

Seasonal CO₂ exchange in a coastal heathland in western Norway – effects of drought and bryophyte removal



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Cover photo: The plexiglass chamber in use while measuring at Lygra, by Alexander Sæle Vågenes

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Abstract

Climate models project that Western Norway will experience warmer temperatures with more frequent and extreme drought periods during the 21st century. Such climatic changes are likely to alter many vital ecosystem processes, such as plant CO₂ sequestration and soil carbon storage, which ultimately may lead to a shift in ecosystem function. In Western Norway, coastal heathlands contain relatively large amounts of soil carbon due to their cold and wet climate, resulting in low microbial decomposition rates relative to plant productivity. In a warmer and drier climate, the carbon balance of coastal heathlands could be particularly vulnerable to changes, potentially shifting these ecosystems from being net sinks of atmospheric carbon to net sources. Here, we measured seasonal variation in ecosystem CO₂-fluxes from above- and belowground sources in a coastal heathland site near Lygra/Bergen, Norhordland. To investigate how extreme drought events may affect future carbon dynamics in this ecosystem, we constructed an experimental drought gradient, manipulating rainfall inputs by 0, 50, and 90% using rainout shelters. Bryophytes constitute a major functional group in coastal heathlands and bryophyte water holding capacity and soil insulation properties could potentially mediate effects of drought stress on ecosystem carbon balance. To investigate the role of bryophytes in a drier climate, we also removed bryophyte cover in a factorial setup within our drought gradient. Results show limited response to treatment where an effect could only be detected statistically for net ecosystem exchange. Ecosystem respiration, gross ecosystem production and soil respiration showed no significance to either bryophyte removal or drought treatment. Ultimately the results from this study will be part of increased understanding of drought effects on the coastal heathlands but also to piecing apart how carbon storage in other similar ecosystems will react to projected changes.

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Introduction

The future is projected to have more extreme weather events with changes in rainfall patterns and increased temperatures (Coumou & Rahmstorf, 2012; IPCC, 2014). Frequently used climate projection models, as for example used in the IPCC report, are used to predict how averages across larger timescales will change. This focus on averages is useful when looking at trends on global scales, but averages can also be misleading when trying to understand how ecosystems will be impacted by future extreme weather. In fact, it is often the most extreme weather events, which occur over relatively short time periods, that have the greatest consequences for ecosystems (Parmesan et al., 2000). While there is little doubt that extreme weather will affect many if not all ecosystems in the future, there are large uncertainties in how and by how much for many ecosystems (Shaver et al., 2000). When ecosystems are disturbed by more extreme weather and changes in weather patterns their ability to perform ecosystem services will be impacted (De Luís et al., 2001). Fundamental ecosystem processes part of the carbon cycle is likely to be altered which will change the system's ability to perform important climate services such as carbon sequestration (Bala et al., 2005).

The carbon cycle

The carbon cycle is the cyclical movement of carbon in and out of ecosystems. The rate movement of carbon can be measured and is referred to as fluxes. e.g. from CO₂ in the atmosphere, which is one pool, to carbon in plant biomass – another pool – by photosynthesis.

Terrestrial ecosystems contain many minor and major fluxes that contribute unevenly to the system being a carbon sink or source of carbon. The process of carbon sequestration is when plants take up carbon as CO₂ from the atmosphere and transform it by photosynthesis into plant material as either standing biomass or belowground in roots. The plant matter will eventually decay and can be stored in the soil as plant organic matter. Thus, carbon comes into a system in a single way through photosynthesis and this is measured as gross ecosystem production (GEP). Carbon leaves the system through respiration processes. Ecosystem respiration (ER) must be measured to find the net balance of carbon. Respiration happens in all living organisms which creates many sources for respiration which is separated into aboveground as ecosystem respiration and belowground as soil respiration (R_s). Aboveground we have the plants and animals, and belowground sources include respiration from plant roots

and fungi, bacteria and other small organisms and the breakdown of soil organic matter. Then the net ecosystem gain, or loss of CO₂ can be calculated by subtracting ER from GEP to get the net ecosystem exchange (NEE), which is equal to the net balance of CO₂ fluxes going in and out of the ecosystem. Another major flux is the respiration from the soil (R_s) which consists of respiration from roots and microbes. It is common that studies either look at above- or belowground carbon pools separately which will miss out on interactions between them (Ciais et al., 2005; Sowerby et al., 2008a).

The primary controller of photosynthesis is light intensity, but any change in precipitation and temperature, whether it being an increase or decrease, will also affect ecosystem carbon fluxes. This is due to the close link between rainfall and temperature, which in combination drives photosynthesis and respiration rates in terrestrial systems. An increase in temperature can vary immensely depending on the system. Systems that experience mostly low temperatures such as the tundra with permafrost will have a larger reaction to increased temperature than desert systems that are already exposed to them. In these cold systems the increased temperature will mean that soil organic matter that previously was locked in ice and therefore inaccessible is now available (Gornall et al., 2007; Stoy et al., 2018). In temperate seasonal ecosystems an increase in temperature is connected to an increase in respiration rates mostly due to increased soil activity but also in plant activity and photosynthesis. The increased activity comes from enzymatic activity becoming easier and more efficient as temperature rise (F. Stuart Chapin III, Pamela A. Matson Harold A. Mooney, 2002). An increase in temperature can therefore result in increased ecosystem respiration, gross ecosystem production and soil respiration but the relative change between them can vary. Too high temperatures on the other hand will be detrimental for plants and is mostly connected to water limitations but can also be directly damaging to as the water flow within the plant increases beyond what internal structures can handle and subsequently breaks. Therefore, higher temperatures indirect effect of a higher water demand on plants forces them to close stomata and reduce photosynthetic activity. Additionally, it can dry out soils reducing soil respiration.

Higher moisture levels can affect soil activity and breakdown of soil organic matter by making more of the soil nutrients accessible in similar fashion as that of temperature. The Increased water content can also have a direct impact on productivity through increased

capacity for photosynthesis as plants do not need to worry about water loss. On the other hand, in waterlogged systems such as peatlands, that have too much water, almost only anaerobic respiration is possible. This prevents nutrients from being released causing very low flux rates for all sources (C. Freeman et al., 1996; Chris Freeman et al., 2001). How important either temperature or moisture is changes depending on the ecosystem.

Understanding changes in photosynthesis rates is important because changes can cause a positive feedback loop to the climate. In such a loop increased CO₂ in atmosphere causes higher temperature and higher frequency of drought events resulting in more carbon to be released from the ecosystem as respiration rates increase and less taken in as productivity is reduced. In turn this will further increase the amount of CO₂ in the atmosphere, which again can potentially further increase respiration and reduce productivity (Heimann & Reichstein, n.d., 2008; IPCC, 2014).

Coastal heathlands

The coastal heathlands of Norway are part of a range of heathlands stretching from northern Norway in the north to Portugal in the south (Kvamme, M., Kaland, P.E., Brekke, 2004). While being a *Calluna vulgaris* dominated shrubland is a unifying feature throughout the range, but there is high variance in annual rainfall, different soils and execution of different management practices (Gimingham, 1989; Kvamme, M., Kaland, P.E., Brekke, 2004; Webb, 2008). As a cultural landscape the heathlands require management to be maintained and would in most areas except the most exposed succeed into forest if left alone. History of management techniques remain similar throughout the range across countries with controlled burning, cutting and grazing as the most important. (Kvamme, M., Kaland, P.E., Brekke, 2004; Webb, N, 1986). Even though history of practices is the same the current practices can differ.

Best management procedures as well as restrictions to when burning is allowed from the state the heathlands should be burned winter or early spring to make sure burning is controlled. Should climate change through drought and make burning problematic this will cause damage to the quality of the heathland. Controlled burning for the heathland is required for biodiversity but also for agriculture (Aarrestad & Vandvik, 2000). Burning provides an

increased diversity of available habitats in the heathlands which is correlated to increased biodiversity in many ecosystems (Aarrestad & Vandvik, 2000; Vandvik et al., 2014).

Coastal Heathlands and similarly cold and wet systems in the northern hemisphere contain a substantial amount of carbon stored as soil organic matter. For the coastal heathlands of Norway, the high carbon content comes from forest and peatland history. The area was completely covered in forest and as the forest disappeared, or was removed by humans, it turned into peatlands, which has preserved the carbon as soil organic matter until today. The high amounts of moisture together with low temperatures creates a system with low turnover rates and low productivity compared to other systems. This has made the coastal heathlands act as sinks for carbon for a long time, but the source/sink dynamics are likely to be impacted by increased drought frequency and temperature. The soil organic matter could be more readily accessible for soil microbes and fungi releasing it into the atmosphere as CO₂.

The coastal heathland is a system where photosynthesis continues through all parts of the year, with low productivity in the winter due to low temperatures and poor light conditions and high productivity during the warm and bright summer months. This seasonality is also represented in the below ground respiration flux, but soil respiration is more linked to soil temperature and does not need light. Therefore, there can be an increase in soil respiration earlier in the year, compared to photosynthesis, as temperature increases which is decoupled from photosynthesis. The same seasonality will also make the timing of drought events more important where growing periods are more vulnerable to drought as the water requirements from vegetation is higher. A major part of the coastal heathlands which has the potential to change soil temperature and moisture and by doing so change productivity and respiration is the often neglected bryophytes.

Bryophytes

Bryophytes are a group of non-vascular plants that cover vast areas in the northern hemisphere and are able to survive in cold and nutrient poor ecosystems (Tuba et al., 2011). They are a major functional plant group of the coastal heathlands and most of the northern hemisphere with physiological traits that can alter the microclimate.

Bryophytes grow tightly together creating dense mats that excel at holding water and shelter the soil from weather causing considerable temperature difference for soil

temperature with bryophyte cover compared to soil with no cover (Bonan & Shugart, 1989; Buscà, 2018; Stoy et al., 2018). The direction of effect can change depending of time of year. Bryophytes act as insulators preventing heat loss increasing soil temperature during cold winter periods and decrease surface and soil temperature during warm summer periods due to shading and high reflection (Stoy et al., 2018).

In coastal heathlands, there is additional interest in the bryophytes because of how the heathlands are managed. A well-managed heathland will be partially managed by controlled fire, and how this fire is control can though fire intensity determines how much bryophytes are impacted by the fire i.e. how much of the bryophytes are left after the fire (Kvamme, M., Kaland, P.E., Brekke, 2004). Because the bryophytes can control the microclimate, management can plan to minimize carbon loss from the heathlands, but at the current time we do not know if it is best to keep or to burn away the bryophytes. Thus, bryophyte preservation constitutes an important knowledge gap with regards to how drought may affect heathlands – and their carbon balance – in the future.

Aims of this study

In this study, I investigate the impact of increased drought frequency on the annual CO₂ exchange in a coastal heathland in western Norway. I do this by experimentally reducing precipitation through rainout shelters while also looking at how bryophytes can ameliorate the effects of reduced precipitation. Here, I focus on the main components of the heathland carbon cycle by looking at net ecosystem exchange (NEE), ecosystem respiration (ER), gross ecosystem production (GEP), and soil respiration (Rs). These fluxes represent the main pathways of carbon in and out of the ecosystem.

The study site also represents a system that is understudied when it comes to drought based on its 2000mm annual precipitation. Other similar drought studies conducted in heath and shrublands are situated in less than 1400 mm annual precipitation (Carter et al., 2012; Heimann & Reichstein, n.d.; Maria et al., 2017; Reinsch et al., 2017; Sowerby et al., 2008b; Treharne et al., 2018). Also, none have to my knowledge also look at the importance of bryophytes on the fluxes which has been highlighted in a previous study by Kopittke simply

based on their large biomass in the heathland and contribution to carbon cycle in other systems (Kopittke et al., 2012; Street et al., 2012).

Aim: To quantify effects of increased drought frequency on Net ecosystem exchange, ecosystem respiration, gross ecosystem production and soil respiration and how the presence/absence of bryophytes mediate the effects of increased drought frequency in the pioneer stage of a coastal heathland.

Q1: How does experimentally increased drought frequency impact the changes in Net ecosystem CO₂ change in a wet coastal heathland throughout the year?

H1: Extreme drought has the potential to cause stress in ecosystems which can alter the ecosystems ability to perform various services such as carbon sequestration. The systems performance and productivity is likely to decrease with more severe drought. I hypothesise that there will be a decrease in all fluxes across the drought gradient as water stress increases.

Q2: How does the insulating properties of bryophytes influence the microclimate of the coastal heathland and how does this impact the different ecosystem carbon fluxes?

H2: Bryophytes have temperature insulating properties that can cause the immediate environment of the bryophyte to be substantially different than compared to other plants. Bryophytes have been shown to reduce seasonal and daily temperature fluctuations which can affect plant and microbe activity. I hypothesise that bryophyte presence will cause a smaller reaction to the drought gradient across all fluxes compared to control plots.

Q3: How does the water holding capacity of bryophyte impact the effects of drought on the microclimate and what effect does this have on the carbon fluxes.

H3: Bryophytes have a high capability to hold and retain water within itself reducing the drought impacts. I hypothesise plots with bryophytes present show lower effects through the drought gradient.

Methods

Study site

The experiment was done in a coastal heathland in western Norway at the Lygra island, Lindås (60°42'N, 5°50'E). The island is situated in Lurefjorden approximately 20 km inland from North Sea and the highest point is 54 m.a.s.l. The climate is oceanic with a mean June temperature of 12 °C and mean January temperature of 2 °C, with mean annual precipitation of 2000 mm per year, and a relatively long growing season of about 220 days (above 5 °C) (Kvamme, M., Kaland, P.E., Brekke, 2004; Vandvik et al., 2014).

The study site is situated in a *Calluna* dominated coastal heathland that is managed by grazing, cutting and controlled burning. The study site was last burned in 2013.

Dominant vegetation types are *Calluna* heath, mires, willow shrubs and mixed grass heaths. The most dominant graminoids are *Avenella flexuosa*, *Agrotis capillaris*, *A. canina* and *Carex pilulifera*, and the most dominant forbs are *Calluna vulgaris*, *Erica tetralix*, *Vaccinium vitis-idea*, *V. myrtillus*, *Potentilla erecta*. Within study site in the pioneer stage forbs, graminoids and bryophytes are most abundant with a few young *Calluna* heath plants.

Study Design

The study site is a part of DroughtNet and follows a modified experimental setup protocol with an extra level of drought, sturdier roof support and with fences (Smith, 2017). A manipulation with two different levels of drought is created using permanent fixed shelters. A moderate drought is imposed with 50% roof cover, and an extreme drought is imposed with 90% roof cover (Figure 1). The shelters were set up in spring 2017. The plastic roofs are made of Icopal Fastlock Uni clear. In addition, an ambient precipitation treatment was used as a control (unsheltered). Each plot is 2*2m with roofs covering 3*3m to create a 50cm buffer zone (Figure 2). Treatment is replicated 3 times. Within the 2*2m plots two 25x25cm subplots were permanently marked for consistency in flux measurement. Permanent soil tubes were set one in each of the subplots made from drainpipes classified for use underground. They are 50mm diameter set ca 6cm into the ground stretching ca 14 cm

above ground. In one of the subplots all bryophytes were removed by hand prior to the start of measurements during the summer of 2017.

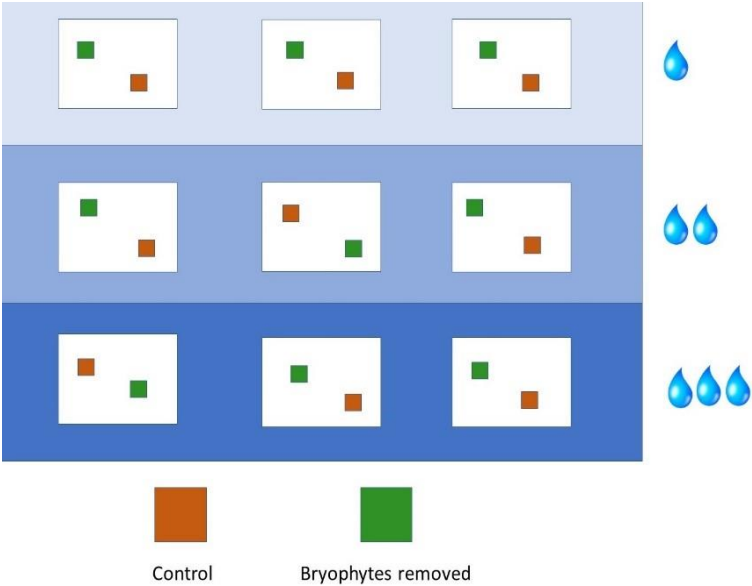


Figure 1. Showing experimental design using full factorial set up for the study with drought gradient and bryophyte removal integrated. Raindrops and colour gradient from light blue to blue show 90, 50 and 0% rainfall reduction. Bryophyte removal treatment is shown with control in orange and bryophytes removed in green within the white squares which represent study plots.

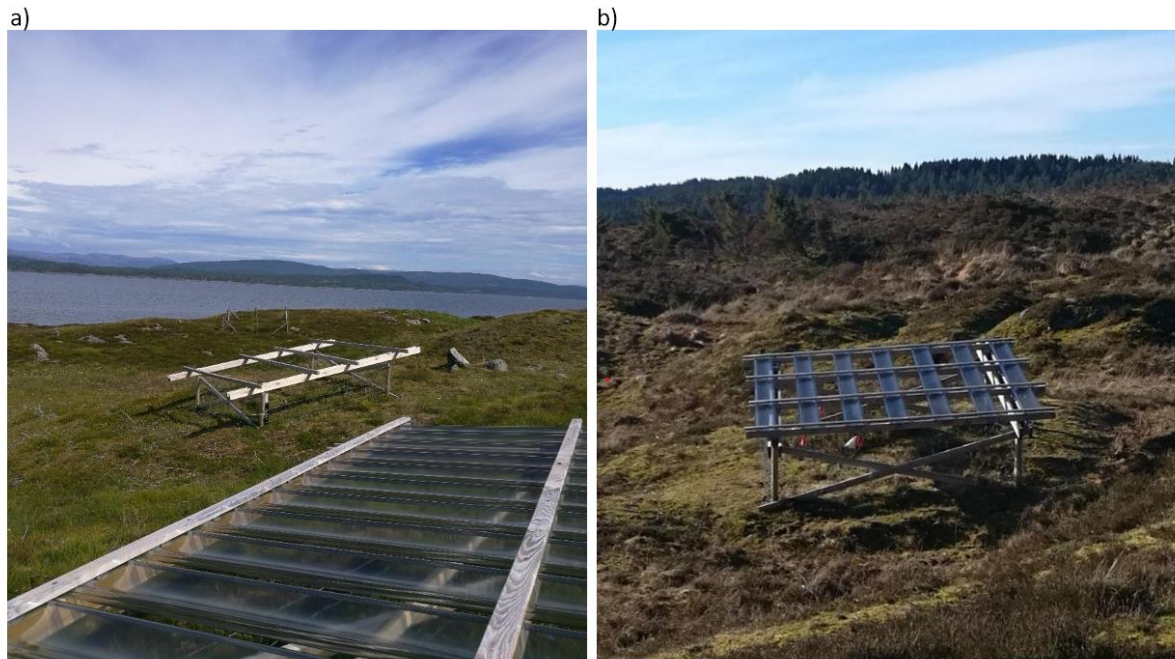


Figure 2. Shows rainout shelters at the study site 90% cover and control plot in a) and 50%cover plot in b).

Field measurements

Measurements were taken in the period 22.05.2018 to 08.07.2019 with weekly to biweekly measurements summer and monthly during winter.

For net ecosystem exchange (NEE) and ecosystem respiration (ER) the closed chamber method was used (Heinemeyer & McNamara, 2011; Sowerby et al., 2008a). Here a clear plexiglas chamber (25 x 25 x 40 cm) was used equipped with two fans for air circulation and connected to an infrared gas analyser (Li-840, LI-COR Biosciences, Lincoln, NE, USA). A tarp windshield was attached to the bottom of the chamber and weighed down to the ground by a heavy chain to keep system closed from outside wind/air. For ER a tarp cover was used to exclude light from the system. Soil respiration (SR) was measured from Polypropylene tubes within the 25x25 cm sub plots. When measuring, the infrared gas analyser tubes were connected through a lid on top of the soil tubes to prevent air mixing (Figure 3).

For each flux measurement, CO₂ concentration was recorded at 1 s intervals over a period of at least 120 s. The chamber was aired out between NEE and ER until atmospheric

CO₂ concentration were reached. Measurements were set to days with as similar weather conditions as possible and set to overcast, no rain and wind less than 7 sec

A range of environmental variables were also measured to control for variation and to investigate treatment effect. Light intensity was measured as photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) using a quantum sensor (Li-190, LICOR Biosciences, Lincoln, NE, USA) placed to represent light presence inside chamber. Temperature inside the chamber was measured using an iButton temperature logger (DS1922L, Maxim Integrated, San Jose, CA, USA). For dates when iButton data is not available climate data was collected from a close by weather station and used instead. Volumetric soil moisture content ($\text{m}^3 \text{ water}/\text{m}^3 \text{ soil}$) was measured by calculating the average of three measurements with a soil moisture sensor (SM300, Delta-T Devices, Cambridge, UK) at three separate places within a plot to best represent it i.e. no overlap. Soil temperature was measured twice for each subplot using digital thermometers. All measurements were done per sampling time

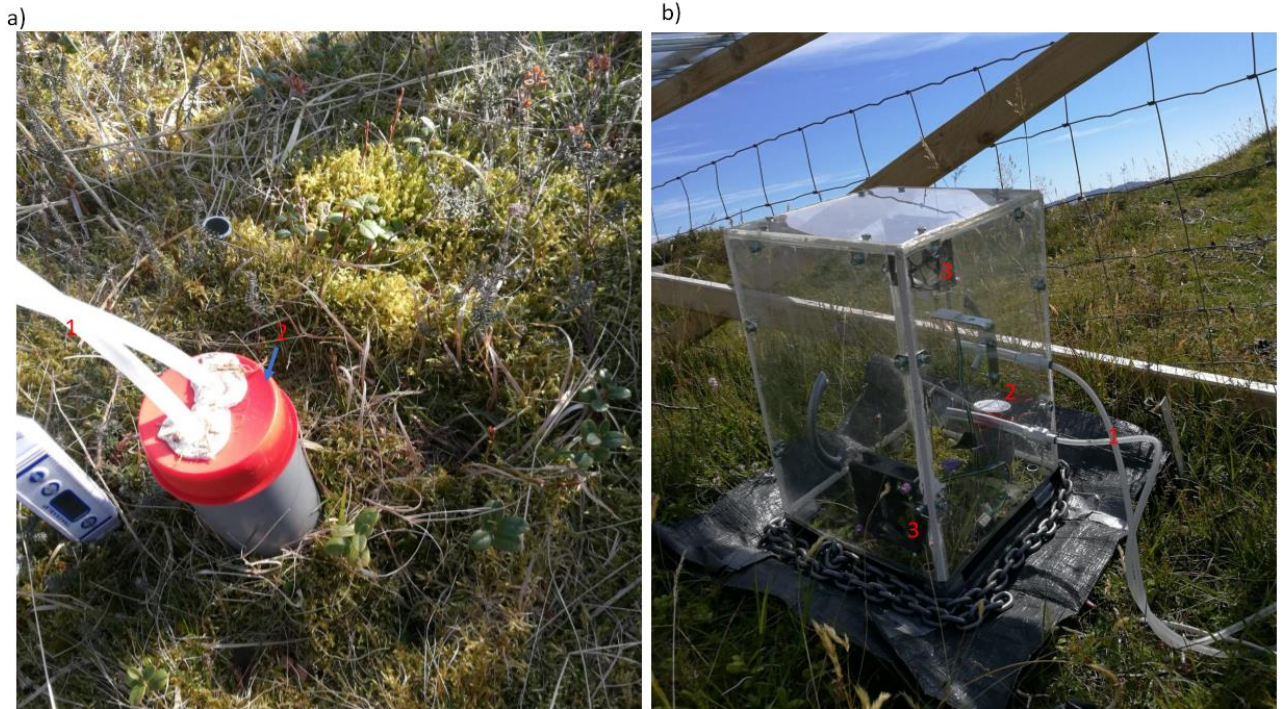


Figure 3. Shows the closed chamber technique being used at one of the rainout shelters for soil respiration a), and ecosystem respiration and gross ecosystem production b). Some primary features are listed with numbers within: tubes going to and from infrared gas analyser **1**, plastic cover used to keep soil respiration from mixing while measuring fluxes **2**, fans used for air circulation **3**.

Statistical analysis

All carbon fluxes were calculated using HMR function in R (version 3.4.3) (Pedersen, 2019). The topography made particularly the chamber measurements difficult at times causing effects on the fluxes not noticeable until data analysis was performed. Fluxes that had obvious faults such as air mixing were cut to a minimum 60sec, where this was not possible the flux was discarded.

A repeated measurements analysis of variance (R.3.4.3) with first-order autoregressive correlation (AR(1)) to account for temporal autocorrelation was performed to test for significance of drought and moss treatment on each flux separately. The same analysis was run for soil moisture and temperature to test for treatment effect. Regression analysis was done to find if photosynthetic active radiation differed between treatments. Linear regression analysis was also done to investigate relative importance of soil moisture and soil

temperature for soil respiration in the study system and to see if drought treatment received different amounts of photosynthetic active radiation.

Results

For the entire study period a treatment effect of the rainout shelters is observed (figure.2 $p < 0.05$). Drought treatment reduced soil moisture by 10 – 25% for each level of drought where means were closer together during spring and winter while further apart for fall and summer. In vegetation control plots where bryophytes are present 0% and 50% cover plots show similar moisture content and only show treatment effect for 90% cover plots revealing a threshold effect. Winter has slightly higher soil moisture across all treatments. Soil and surface temperature show no response to treatment and has very large spread. Highest temperature found during summer, followed by fall, spring and then winter with the lowest.

Total chamber measurements for NEE, ER and GEP is 25 while for Soil respiration total number of measurements is 27. Due to bad weather conditions for chamber measurements with high winds measurements had to be stopped causing the higher number of Soil respiration samples.

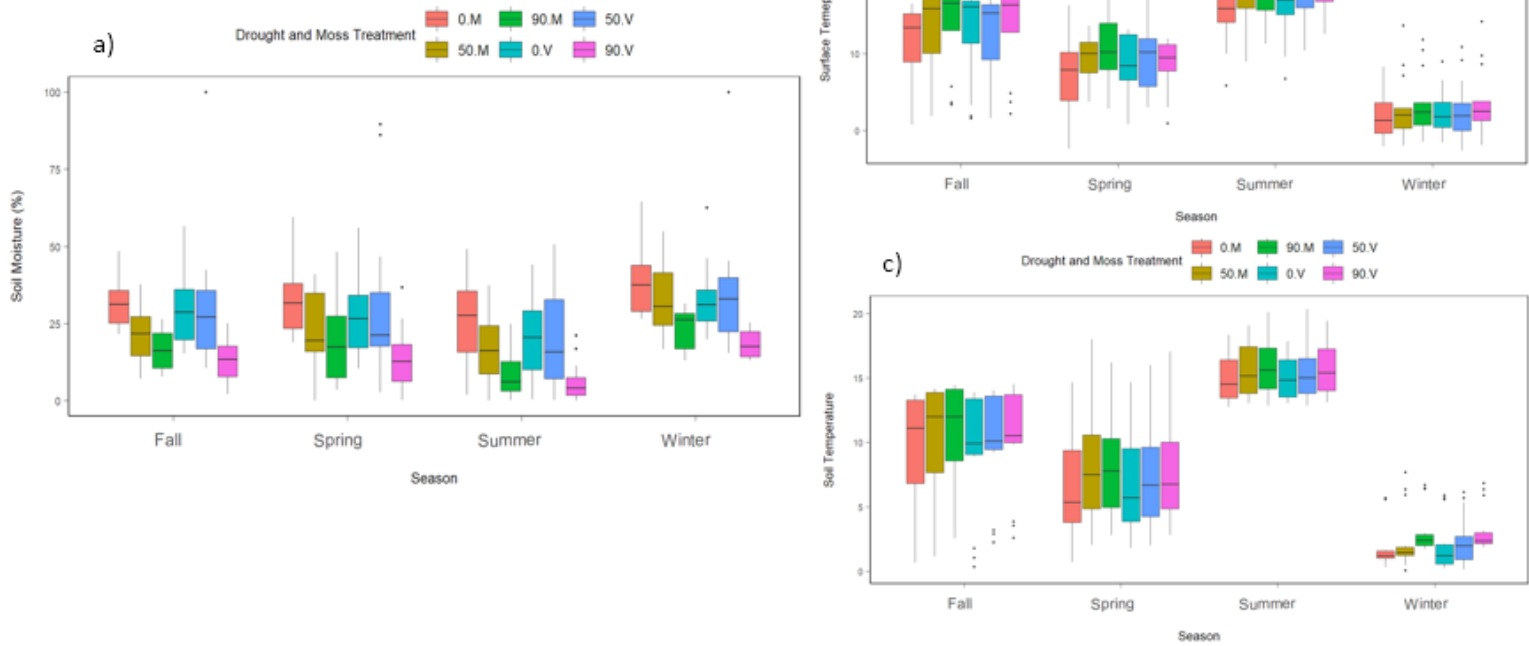


Figure 4. Mean values in soil moisture a), surface temperature b) and soil temperature c) for drought and bryophyte removal treatments. 0, 50, 90 represents the drought gradient. M and V represents moss removal experiment with moss removed in M and control V.

The fluxes

Net ecosystem exchange was the only flux to show a significant reaction to the drought treatment. No fluxes showed an effect of bryophyte treatment (table 1, figure). NEE show increased flux for summer and fall where variability also is high. Ecosystem respiration show highest flux rate during summer and fall with very low rates in spring and winter. Gross ecosystem production has highest rates during summer with similar rates for the other seasons and with no effect from treatments. Soil respiration behaves similarly with highest flux rates in the summer with spring and fall close behind and winter last, also with no treatment effect.

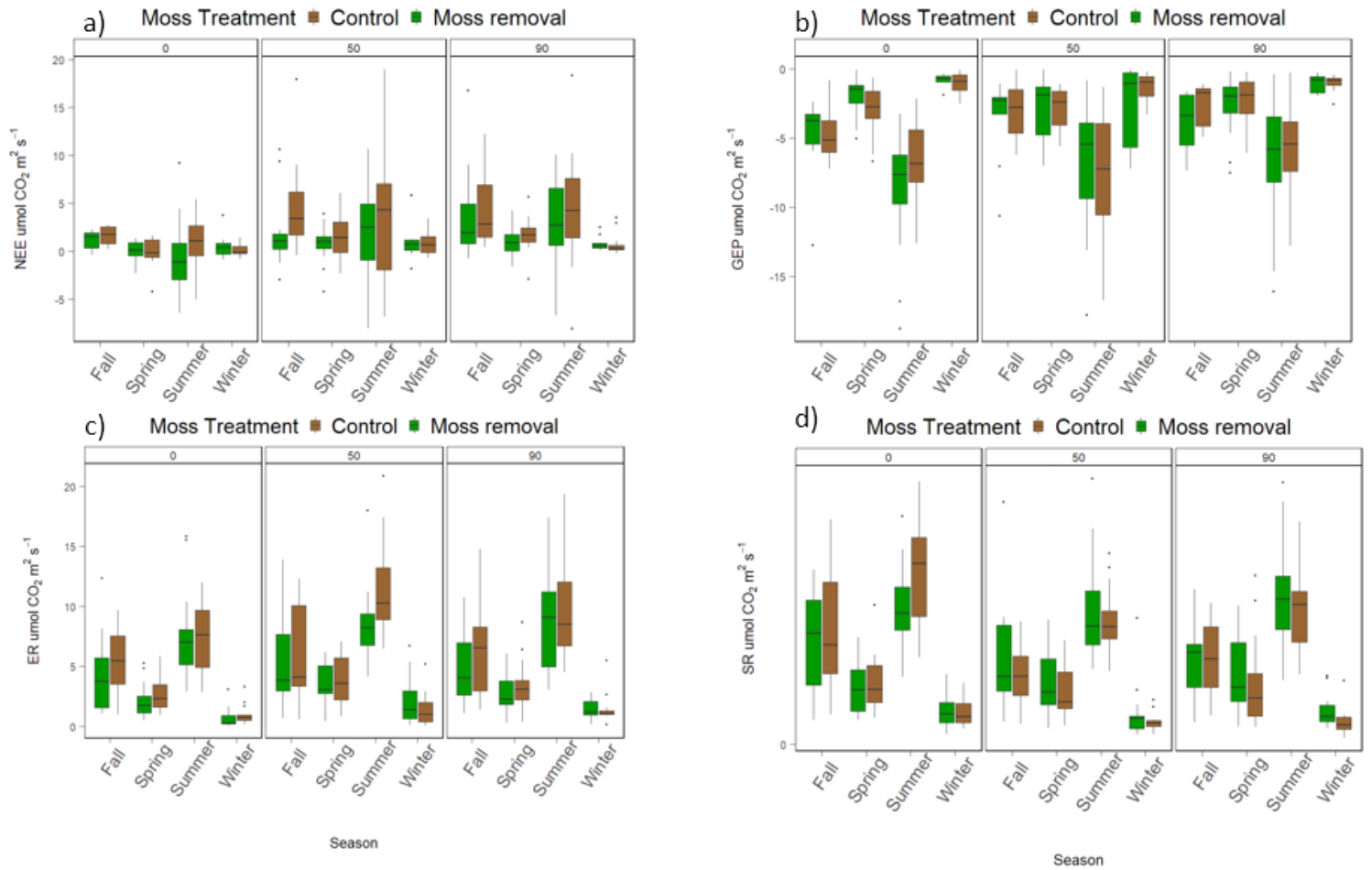


Figure 5. Box plots of how the fluxes differ for different seasons across drought treatment and for bryophyte removal with Net ecosystem exchange (NEE) a), gross ecosystem production (GEP) b), ecosystem respiration (ER) c) and Soil respiration (SR) in d). Bryophyte treatment controls are shown in brown, and bryophyte removal in green.

Soil respiration showed a stronger relationship to soil temperature ($F=647$, $P<0.001$, $AIC=560$) compared to soil moisture ($F=33.343$, $P<0.001$, $AIC=899$) (figure 6).

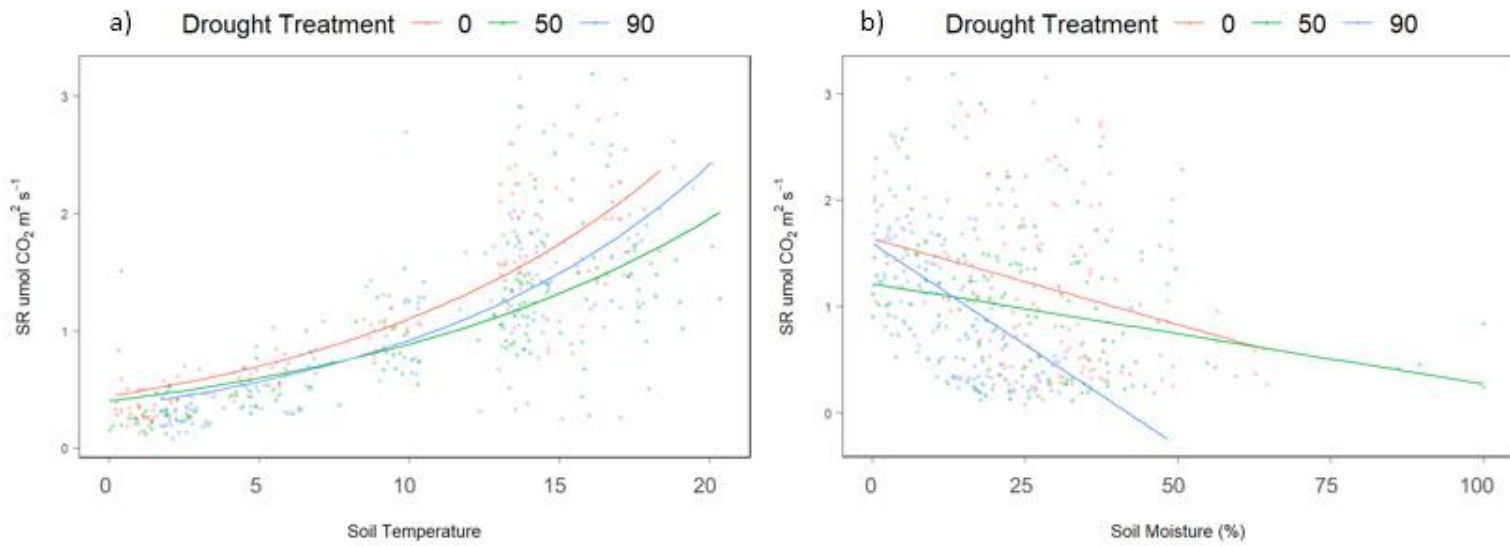


Figure 6. Scatter plot with linear regression lines showing soil respiration relationship with soil temp a) and soil moisture b) across drought gradient shown in orange(control), green (50% rainout shelters) and blue (90% rainout shelters)

Photosynthetic active radiation did not vary across drought treatments ($F=0.1152, P=0.7345$)

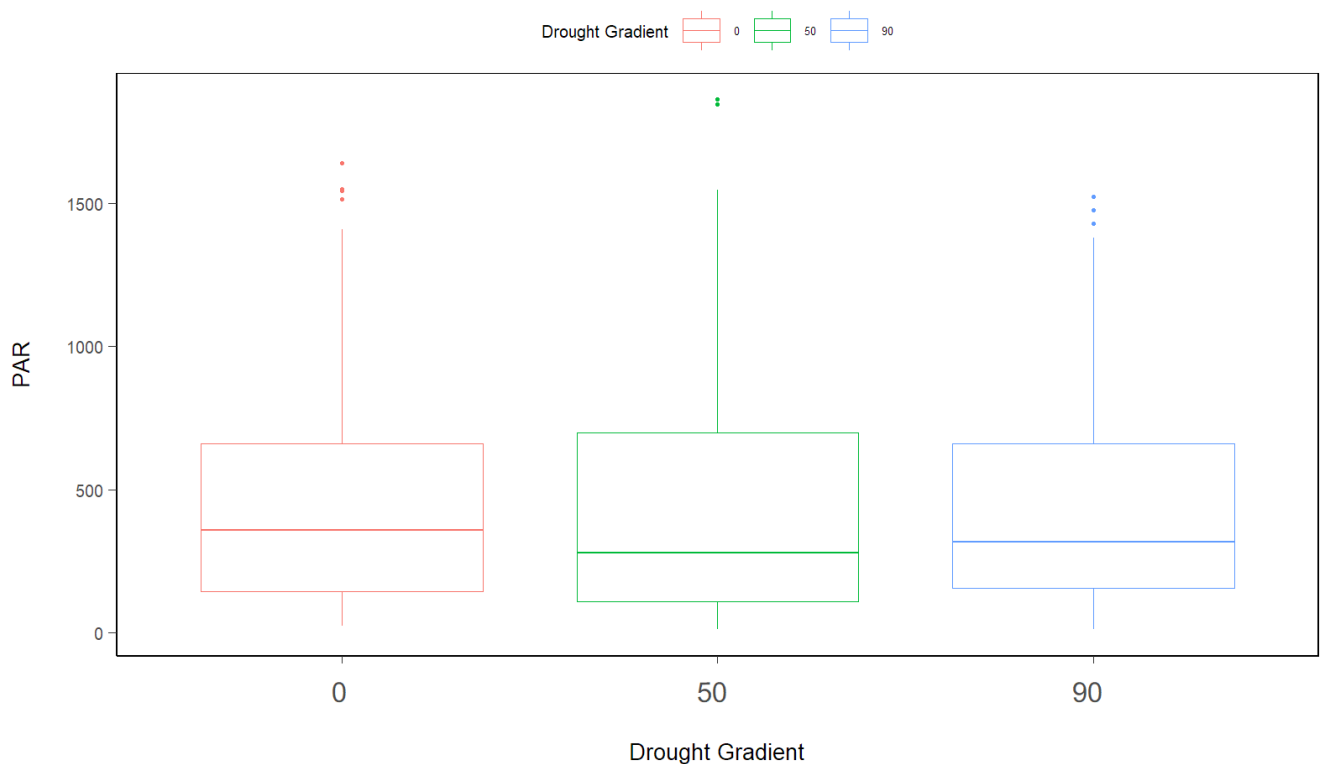


Figure 7. Boxplot showing photosynthetic active radiation received across drought treatment for across the whole year for the study period.

Table 1. Shows results from multiple measurements analysis of variance for the ecosystem fluxes. Statistically significant response to treatment marked with asterisk (*).

Flux	Variables	numDF	denDF	F-value	AIC	P-values
NEE	intercept	1	340	28.476	1939	<0.0001
	Drought treatment	2	14	4.580		0.0295 *
	Bryophyte treatment	1	14	2.550		0.1326
	Season	3	340	9.000		<0.0001
SR	Intercept	1	431	19.887	580	<0.0001
	Drought treatment	2	14	1.027		0.3837
	Bryophyte treatment	1	14	0.176		0.6815
	Season	3	431	190.723		<0.0001
ER	Intercept	1	401	333.712	2033	<0.0001
	Drought treatment	2	14	2.255		0.1416
	Bryophyte treatment	1	14	1.567		0.2311
	Season	3	401	170.190		<0.0001
GEP	Intercept	1	304	213.119	1609	<0.0001
	Drought treatment	2	14	1.187		0.3340
	Bryophyte treatment	1	14	0.253		0.6227
	Season	3	304	60.798		<0.0001

Discussion

In this study I measured ecosystem CO₂ fluxes and how they over the year when subjected to a drought gradient and bryophyte removal.

The NEE increased from control into the drought treatments causing higher amounts of carbon to be released as CO₂ from the system into the atmosphere. The major contributor to this change has not been picked up by the analysis possibly due to high variation in the data. However, trends can be found with a closer look at GEP and ER the two components of NEE. ER increased the most between the two components, where particularly during summer for both moss treatments ER showed larger difference than GEP. This finding is in agreement with the literature which claims high respiration as moisture is reduced (Ciais et al., 2005; Sowerby et al., 2008b). Gross ecosystem production has not been standardised for light conditions in photosynthetic active radiation (PAR) which could explain additional

variation. Difference in PAR for GEP across drought treatment was investigated and no such difference was found. The limiting factors of the coastal heathland must be considered. In this system water limitation is rare due to large amount of yearly rainfall, the rainout shelters have reduced the soil moisture considerable but possibly not enough to make water limiting for longer periods of time and that the system possess a high ability to recover from drought as previously found by Sowerby (Reinsch et al., 2017; Sowerby et al., 2008b)

No reduction has become evident for soil respiration in this study which is in contrast to previous studies as well (Liu et al., 2016; Sowerby et al., 2008a). This could be a result of the relationship between soil moisture and temperature on R_s . Soil temperature explained much more of the difference in soil respiration than soil moisture. It is likely that the induced drought gradient is not strong enough over time to show any changes in soil respiration.

Explanations to why little response to drought gradient has been in the carbon fluxes can be many, here I propose three. Firstly, as previously mentioned it is possible that recovery is fast and efficient enough to prevent effects from showing. Secondly, because large amounts of the data were gathered during what was already considered extraordinary drought and therefore impacting the control as well which can hide some of the response and increase uncertainty. Thirdly, the response of the drought gives results that are not possible to pick up over this short of a period considering the study system grows slowly. As drought is imposed and the plants react this could further down the successional stages cause a change in community structure and composition that will alter the carbon dynamics much later and not within the pioneer stage which is rapidly changing.

Bryophytes treatment effect on soil moisture suggest a threshold effect where control plots and 50% cover plots are the same. Bryophytes were able to change the soil moisture content but showed no change soil and surface temperature. No impact of the mosses was found for the fluxes. This contrasts with the second hypothesis where the insulating properties of mosses were hypothesised to have an ameliorating effect on the response to drought for the carbon fluxes. This could be because insulating properties are not as important for this system because of seasonal temperatures are relatively high compared to colder systems where mosses have been shown to have effect (Gornall et al., 2007; Grogan & Jonasson, 2006; Street et al., 2012). For this study lack of response in fluxes can be explained by the lack of change in environmental variables where only soil moisture was altered by moss

presence. Changes in soil moisture is in accordance with the third hypothesis where the water holding capacity of mosses were hypothesised to reduce impact of drought. However, the retention of water within the mosses could also prevent water from entering the soil and thereby increasing the effects of drought which has been shown in earlier studies(Gornall et al., 2007), but since no effect was found it is difficult to determine which effect is the strongest for this study. Since no reaction in the fluxes can be found it is more likely that the moss layer has retained water as seen for the 50% cover and prevented it from entering the soil resulting in a similar effect as that of the 90% cover plots. Bryophyte depth has not been measured which is unlikely to have affect for ground surface temperature but could mean differences in insulation and water holding properties(Gornall et al., 2007). Deeper and denser bryophyte cover would be able to hold more water and a stronger temperature buffer.

The ecosystem fluxes measured here are the major pathways of carbon in the system, but they are not the only pathways. Leeching would be of interest in this system due to large amounts of rainfall and rugged topography that could lead to stronger water movement. Overall leeching is not being explored but soluble carbon in the soil water is being analysed as part of a different ongoing study. Impact of herbivory which can be a major loss of carbon from a system has been excluded in this study by fences. It is likely that had herbivory not been excluded it would represent a major loss as the pioneer stage of the heathland which consist of much more palatable species and primary food source for grazing sheep in the are during spring and summer. However, this would further obscure any response of drought and bryophyte removal treatment.

For the future it will be important to look at how drought frequency will impact the heathlands over time and across successional stages to better understand the future projected changes in extreme weather events will cause.

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