desiccation rate by placing them in an equilibrium chamber and weighing the samples at set time intervals over a period of 24 hours.

Results – Only *Dicranum* sp. and *Sphagnum* sp. showed a statistically significant decrease in net photosynthesic assimilation rate as the temperature increased, though all species show a tendency for decrease up to 19°C. After 19°C *Sphagnum* sp. stops decreasing and *A. palustre* and *H. splendens* shows a slight increase at 22°C. The rest continues to decrease. By comparing the species at the different temperatures, *P. commune* were found to have the highest assimilation rate at all temperatures and *P. schreberi* and *Sphagnum* sp. to have the lowest. For the desiccation rate, there were statistically significant differences in the desiccation rate for the first 30 min, and after that all the six species desiccation rate were more or less the same.

Conclusion – I have found that as the temperature increases, the differences in A_{net} between the species decreased indicating that they respond differently to higher temperatures. 19°C seemed to be where the species diverged in response where some continue to have a decrease in A_{net}, while others stops decreasing or even have an increase as the temperature increases. *Sphagnum* sp. were found to be the better of the species at retaining water while *P. commune* were the weakest for the first 30 min.

Sammendrag

Bakgrunn og mål – Det er forutsett at temperature i alpine områder vil øke som en følge av klima endringer, og det vil være en nedgang i bryofytter sammenlignet med karplanter. Det er derfor av intresse å se om fotosyntese aktiviteten hos moser blir påvirket av en økning i temperatur, og vis dette ikke er tilfellet, så kan nedgangen i bryofytt dekke skyldes konkuranse fra buskplanter.

Metode – Prøver fra seks forskjellige arter (*Aulacomnium palustre*, *Dicranum* sp., *Hylocomium splendens Pleurozium schreberi*, *Polytrichum commune* og *Sphagnum* sp) ble brukt til gassutvekslingsmålinger ved fire forskjellige temperaturer (13, 16, 19 og 22°C). Prøver fra de seks artene ble også brukt til å måle uttørkningshastighet ved bruk av et ekvilibriumskammer, der prøvene ble veid ved faste tidsinterval over en 24 timers periode.

Resultater – Det ble kun funnet en statistisk signifikant nedgang i fotosyntetisk CO_2 assimilasjon ved økning i temperaturer hos *Dicranum* sp. og *Sphagnum* sp, men alle artene viste en tendens til nedgang opp til en temperatur på 19°C. Ved temperaturer høyere enn 19°C stopper nedgangen hos *Sphagnum* sp, og *A. palustre* og *H. splendens* hadde en svak økning fra 19 til 22°C. Resten av artene hadde en nedgang etter 19°C. Ved å sammenligne artene for hver temperatur, så ble det funnet at *P. commune* hadde høyest netto assimilasjon ved alle temperaturene, og *P. schreberi* og *Sphagnum* sp. hadde den laveste. Under utørkning så var det en statistisk signifikant forskjell i vanntap de første 30 min, og etter det så var vanntapshastigheten mer eller mindre lik for alle artene.

Konklusjon – Jeg fant at når temperaturen øker, så minker forskjellen i A_{net} mellom artene, noe som indikerer at de påvirkes forskjellig ved økning i temperatur. 19°C ser ut som punktet hvor artene får størst forskjellig påvirkning av økende temperature, der noen fortsetter å ha en nedgang i A_{net}, hos andre stopper nedgangen opp, og noen har en svak økning i A_{net} når temperaturen øker. Jeg fant at *Sphagnum* sp. er best til å holde på vann av artene og *P. commune* er den dårligste under de første 30 min av forsøket.

Introduction

Global climate change is projected to have large impacts in arctic and alpine areas. By the end of the century, large regions of the terrestrial arctic are predicted to experience a warming of 6˚C or more (Sanderson et al. 2011), which makes it important to see how this increase in temperature will affect plant life. A study done by Sandvik and Heegaard (2003) showed that as long as water is freely available, mostly from precipitation and meltwater, an increase in nutrients and temperature may favour bryophytes. Bjork and Molau (2007) showed that bryophytes will mostly be negatively impacted by vascular plant species from adjacent plant communities.

A meta-analysis of numerous studies concludes that warming significantly alters biomass accumulation of terrestrial plants, with woody plants showing the highest increase while spore plants suffer a suppression in growth(Lin et al. 2010). In a factorial field study by Potter *et. al.* (1995), where temperature, water supply and nutrients (NPK fertilizer) were increased, the total moss coverage were less than 50% of total plant biomass compared to an unfertilized field. Klanderud (2008) did a similar study and found that after four years of warming and nutrient addition 57% of the mosses had disappeared, and hypotheses that this might not be from the increase in temperature but rather that tall species may expand at the expense of low stature species. This hypothesis is shared by others, including Cornelissen *et al.* (2001) who hypothesised that the increased temperature and/or nutrients lead to a decline as a function of increased abundance of vascular plants. In addition to this, Vellak et al. (2003) shows that “distance from nearest tree” is the strongest influence of diversity and distribution of bryophytes. Species richness increases the further from trees they are.

A study on moss species (Waite and Sack, 2009) found that mosses have a low leaf mass per area and low gas exchange rate. It is expected that mosses have a low light saturated photosynthesis rate, given their growth form and biochemical tolerance of shade and desiccation (Waite and Sack, 2009). Unlike vascular plants, light-saturated photosynthesic rate per mass did not correlate with habitat irradiance. Mosses are becoming increasingly recognized as a major contributor to ecosystem carbon cycling (Gorham 1991, Street et al 2013). This is both as a substantial contribution to cumulative sub-arctic land-surface carbon uptake (Street et al 2013), and insulation on soil and permafrost layers. Mosses contribute to

resistance to directional climate change and climate-mediated disturbance such as permafrost thaw (Turetsky et al. 2010).

Unlike vascular plants, mosses lack the means to store and regulate water loss, since they don't have either a cuticle or stomata, and take up water directly from the air moisture, so that desiccation might be the affecting factor rather than temperature in moss photosynthesis. A study done in Antarctica by Robinson et al. (2000), indicates that desiccation may lead to not only reductions in moss communities but also changes in community composition.

Few studies have focused on carbon fluxes in mosses and as mosses are very abundant in the field sites in the Dovre Mountains of Central Norway, this study will focus on the carbon fluxes at different temperatures and desiccation rates in the six most common moss species found at the study site. The species I will look at are ribbed bog moss (*Aulacomnium palustre*), fork moss (*Dicranum* sp.), stairstep moss (*Hylocomium splendens*), big red stem moss (*Pleurozium schreberi*), common haircap moss (*Polytrichum commune*) and a peat moss (*Sphagnum* sp.). I will look at the photosynthesic assimilation rate for each species at four different temperatures, 13, 16, 19 and 22°C, and compare the difference both between the different temperatures for each species individually and between each species at each given temperatures. From this I hope to see how temperature affects the photosynthesic activity for each species and which species is most affected by changes in temperature. I will also be looking at the desiccation rate for each species over a period, as water may also be an important factor for photosynthesic activity in mosses. For this study my research questions are:

1. How does temperature affect the net photosynthesic assimilation for each species?
2. Does one or more species perform better or worse at a specific temperature?
3. At what rate do the species desiccate?

Materials and methods.

All samples used in the study were collected at the study site at Norsk Villreinsenter Nord (62°13′ N, 9°32′E), Hjerkinn, in Dovrefjell-Sunndalsfjella National Park in central Norway. It is within the lower alpine zone 1012 m.a.s.l. The characteristic climate there is a mean temperature of -11.8 °C in January and 10.1°C in July, and a mean annual precipitation of 787 mm (1961-1990). The climate in 2015 had a mean temperature of 9.1°C in July and the warmest measured day were 24.2°C, with a total annual precipitation of 641,7mm (Norwegian meteorological institute 2016).

Two different analyses were done, the first being a measurement of photosynthesic activity at different temperatures and the second a measurement of desiccation rate.

A third analysis were planned where I would look at the photosynthesis at different levels of desiccation. This part had to be scrapped due to a breakdown of the portable photosynthesis system, requiring it to be sent off to maintenance. The plan were to use five different 1 litre solutes made of H_2O and PEG 400 (polyethylene glycol 400). The solutes were to have 10%, 20%, 30%, 40% and 50% PEG 400 in weight percent and the rest H_2O, giving a range of different equilibrium water potentials.

Photosynthesis measurements

The measurements of photosynthesic activity in mosses were conducted at the study cite in the period from 11.06.15 to 18.06.15, by measuring gas exchange using a portable photosynthesis system (CIRAS-3) and a PLC3 leaf cuvette modified with a 4.5 cm diameter cup to hold moss samples. The reference air were taken from outside and had a mean of 416.3 μmol CO_2 mol^{-1}, and 60% of the humidity were removed before it reached the cuvette. At the start of each day, fresh samples of each species were collected and brought inside, and prepared by cutting of the top “green” part of the mosses. The cut parts were measured to fit the bryophyte chamber, put in small 4cl plastic and stored inside a small equilibrium chamber, a sealed plastic box fitting six of the sample cups (one for each species) elevated above a small pool of water. Each species sample were measured in a random order each day at four different temperatures 13, 16, 19 and 22°C. All samples were first measured at 19°C

in their given random order for the day, then 16, 13 and finally 22°C. Each sample were returned to the equilibrium chamber after being measured to ensure they were fully saturated before a new temperature measurement were conducted on the same sample. A custom script I made were used for each temperature measurement lasting for a total of 5 min and 20 sec. The script for each temperature followed the same procedure: 1 min of dark acclimation followed by three measurements with a ten second interval, then a 3 min period of acclimation to light exposure followed by five measurements with a ten second. The multiple recorded measurements at the end of each acclimation period were used to ensure the measurements were stable, and a mean value were calculated for each measurement interval to correct small changes. The basis for light intensity (µmol m^{-2} s^{-1}) were determined by creating a light response curve for each species to see at which PARi (photosynthetically active radiation intensity) the curve started to horizontally align, which is the point where the mosses reach full light saturation. From running light response curve measurements for each species, the optimal PARi were found to be around 1000 (Appendix A).

Since I were using a custom made bryophyte chamber for my measurements I had to recalculate A (photosynthesic rate per µmol kg^{-1} s^{-1}). The bryophyte chamber were 4.5 cm^2, and for each sample, the chamber were as closely filled with moss as possible without being packed tightly, allowing some small breathing room. The measured value for A is originally based on leaf area (m^2), but since I were using a large sample of moss instead of an individual leaf I had to recalculate A based on dry weight (g) instead. A is given as:

$$\mathrm{A} = \frac{\mu mol}{m^2 s}$$

To correct it for sample dry weight:

$$A = \frac{\mu mol}{m^2 s} * \frac{m^2}{kg} = \frac{\mu mol}{kg\ s}$$

$$\frac{m^2}{kg} = chamber\ area\ (cm^2) * \frac{1m^2}{10^4 cm^2} * \frac{1}{dry\ weight\ (g)} * \frac{10^3 g}{kg}$$

Desiccation rate

The samples were collected at the study site and brought back to the lab at NTNU, where 10 samples of each species were prepared by cutting of the top "green" part of the mosses and giving the samples roughly the same size. The samples were divided into two sets where five of each species were placed in two separate 30 x 30 x 7cm equilibrium chambers containing 1 litre of distilled water each. Both boxes were stored at room temperature and without access to direct sunlight both before and during the desiccation measurements. The first sample set were kept in the chamber for 12 hours before weighing to ensure they were all fully saturated. Each sample were weighed at full saturation then transferred to a new equilibrium chamber containing 500g PEG 400 (polyethylene glycol 400) weight % then), a strong hydrophilic liquid, and 500g distilled water giving the chambers an equilibrium water potential of about -15 MPa, to start a controlled desiccation process. The samples were then weighted at the intervals 15 min, 30 min, 1 hour, 2 hours, 4 hours, 8 hours and 24 hours after being placed in the desiccation chamber. The process were repeated once more for the second sample set right after the last measurement from the first set. After each sample were weighted they were put in a drying oven and dried at 50°C for 3 days to ensure they were completely dry before being weighted.

Since each species had some differences in weight, the sample measurements were recalculated to show the relative water content (Rwc) to better be able to compare them.

Rwc were calculated using this formula:

$$Rwc = \frac{FW\ (weight\ at\ the\ time\ of\ measurement) - DW\ (dry\ weight)}{HW\ (hydrated\ weight) - DW}$$

Statistical analysis

The statistical analyses were performed using Minitab software. Analysis of variance (ANOVA) and Tukey tests were used to analyse the data. Analyses were run to look at the relationship between A_{gross}, R and A_{net} and temperature for each individual species, the difference between each species at each temperature, and to look at the differences in desiccation for the first 30 min.

Results

Gross Photosynthesis

The means of the gross photosynthesic rate per µmol kg^{-1} s^{-1} (A_{gross}) for each species at different temperatures is small. Of all the species, only *P. schreberi* has a statistically significant difference between the measured temperatures (table 1), 13 and 19°C (figure 1). The overall (A_{gross}) ranges from 11 µmol kg^{-1} s^{-1} (*P. commune*, 16°C) to a negative -4 µmol kg^{-1} s^{-1} (*P. schreberi*, 19°C). There is no clear indication of an overall trend for the species when the temperature increases. Where *A. palustre*, *Dicranum* sp. and *Sphagnum* sp. gets a lower but not statistically significant A_{gross} with increased temperature, H. *splendens* and *P. schreberi* has a slight but not significant increase from 19 to 22°C, and *P. commune* has its highest A_{gross} at 16°C.

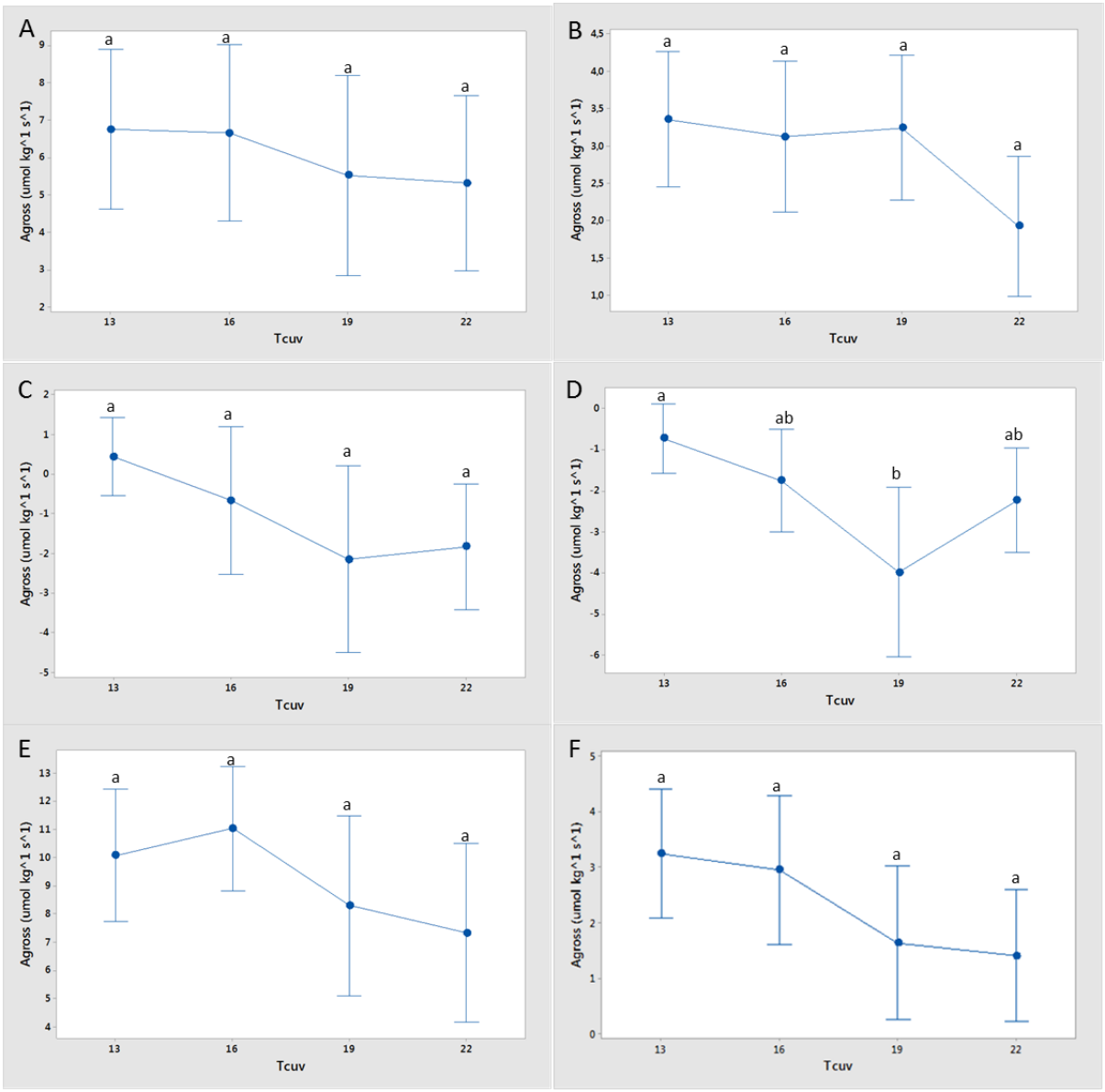

Figure 1: *Gross photosynthesic assimilation rate per µmol* kg^{-1} s^{-1} *for each individual species at four different temperatures. A = A. palustre. B = Dicranum sp. C = H. splendens. D = P. schreberi. E = P. commune. F = Sphagnum sp.*

Table 1: *The results from analysis of variance between A_{gross} and four different temperatures for each individual species. Statistical significance (P<0.005) is marked in bold.*

Source	DF	Sum of Squares	Mean Square	F	p
Temperature					
A. Palustre	3	16,94	5,647	0,51	0,681
Error	36	402,12	11,170		
***Dicranum* sp.**	3	13,25	4,416	2,45	0,080
Error	36	65,00	1,806		
H. Splendens	3	42,23	14,076	2,30	0,094
Error	36	220,21	6,117		
P. Schreberi	3	55,94	18,648	4,68	**0,005**
Error	36	143,30	3,981		
P. Commune	3	84,89	28,300	1,89	0,149
Error	36	538,95	14,970		
***Sphagnum* sp.**	3	18,72	5,240	2,62	0,065
Error	36	71,93	1,998		

When looking at the difference between each species at the four temperatures we can see a clear difference in A_{gross} (figure 2) and there is a statistical difference between the six species at all four temperatures (table 2). *P. commune* have a higher A_{gross} across all temperatures compared to the other species but is only significantly higher at 13°C. As the temperature increases, there is less significant difference between the species.

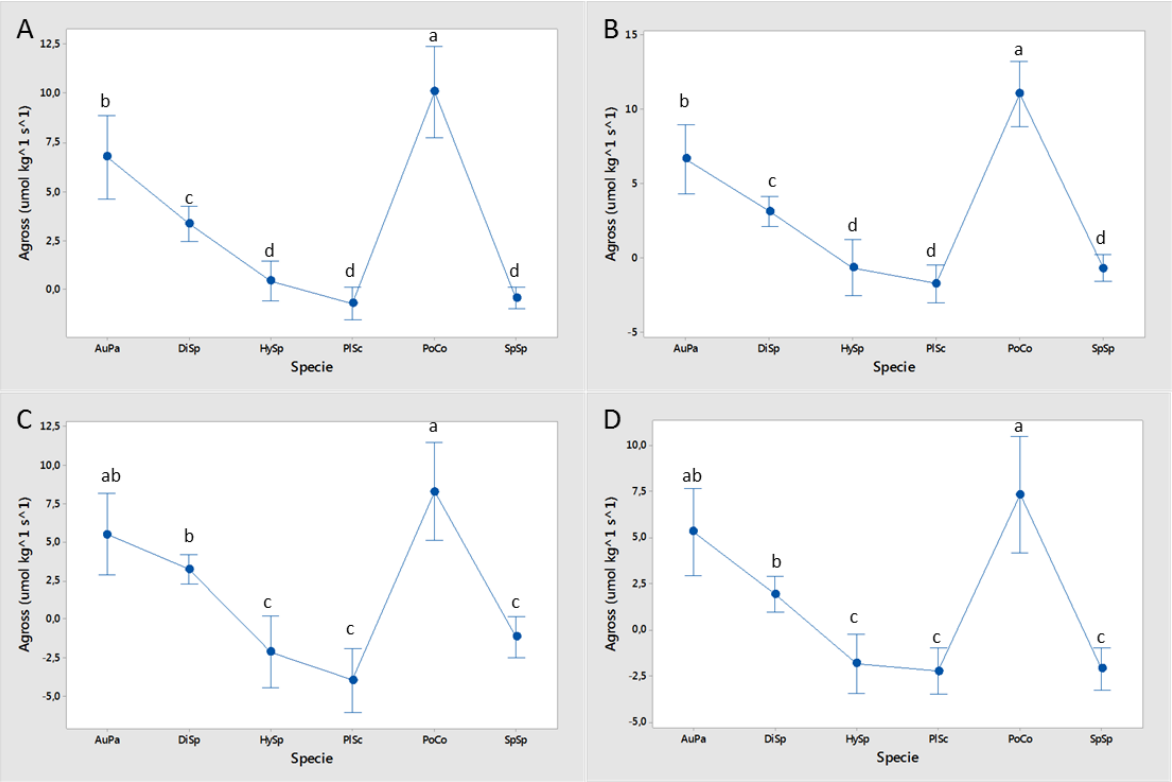

Figure 2: *Gross photosynthesic assimilation rate per µmol kg^{-1} s^{-1} compared between the six species at the four different temperatures. A = 13°C, B = 16°C, C = 19°C, D = 22°C.*

Table 2: *The results from analysis of variance between A_{gross} for each species at the four different temperatures. Statistical significance (P<0.005) is marked in bold.*

Source	DF	Sum of Squares	Mean Square	F	p
Species					
13°C	5	963,10	192,650	45,78	p<0,001
Error	54	227,20	4,208		
16°C	5	1277,00	255,391	45,43	p<0,001
Error	54	303,60	5,622		
19°C	5	1161,10	232,226	23,90	p<0,001
Error	54	524,70	9,717		
22°C	5	865,10	173,011	24,20	p<0,001
Error	54	386,00	7,148		

Respiration

The means of respiration rate per µmol kg^{-1} s^{-1} (R) for each species varies greatly at each measured temperature. The analysis of variance shows that half the species have a statistically difference in respiration (table 3), and the Tukey test shows there is differences in the rest of the species as well (figure 3). *Dicranum* sp., *P. commune* and *Sphagnum* sp. shows an increase in R as the temperature increases (lower R is an increase), as does *A. palustre*, *H. splendens* and *P. schreberi* but with a decrease from 19 to 22°C.

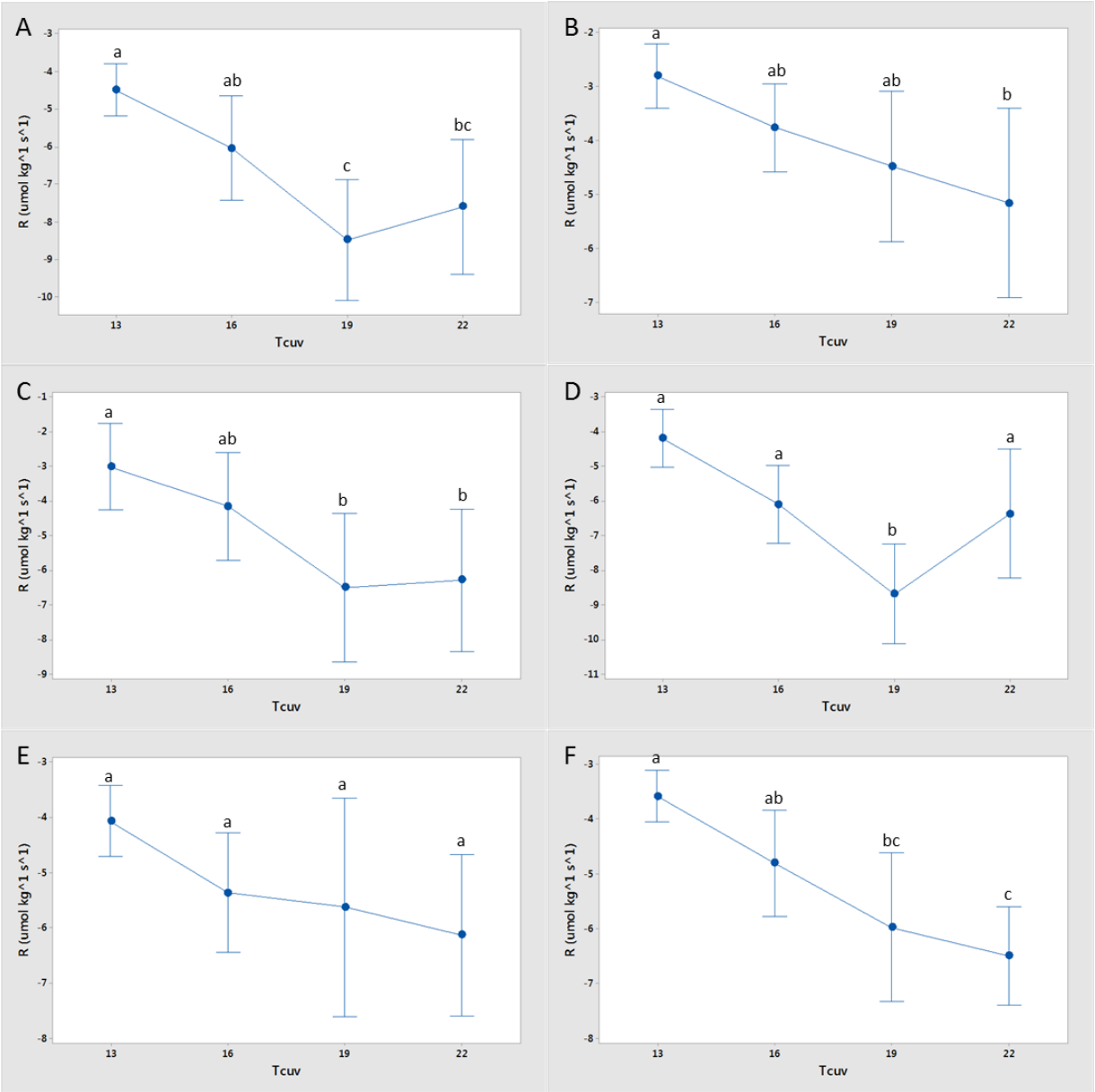

Figure 3: *Respiration rate per µmol kg^{-1} s^{-}1 for each species at the four different temperatures. Increase in respiration rate is showns as a lower negative. A = A. palustre. B = Dicranum sp. C = H. splendens. D = P. schreberi. E = P. commune. F = Sphagnum sp.*

Table 3: *The results from analysis of variance between R and the four temperatures for each individual species. Statistical significance (P<0.005) is marked in bold.*

Source	**DF**	**Sum of Squares**	**Mean Square**	**F**	**p**
Temperature					
A. palustre	3	92,56	30,855	7,70	**p<0,001**
Error	36	144,26	4,007		
***Dicranum* sp.**	3	30,68	10,228	3,46	0,026
Error	36	106,48	2,958		
H. splendens	3	85,78	28,593	4,56	0,005
Error	36	225,52	6,264		
P. schreberi	3	102,10	34,033	9,32	**p<0,001**
Error	36	131,50	3,653		
P. commune	3	23,09	7,695	2,07	0,122
Error	36	133,89	3,719		
***Sphagnum* sp.**	3	50,62	16,873	9,09	**p<0,001**
Error	36	66,83	1,856		

When the rate of respiration is compared between each species at the different temperatures ANOVA shows that there is a statistical difference between the species for all temperatures except 22°C (table 4). The greatest difference between the species is found at 16 and 19°C (figure 4).

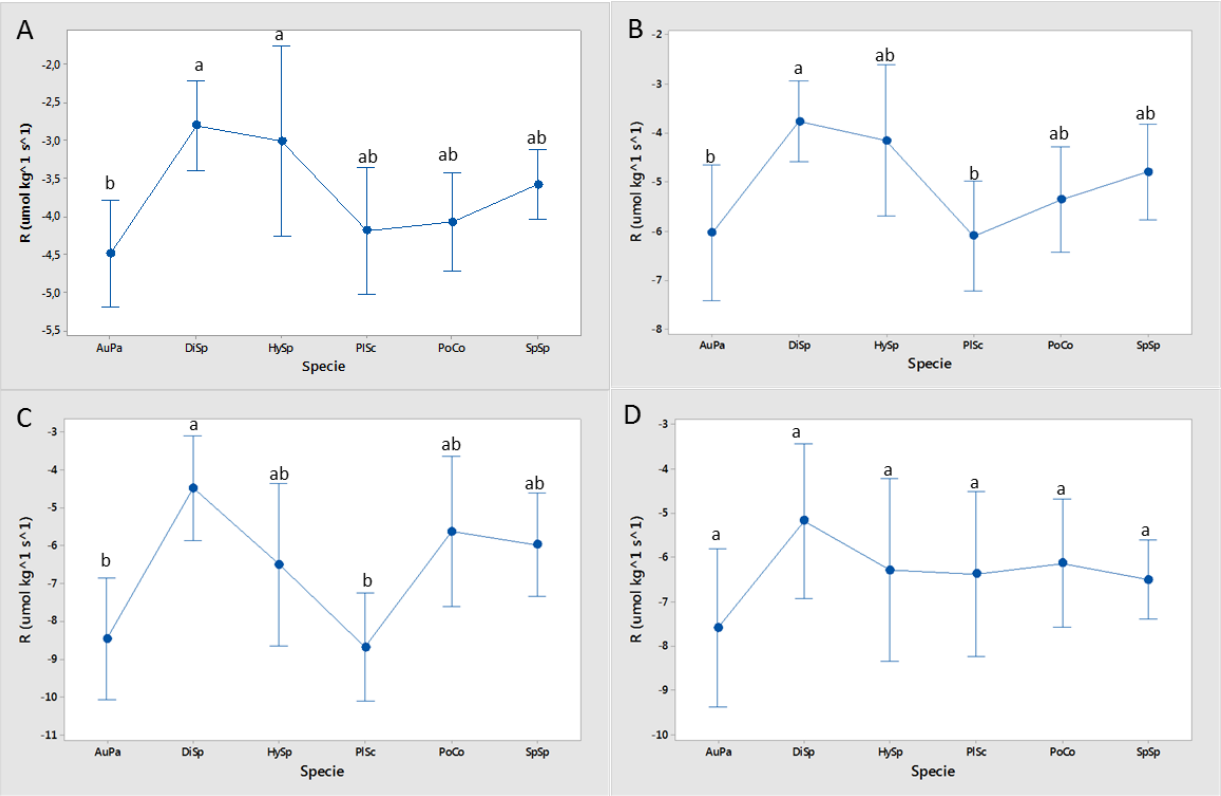

Figure 4: *Respiration rate per µmol kg^{-1} s^{-}1 compared between the six species at the four different temperatures. A = 13°C, B = 16°C, C = 19°C, D = 22°C.*

Table 4: *The results from analysis of variance between R for each species at the four different temperatures. Statistical significance (P<0.005) is marked in bold.*

Source	DF	Sum of Squares	Mean Square	F	p
Species					
13°C	5	22,93	4,585	3,77	**0,005**
Error	54	65,62	1,215		
16°C	5	47,03	9,405	3,46	**0,005**
Error	54	146,81	2,719		
19°C	5	137,10	27,420	4,96	**0,001**
Error	54	298,60	5,529		
22°C	5	30,23	6,046	1,10	0,373
Error	54	297,50	5,509		

Net Photosynthesis

The mean net photosynthesic assimilation rate per µmol kg^{-1} s^{-1} (A_{net}) at each temperature for each species individually are quite different. Of the six species, only *A. palustre*, *Dicranum* sp. and *P. commune* have a net gain, and only *P. commune* stays positive for all four temperatures (figure 5). ANOVA shows that with temperature increase there is only a statistical difference in Anet for *Dicranum* sp. and *Sphagnum* sp. (table 5). An increase in temperature seems to indicate a decrease in A_{net} for *Dicranum* sp., *H. splendens* and *P. commune*. *A. palustre* and *P. schreberi* shows a decrease in A_{net} until 19°C but have a small increase at 22°C, while *Sphagnum* sp. seems to stabilize and have a near same A_{net} at 19 and 22°C.

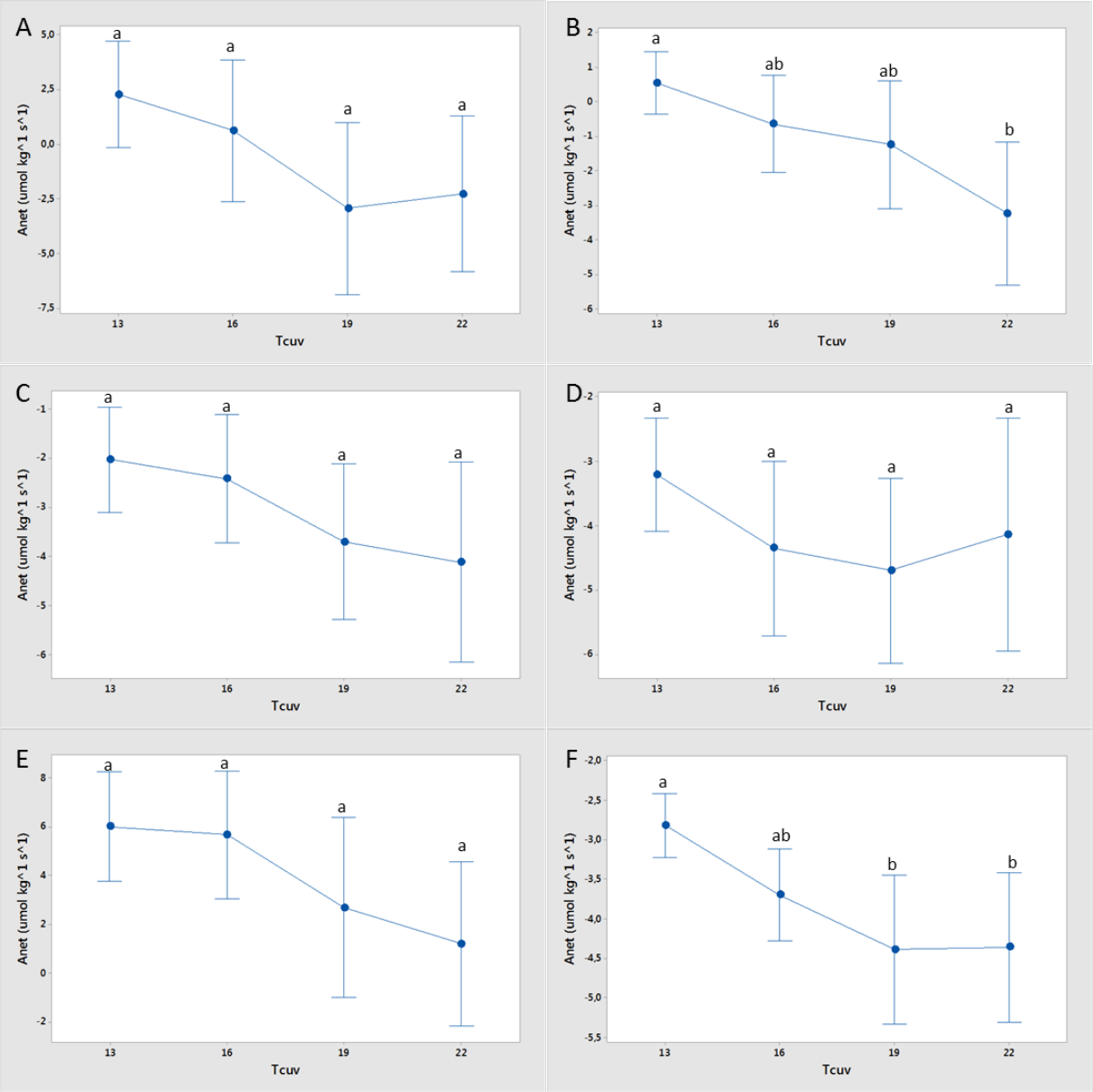

Figure 5: *Net photosynthesic assimilation rate of CO_2 per µmol kg^{-1} $s^{-}1$ for each species at the four different temperatures. A = A. palustre. B = Dicranum sp. C = H. splendens. D = P. schreberi. E = P. commune. F = Sphagnum sp.*

Table 5: *The results from the analyses of variance between A_{net} and temperatures for each individual species. Statistical significance (P<0.005) is marked in bold.*

Source	DF	Sum of Squares	Mean Square	F	p
Temperature					
A. palustre	3	180,70	60,23	2,77	0,055
Error		781,70	21,72		
***Dicranum* sp.**	3	75,38	25,13	4,86	**0,005**
Error		186,30	5,18		
H. splendens	3	30,21	10,071	2,15	0,111
Error		168,73	4,687		
P. schreberi	3	12,21	4,069	1,04	0,385
Error		140,25	3,896		
P. commune	3	164,40	54,81	3,02	0,042
Error		652,70	18,13		
***Sphagnum* sp.**	3	16,39	5,46	4,86	**0,005**
Error	36	40,44	1,12		

When we compare the species at each temperature, *P. commune* have a statistically higher A_{net} than the other species at all temperatures (figure 6, table 6). Here as well we see a trend to that an increase in temperature makes the differences in A_{net} less between the species.

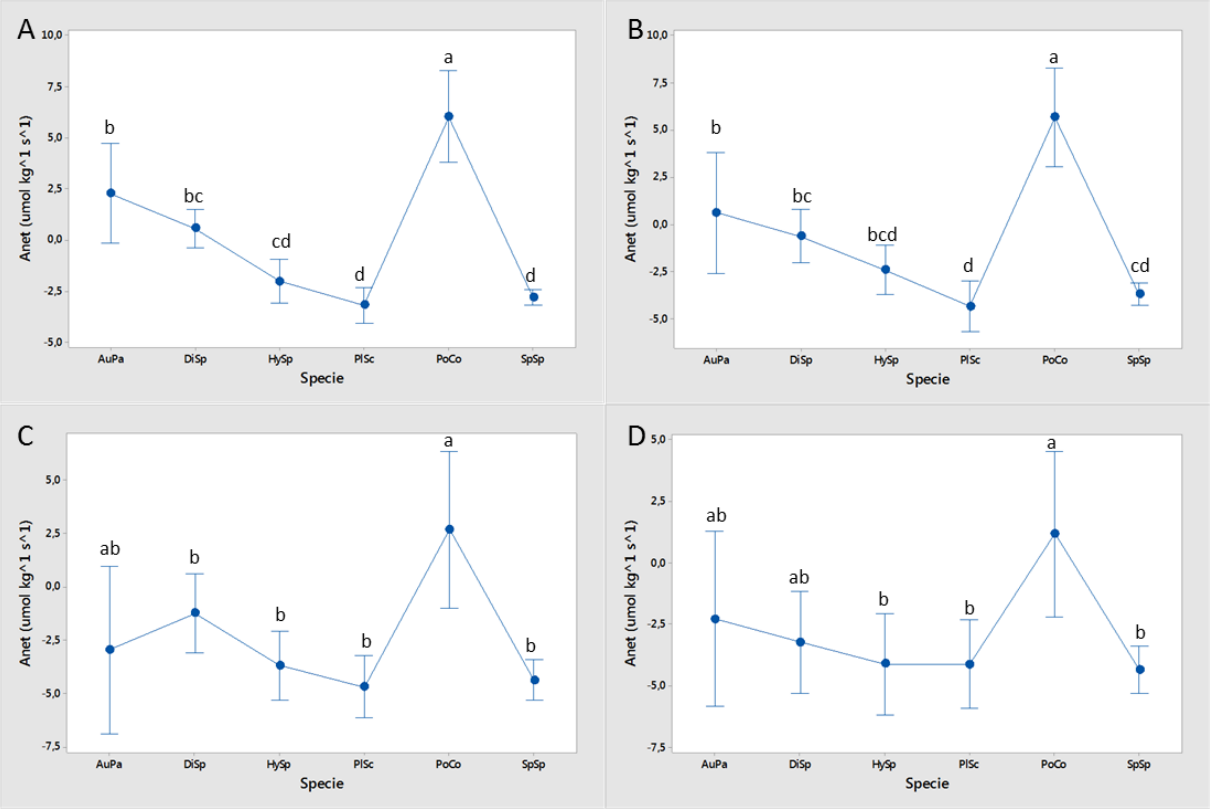

Figure 6: *Net photosynthesic assimilation rate of CO_2 per µmol kg^{-1} $s^{-}1$ compared between the six species at the four different temperatures. A = A. palustre. B = Dicranum sp. C = H. splendens. D = P. schreberi. E = P. commune. F = Sphagnum sp.*

Table 6: *The results from analysis of variance between A_{net} and species for each temperature. Statistical significance (P<0.005) is marked in bold.*

Source	DF	Sum of Squares	Mean Square	F	p
Species					
13°C	5	637,40	127,479	28,32	**p<0,001**
Error	54	243,00	4,501		
16°C	5	675,90	125,188	17,84	**p<0,001**
Error	54	409,20	7,577		
19°C	5	384,20	76,830	6,19	**p<0,001**
Error	54	669,70	12,400		
22°C	5	223,00	44,600	3,71	**0,005**
Error	54	648,30	12,010		

Relative water content

The desiccation rate for all six species is almost the same except the first 30 min (figure 7), thus it is only of interest to look at the difference in desiccation rate at the start of the period. From the analysis of variance test, we can see that there is a clear statistical difference in desiccation after the first 15 min (p<0,001), and that *Sphagnum* sp. seems to be the best and *P. commune* is the weakest of the species when it comes to the ability to retain water (figure 8).

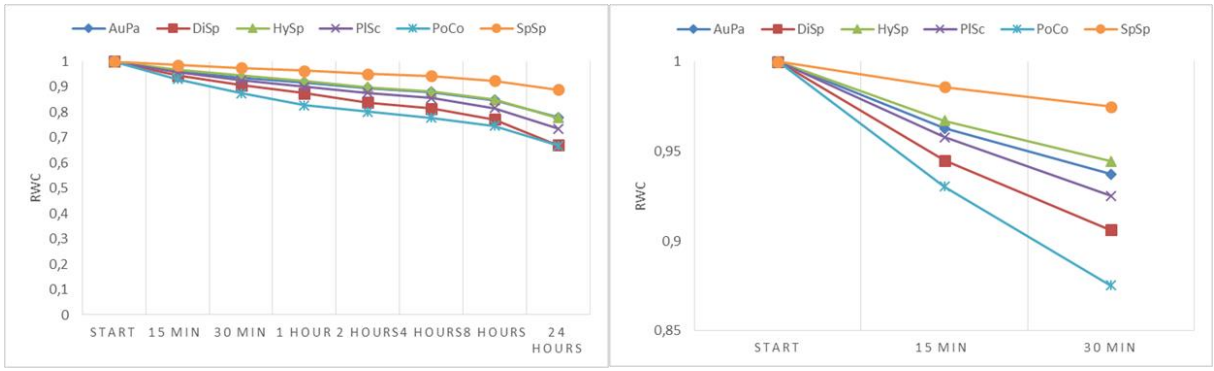

Figure 7: *Rate of desiccation. The figure to the left shows the whole 24 hours period, while the right one shows the first 30 min.*

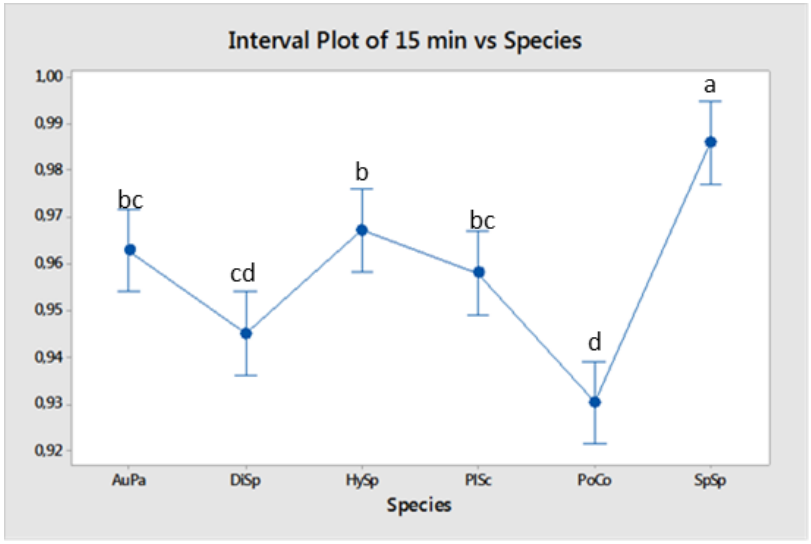

Figure 8: *The relative water content of all six species after the first 15 min of desiccation. ANOVA: DF =5, SS = 0.0182, MS = 0,004, F = 18.68,* ***P<0.001****. Error: DF = 54, SS = 0.01, MS = 0.0001.*

Discussion

Overall temperature effect

From ANOVA I found that temperature had a significant effect on photosynthesic activity and respiration in only a few of the species, and the effect varies between the species.

P. schreberi were the only specie with a significant difference in gross photosynthesic assimilation rate (table 1) were it were significantly lower at 19°C than at 13°C (figure 1). Although not statistically significant, A_{gross} for all species reacts differently to an increase in temperature, were *H. splendens* and *P. schreberi* have a slight increase in A_{gross} from 19 to 22°C, *A. palustre* and *Sphagnum* sp. have a noticeable decrease from 16 to 19°C, *Dicranum* sp. have a noticeable decrease at 22°C and *P. commune* slightly increases at 16°C and continues to drop after. This indicates that lower temperatures are better for photosynthesic assimilation as it decreases in all species at temperatures higher than 13°C, but at some point the increase in temperature have less of an effect, and for some species a large increase in temperature turns out to be beneficial as indicated in the short term measurements.

When we compare the species at the different temperatures we see that the differences in A_{gross} are more or less the same at all four temperatures (figure 2). This indicates that an increase in temperature does not have a different effect on each species A_{gross}.

When we look at the respiration rate, *A. palustre*, *P. schreberi* and *Sphagnum* sp. are the only species with a significant difference (table 3). *A. palustre*, *H. splendens* and *P. schreberi* and have a decrease in R between 19 and 22°C, while *Dicranum* sp., *P. commune* and *Sphagnum* sp. have a steady increase in R as the temperature increase (figure 3). Here as well we can see an indication that for some of the species temperatures lower or higher than 19°C is results in less respiration and are more optimal to operate at.

When we compare the species (figure 4) we see that the differences between the species is almost the same for 13 and 16°C with a small difference at 19°C. At 22°C the difference in R between each species is much smaller, indicating that higher temperatures have large effects on each species respiration.

When we look at the net photosynthesic assimilation rate of the six species only three of the species has a positive net gain. *A. palustre* have a positive net gain at 13 and 16°C, *Dicranum*

sp. only have a net gain at 13°C and *P. commune* have a positive net gain for all four temperatures (figure 5). ANOVA shows that *Dicranum* sp. and *Sphagnum* sp. were the only species with a significant difference in A_{net} between the four temperatures (table 5). All species have a decrease in A_{net} as the temperature increases with a few exceptions. A_{net} for *Sphagnum* sp. shows no decrease from 19 to 22°C indicating that the effect of increased temperature lessens after a certain point. For *A. palustre* and *H. splendens* the A_{net} increases from 19 to 22°C. This could be explained from the decrease in respiration at 22°C for both species. *H. splendens* also have an increase in A_{gross} at 22°C. William and Flanagan (1996) showed in a study that the photosynthesic assimilation rate of both *P. shreberi* and *Sphagnum* sp. have two different optimal water content ranges which are lower than 100% saturation, and since all my samples were fully hydrated this might explain why my measured A_{net} for the species were in the negative.

When we compare the species at each temperature (figure 6), it is clear that *P. commune* have the highest net photosynthesic assimilation rate of CO_2 per µmol kg^{-1} $s^{-}1$ of the six species. It were found that for all four temperatures *P. commune* is statistically significantly higher than the other species. For every temperature except 16°C, *P. schreberi* and *Sphagnum* sp. were shown to have the lowest A_{net} of the six species. We see that the difference between the species decreases as the temperature increases indicating that an increase in temperature have a different effect on the A_{net} for each species. All species suffers a decrease in net photosynthesic assimilation as the temperature increase from 13°C, but for some of them 19°C is the least optimal temperature for photosynthesis and the assimilation rate increases as the temperature increases. If the mosses have had a longer acclimation period to each temperature the resulting A_{net} might have been higher, as some bryophyte species are known to acclimate by shifting the temperature optimum for photosynthesis (Longton 1988).

Desiccation

The desiccation rate for each of the six species seems to be the same where they all follow a linear curve of water loss, but what separates them is how quickly they lose water the first 30 min (figure 7). The analysis of variance shows that there is a significant difference in each species relative water content after the first 15 min, where *Sphagnum* sp. retains the most water and *P. commune* have lost the most. This came as a surprise as the *Polytrichum* genus are known for having a high desiccation tolerance due to possessing thin wax-like cuticles,

but since they are an endohydric specie with widespread leafs (Shaw and Goffinet 2000), the process of cutting it to sample size might have damaged its ability to retain water.

A problem with doing gas exchange on mosses

In doing measurements on mosses, I found humidity to be a problem. The mosses lack of ability to store and regulate water loss provided difficulties for the portable photosynthesis system, as it warns that measurements might become inaccurate or faulty if the air humidity is too high. This is because the measured air might create condense inside the tubing and this in turn might absorb CO_2. To work around this I had to limit the humidity of the air intake by 60%, and even then there were a cuvette humidity of 90%+ when running at 13°C. This might have caused a small increase in desiccation rate and affected the measurements of the mosses, such as *A. palustre* which is greatly affected by humidity (Garcia et al. 2016).

Conclusion

I have found that temperatures effect on respiration rate, gross and net photosynthesic assimilation rate are only significant for a few of the species, but a change can be observed for all the species none the less. I also found that 19°C seems to be the least optimal temperature for most of the species. Some species have no change in the temperatures measured after, and some even show an increase in A_{gross}/A_{net} and a decrease in R as the temperature increase further. This indicates that a small increase in temperature might have more of a negative effect on the mosses, than a large one. Though, an increase in temperature might result in the mosses drying out faster if they have no access to a reliable water source.

When looking at the mosses desiccation I found that the biggest difference in desiccation rate takes place in the first 30 min, and I do not know how this would affect the photosynthesis in the mosses since I were not able to conduct the photosynthesis measurements at different levels of desiccation. Seeing how the rate of desiccation changes after such a short time to a more stable rate, I would assume that the mosses adapts to this sudden loss of water. It might be that they limit the photosynthesic activity to reduce the water loss, but this is only conjecture.

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Appendix A

Light intensity curves for the six species of moss. It were found by using CIRAS original light intensity curve script were the sample were irradiated for 3 min at each level of PARi. The order each level of PARi were measured is: 700, 1500, 0, 15, 50, 100, 200, 250, 500, 1000, 1500, 2000, 1000, 500, 50, 0. The curve for *Polytrichum commune* (PoCo) is strange because the sample decreased its photosynthesis in the middle of the measurements and it affected the mean value used in the curve.