

Land-use and climate impacts on drought resistance and resilience in coastal heathland ecosystems

Siri Vatsø Haugum

Thesis for the degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
2021

UNIVERSITY OF BERGEN



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Date of defense: 15.12.2021

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Year: 2021

Title: Land-use and climate impacts on drought resistance and resilience in coastal heathland ecosystems

Name: Siri Vatsø Haugum

Print: Skipnes Kommunikasjon / University of Bergen

Scientific environment

This PhD dissertation was written at the University of Bergen at the Faculty of Mathematics and Sciences, and the Department of Biological Sciences.

The thesis was conducted as part of the LandPress project, funded by the Research Council of Norway (RCN project 255090) and was conducted at the Department of Biological Sciences, University of Bergen, in collaboration with Møreforskning and the Norwegian Institute for Bioeconomy Research (NIBIO). The project received additional funding and support from the RECITE project (RCN project 274831), the Meltzer Foundation, and Grolle Olsen's Legat til Universitetet i Bergen med tilførsel av arv etter Miranda Bødker, the European Cooperation in Science and Technology (EU COST Action ES1308), the Heathland Centre at Lygra, and the County Governor of Hordaland.



Acknowledgements

I am grateful for the support I have received from my supervisors through my four years of study - especially during the final run towards the finish line. Thank you for designing two fantastic experiments to work in, and build upon, and for enthusiastically discussing my work. Thank you for letting me explore numerous side-track projects, such as anthropogenic fire systems in the Peruvian Puna, and multiple variations of scientific and public outreach. Indeed, some of these side quests ended up being quite fruitful! Thank you, Vigdis, for teaching me so many of your skills (and a few bad habits too), and thank you, Liv Guri, for being ever so optimistic and for having a well-developed sixth sense for when an encouraging phone call was due. Thank you, Richard, for patient R support, and last but not least, thank you, Pål, for teaching me so much about the northern heathlands. I look forward to more collaborations in the future!

To teach is the best way to learn. I wish to thank BIO and bioCEED for hosting the most exciting lab and field courses, and for facilitating the large amount of student engagement in our research. No one expresses enthusiasm and fascination over the natural world better than our biology students do. The number of students that played a role in this thesis is far too many to mention. However, I advise readers to look thoroughly on the author list of paper IV and in the Acknowledgements sections of individual papers.

The EECRG and the Between the Fjords lab are great places to 'grow up' as a scientist. Linn, Arild, and Jonathan have been incredibly supportive as technicians and friends. Sharing numerous academic experiences with Ragnhild has been a great pleasure, and I truly admire her dedication to everything she does. Kristine and Ruben have come to the rescue more than once and I enjoy so much to follow their progress in research, teaching, and scientific outreach. I have spent many hours in the offices of Inger and Anne discussing whatever was on my heart while getting inspired by their work and their warm personalities. John-Arvid made sure that field course teaching was a recurring highlight of my summers. I have enjoyed progressing

through my PhD in parallel with Beate and I look forward to my next visit to Scotland. Thank you also to the Bjerknes Centre for taking scientific outreach seriously and for inviting me in with open arms.

Thank you, Inger K. Schmidt, for welcoming me to Copenhagen and IGN and for expanding my understanding of the European heathlands. Thank you, to the fellow students and employees at IGN who made my many long and short stays cheerful, both during and after office hours.

The work presented in this thesis would not be possible without the landowners who provided us with the most exciting field sites - and especially Sigmund and Johan who also assisted greatly with logistics. Lyngheiseret has often felt like my second home and I feel incredibly lucky to return now as an employee.

Thank you to everyone in the “Heathland family” for sharing your knowledge and love for the heathlands with me. This goes well beyond numerous scientific and social events. I have followed the footsteps of Inger, Liv Guri, Heidi, Tessa, and Jan Håkon, and you have always shown enthusiasm for my PhD project. Mons and Peter Emil taught me the history of heathlands, and they instructed me in how to keep heathlands sound and happy with flames. Amy always kept an eye on me and her contribution to the heathland family expresses a genuine love for the old landscape and its inhabitants.

Friends and family provided helping hands in the field when my notoriously poor time-optimism peaked. My doppelganger, Siri Ane, even showed up to help three years in a row! I am grateful that my friends and family also made sure I enjoyed life outside the office and the field sites. Thank you for taking me out into nature without my notebook. Thank you, June, for being sister of the year, and many thanks to my parents for reminding me that there is more to life than a PhD. Last but not least, thank you, Casper, for all your support and for the many small and big adventures.

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Abstract

Background: Coastal heathlands of north-western Europe are semi-natural landscapes of high conservation value. These are ancient and historically widespread landscapes, but anthropogenic land-use and climate change are now increasingly threatening coastal heathland biodiversity, structure, and ecosystem functioning. Semi-natural ecosystems depend on management practices to maintain their ecosystem functioning. In coastal heathlands, prescribed burning and grazing have been key management tools for millennia, keeping the vegetation within alternating post-fire successional phases. Abandonment of these practices, leading to degraded heathlands, combined with agricultural intensification and infrastructure development, has reduced coastal heathland area in Norway to a tenth of its former distribution, paralleling heathland loss trends across their European distributional range. Recently, extreme drought events have led to severe diebacks of the key-stone species *Calluna vulgaris* in heathlands along the Norwegian coast, the northernmost distribution area of European coastal heathlands. These relatively short-term drought events dramatically alter ecosystem functions, and yet we know little of the system's ability to recover from such events. Extreme climatic events, including droughts, are projected to increase along the Norwegian coast due to anthropogenic climate change, raising concerns about the resistance and resilience of coastal heathland ecosystems to intensified drought, and consequences for future heathland biodiversity and ecosystem functioning. Quantifying ecological drought and its impacts on ecosystems is challenging due to the intrinsic complexity of ecological and ecosystem responses to global changes. To date, most studies aiming at quantifying ecological response to drought are performed in dry climates, leaving a knowledge gap on how intensified drought affects precipitation-rich ecosystems. Moreover, few studies on ecosystem responses to climate change include the interaction with land-use changes, despite the latter being the main driver of biodiversity loss and habitat changes globally.

Objectives: The objectives of this thesis are i) to assess how resistant Norwegian coastal heathland ecosystems are to experimental drought, ii) to discover how

resilient these heathlands are in recovering ecosystem functioning after a major natural drought event and to what extent this is affected by prescribed burning, and iii) to contribute to the general understanding of ecological responses to increased frequency, duration and intensity of drought in a precipitation-rich ecosystem, in interaction with land-use change.

Main results: I find that plant community dynamics and primary production in coastal heathlands are largely resistant to experimental drought. However, I also find that in the late post-fire successional phase, heathland ecosystem carbon dynamics are affected by experimental drought. A natural drought caused variable drought damage and mortality across the study sites, but mortality was highest in the northernmost sites. Whilst the recovery of *Calluna* in unburnt stands varied from high to very low over the study period, all sites show high recovery after fire. Overall, prescribed fire seems to be an efficient restoration tool in drought-damaged coastal heathland vegetation, regardless of pre-fire damage and recovery rate of unburnt stands.

Conclusion: Intensified drought can alter ecosystem functions in coastal heathlands but predicting ecosystem responses and recovery remains difficult. Early post-fire successional heathlands seem to be more resistant to experimental drought than late successional heathlands. Ecological resilience after drought is dependent on more factors than this study uncovers, but prescribed fire seems to be an efficient restoration tool across ecological and climatic gradients. Consequently, continued traditional management can buffer impacts of climate change on the coastal heathlands of north-western Europe, and be an important tool in restoration.

Keywords: Coastal heathlands, Atlantic heath, drought experiment, *Calluna vulgaris*, resistance, resilience, recovery, land-use, prescribed burning, semi-natural habitats, plant community, carbon storage, functional traits, succession

Samandrag

Bakgrunn: Kystlyngheiene i nordvest-Europa er seminaturlege landskap med høg forvaltningsverdi. Dette er svært gamle og historisk vidt utbreidde landskap, men menneskeskapte arealbruks- og klimaendringar utgjer i dag ein stadig aukande trugsel for biodiversitet, utforming og økosystemfunksjonar i kystlynghei. Semi-naturlege økosystem er avhengige av skjøtsels for å oppretthalde økosystemfunksjonar. For kystlyngheia har lyngsviing og beiting vore nøkkelverktøy i skjøttinga i årtusnar, noko som har halde vegetasjonen i vekslende suksesjonsfasar etter lyngsviing. Opphøyr av denne skjøttinga, kombinert med intensivering i landbruket og utbygging av infrastruktur, har redusert arealet av kystlynghei til ein tiandedel av den tidlegare utbreiinga. Det same tapet av kystlynghei finn vi langs heile det Europeiske utbreiingsområdet. Nyleg har ekstremtørke resultert i massedaud av nøkkelarten røsslyng (*Calluna vulgaris*) i lyngheier langs norskekysten, som utgjer den nordlege delen av utbreiingsområdet for kystlynghei i Europa. Slike tørker kan endre økosystemfunksjonane dramatisk i løpet av nokre veker, og vi veit lite om kor godt økosystemet greier å hente seg inn etter ei slik hending. Ekstremver, inkludert tørke, er venta å auke i regionen som følgje av menneskelege klimaforandringar og skapar bekymring for kor motstandsdyktige og resiliente økosystema i kystlyngheia er i møte med meir intens tørke, samt konsekvensar for framtidig biomangfald og økosystemfunksjonar i kystlynghei. Det er vanskeleg å kvantifisere økologisk tørke og effektane den har på økosystemet fordi økologiske responsar til globale endringar er komplekse av natur. Så langt er dei fleste slike studiar utført i tørre system, noko som gir eit kunnskapshol knytt til korleis ekstremtørke påverkar nedbørsrike økosystem. Vidare er det få studiar på økosystemresponsar til klimaendringar som famnar om arealbruksendringar, sjølv om det siste er den viktigaste årsaka til tap av naturmangfald og habitatendringar.

Føremål: Føremåla med denne avhandlinga er å svare på i) kor motstandsdyktig norske kystlyngheier er til eksperimentell tørke, ii) kor resiliente desse lyngheiene er til å rette opp att økosystemfunksjonar etter ei kraftig naturleg tørke, og i kva omfang

dette er påverka av lyngsviing, og iii) bidra til den generelle forståinga av økologiske responsar knytt til auka hyppigheit, varigheit og intensitet av tørke i nedbørsrike økosystem, og i interaksjon med arealbruksendringar.

Hovudfunn: Eg finn at kystlynghei i hovudsak er motstandsdyktig mot eksperimentell tørke. Samstundes finn eg også at karbonomsettinga i økosystemet blir påverka av eksperimentell tørke i den seine suksesjonsfasen etter lyngsviing. Ei naturleg tørke resulterte i varierende grad av tørkeskade og lyngdaud på tvers av studieområda, men dødelegheita var høgst i dei nordlegaste områda. Medan lyngen i dei ubrende forsøksfelta viste låg til høg forbetring gjennom studieperioden fann vi god forbetring av vegetasjonen i alle studieområder etter lyngsviing. Totalt sett ser lyngsviing ut til å vere eit effektivt restaureringsverktøy i tørkeskadd kystlynghei, uavhengig av tilstanden før sviing og forbetringa til den ubrende lyngen.

Konklusjon: Meir ekstreme tørker kan endre økosystemfunksjonar i kystlynghei, men å føresjå økosystemresponsar og vegetasjonsbetring etter tørkeskade er vanskeleg. Kystlynghei i tidlege suksesjonsstadie etter lyngsviing ser ut til å vere meir motstandsdyktige mot eksperimentell tørke. Økologisk resiliens etter tørke avheng av fleire faktorar enn dei som blir avdekka her, men lyngsviing ser ut til å vere eit effektivt restaureringsverktøy på tvers av økologiske og klimatiske gradientar. Følgeleg kan framhald av skjøtsel med brann og beite skape ein buffer mot innverknaden av klimaendringar i kystlyngheier i Nordvest-Europa, samt vere eit viktig verktøy i restaurering.

Nøkkelord: Kystlynghei, Atlantisk hei, tørkeeksperiment, *Calluna vulgaris*, motstandsdugleik, resiliens, tilbakeføring, arealbruk, lyngsviing, semi-naturlege landskap, plantesamfunn, karbonlagring, funksjonelle eigenskapar, suksesjon

List of individual papers

- Paper I** **Haugum SV**, Thorvaldsen P, Vandvik V, and Velle LG. Coastal heathland vegetation is surprisingly resistant to experimental drought across successional stages and latitude.
Oikos. doi:10.1111/oik.08098
- Paper II** **Haugum SV**, Christiansen CT, Vågenes A, Velle LG, Thorvaldsen P, and Vandvik V. Land-use management with prescribed burning stabilizes soil carbon pools under experimental drought in wet coastal heathlands.
Manuscript prepared for Environmental Research Letters.
- Paper III** Velle LG, **Haugum SV**, Telford RJ, Thorvaldsen P, and Vandvik V. Lasting die-back of Atlantic heathlands after an extreme drought event: Can prescribed burning be a tool to promote recovery?
Manuscript submitted to Applied Vegetation Science¹, October 2021.
- Paper IV** **Haugum SV**, Thorvaldsen P, Velle LG, Birkeli K, Thormodsæther R, Christiansen CT, Geange SR, Aamold D, Busca S, Garcia WFE, Grape VH, Guthu H, Mouton L, Nesheim-Hauge E, Pánková K, Sandsten H, Simonsen L, Swat M, Tjøflot H, Vangdal IT, Vestlie T, Vågenes A, and Vandvik V. A comprehensive multi-scale experiment in a coastal heathland: Plant and ecosystem responses to drought across three post-fire successional phases and two latitudinal zones.
*Data Descriptor prepared for Scientific Data**

¹ The original version of the thesis stated that Paper III was submitted to *Journal of Vegetation Science*. This has been corrected before printing.

Specifications of author contributions to the individual papers

Contribution	Paper I	Paper II	Paper III	Paper IV
Project/paper idea and design	VV, LGV, PT	SVH, CTC, VV	LGV, PT, VV	SVH, VV, LGV, PT
Data collection	SVH, PT, LGV	SVH, AV	SVH, PT, LGV	SVH, PT, LGV, KB, CTC, SG, RT, Students**
Data preparation	SVH	SVH, CTC, AV	SVH	SVH, RT, Students*
Statistical analyses	SVH	SVH, CTC	RJT, SVH	SVH, RT
Writing	SVH	SVH, CTC	LGV, VV	SVH, RT
Inputs and editing	PT, LGV, VV	CTC, LGV, AV, VV, PT	SVH, PT, RJT	VV, LGV, PT, RT, KB, CTC, SG, Students**

SVH = Siri Vatsø Haugum^{1,2}, VV = Vigdis Vandvik^{1,2}, LGV = Liv Guri Velle³, PT = Pål Thorvaldsen⁴, RJT = Richard James Telford¹, CTC = Casper Tai Christiansen⁵, AV = Alexander Vågenes¹, KB = Kristine Birkeli¹, RT = Ruben Thormodsæther¹, SRG = Sonya Rita Geange^{1,2}

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**Note: The final published version of this data descriptor will contain links to a permanent and openly available version of all raw and derived datasets in an Open Science Foundation (OSF) project. The thesis version does not contain these links, as the data may be subjected to change during the publication process. The opponents will be granted access to the raw and derived data files which are deposited in an OSF project that will be made publicly available once the data descriptor is published.*

*** Students = BSc and MSc students, mainly from University of Bergen. For names, affiliations and their individual contributions, see author list on paper IV.*

Synthesis

The coastal heathlands of north-western Europe are a rare example globally of anthropogenic ecosystems where remnants of ancient human land-use regimes and their historic ecological and evolutionary impacts on vegetation can still be observed today (Webb 1998, Vandvik et al. 2014). A combination of native, frugal plant species favoured by grazing by traditional agricultural livestock breeds and prescribed burning regimes, as well as the mild climate along the European North Atlantic coast, has supported permanent human settlements for more than 6000 years (Hannon et al. 2005). Today, coastal heathlands provide habitats for red-listed species (Hovstad et al. 2018), store carbon (Bartlett et al. 2020, Friggens et al. 2020), produce food, and provide grounds for recreational activities (Kaland 2014). However, coastal heathlands are increasingly threatened because of agricultural intensification, urban and rural infrastructure development, and abandonment of traditional land use practices (EC Habitats Directive 1992, Janssen et al. 2016, Hovstad et al. 2018). In addition, climatic changes pose new threats to coastal heathlands and their ecosystem services (IPBES 2018), but there are big knowledge gaps on the resistance and resilience of these ecosystems to climate change, and especially to increased climatic variability and extreme climate events (Pinto Correia et al. 2005, Treharne et al. 2020).

Norwegian coastal heathlands are some of the most intact remaining coastal heathlands in Europe, being one of the few regions where traditional management practices are still applied, and where agricultural intensification has been relatively minor (Webb 1998, Kvamme 2004). Nevertheless, Norwegian coastal heathlands have recently faced large-scale diebacks following natural drought periods (Phoenix and Bjerke 2016). Droughts are projected to increase in frequency, intensity, and duration along the Norwegian coast (Wong et al. 2011, IPCC 2021), raising concerns about a new and challenging conservation issue.

In this thesis, I explore drought resistance and resilience in northern coastal heathlands through experimental drought manipulation in combination with a natural

experiment in drought-damaged heathlands. First, the synthesis chapter presents coastal heathland ecology, and current and future threats to coastal heathlands and their ecosystem function and services. Next, I present the objectives and research questions, the methodological approach, and summarise and discuss the main findings of my research. Last, I draw together and discuss the overall scientific conclusions and implications of my work. The synthesis chapter ends with an afterword where I share my experiences and reflections around student-active research, focusing on the benefits and challenges of involving students actively as contributors to data collection in research.

Following the synthesis are the research results written up as four scientific manuscripts presenting I) resistance of coastal heathland plant communities to experimental drought, II) resistance of coastal heathland ecosystem carbon balance to experimental drought, III) recovery and resilience of coastal heathland plant communities after a natural winter drought and the role of prescribed burning in restoring resilience, and IV) a comprehensive data paper on coastal heathland ecosystem responses to experimental drought.

European coastal heathlands

European coastal heathlands, also known as Atlantic heaths, are semi-natural ecosystems on the European west coast, ranging from Portugal (40.5°N) in the south to the Lofoten archipelago in Norway (68.5°N) in the north (Figure 1a). Along this geographical space there are strong gradients in temperature, precipitation, soil properties, nitrogen deposition, management practices, and plant community composition (Kaland 2014). Nevertheless, the heathland vegetation is relatively uniform across this biogeographic extent, consistently dominated by dwarf-shrubs partially resulting from a management regime predominantly with grazing and prescribed burning to promote open habitats and fine-scale vegetation heterogeneity at the landscape scale (Vandvik et al. 2005). Today, heathlands remain important for European cultural and natural heritage (Kaland 2014).(Kaland 2014)

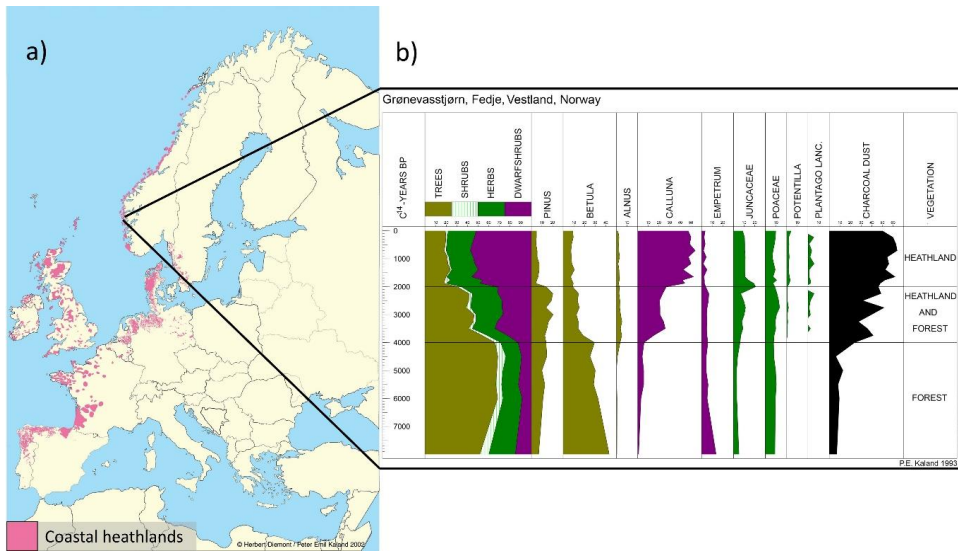


Figure 1: Pollen diagrams are used as important tools for dating the transition from forest to semi-natural coastal heathlands along the distribution area of coastal heathlands. a) The historical distribution of European coastal heathlands in the 19th century. b) Pollen diagram from Grønevasstjørn, Fedje, Norway. At this site, the pollen diagram reveals that the transition from deciduous forest to heathland happened in two phases, both traceable as a decline in pollen from trees and an increase in pollen from the dwarf-shrub *Calluna vulgaris* and forbs at ca. 4000 BP (¹⁴C years before present) and ca. 2000 BP. A sharp increase in charcoal dust at the point of the first heathland expansion indicates the continued presence of fire as a tool for transitioning from forest to heathland and for maintaining heathland. Other sites show similar trends, but with forest clearance occurring at different times between ca. 6000 BP and 500 BP depending on the local land-use history. Lines between a) and b) show the location of Fedje. Figures provided by Peter Emil Kaland and used with permission.

Historically, coastal heathlands supported year-round livestock grazing and supplied settlements with resources such as meat, wool, milk, peat, manure, berries, and honey (Hjelle et al. 2010; Figure 2). Heathlands predominantly replaced forests (Figure 1b and Figure 3). Humans cut down trees and used fire to remove bushes and stumps to change the landscape from forest to heathland (Kaland 2014; Figure 1b). (Hjelle et al. 2010; Figure 2) Enhanced heathland cover followed broadly the expansion of human settlement northwards on the European west coast from ca. 6000 BP (years before present) onwards, with large local variation in the onset of deforestation, and heathlands also increased in abundance regionally as agriculture became established

(Prösch-Danielsen and Simonsen 2000, Pinto Correia et al. 2005, Hjelle et al. 2010). The distribution of coastal heathlands peaked in the 19th century (Figure 1a), before industrialisation started to replace these traditional agricultural practices (see Figure 2 for an overview of agricultural practices). In the following century, heathland habitats were increasingly lost to agricultural intensification, urban and rural developments, infrastructure, and abandonment of land-use resulting in secondary succession in the outfields and a reforestation of the landscape. Today, only one tenth of the original heathland distribution remains, and coastal heathlands are classified as ‘endangered’ or ‘vulnerable’ throughout their distributional range (EC Habitats Directive 1992, Kvamme 2004, Janssen et al. 2016, Hovstad et al. 2018)}.

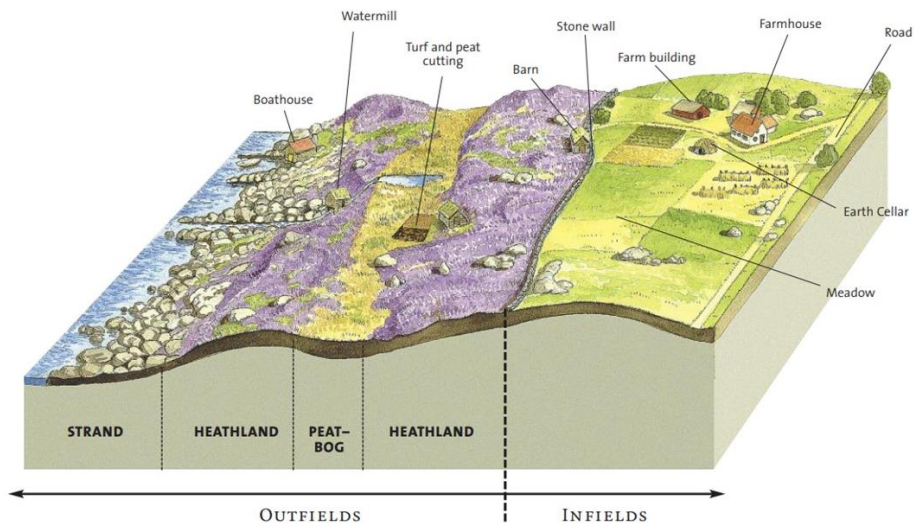


Figure 2: Schematic illustration of a traditional heathland farm in coastal northern-Europe in the 19th century, with a characteristic clear divide between cultivated or mowed infields and grazed outfields dominated by heather. The relatively cold and wet climate of the region facilitates bog formation in landscape depressions, and turf and peat were valuable resources used for e.g., fuel. Illustration by Ed Hazebroek, reproduced from Kaland (2014) with permission.

Heathland management

Burning and grazing continued in a cycle to prevent the return of forest, and over time the cyclical coastal heathland ecosystem emerged, with its predictable post-fire vegetation succession (Gimingham 1988). In coastal heathlands, the vegetation

emerging immediately after burning is dominated by graminoids and forbs which provide valuable fodder for livestock. Later, the evergreen dwarf-shrub *Calluna vulgaris* (L.) Hull (from hereon, *Calluna*) dominates the vegetation, providing access to green, nutritious fodder for livestock throughout winter. This provision of year-round livestock fodder was crucial for the success of human settlements along the coast. The coastal location provided marine proteins, which together with terrestrial meat and milk from livestock husbandry in the heathlands provided more reliable food sources for the coastal human population than those who relied on crop yields (Kvamme 2004).



Figure 3: Remnants of a tree stump from Hopøy, Øygarden, Norway. Coastal heathlands predominantly replaced forest. Peat was the main source of heating fuel after the forest was removed. Photo: Siri V. Haugum.

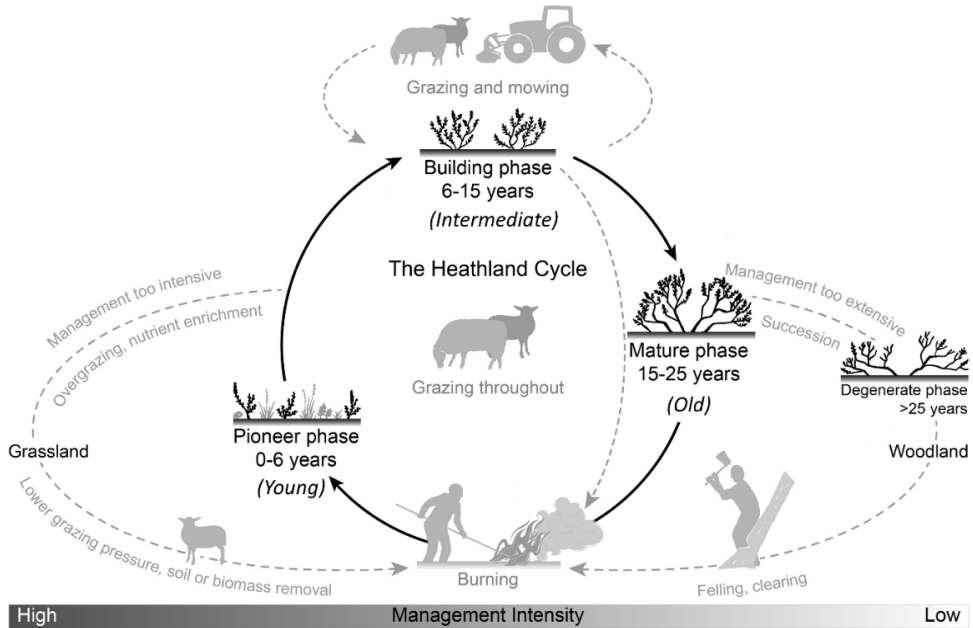
In addition to the livestock fodder resource in the heathland, livestock manure and seaweed provided fertilisers for infield production (Figure 2), which in turn allowed farmers to produce vegetables for their own nutritional supplement and grass to

support more livestock. To compensate for the absence of trees, peat was extracted and used for fuel (Kaland 2014; Figure 2).

In the heathland, *Calluna* stands become coarse and unattractive as fodder after >20 years, thus the heathland was burned to restart the successional cycle (Figure 4). However, other non-fire disturbances, such as cutting and mowing, were also used to renew *Calluna* shoots and increase fodder value. Gimingham (1988) classified the post-fire succession in coastal heathlands into four phases based on the architecture of *Calluna*. In the early post-fire phase, termed the *pioneer phase* by Gimingham, (Gimingham 1988) *Calluna* resprouts from belowground organs or germinate from seeds, but graminoids and forbs dominate the vegetation cover (Barclay-Estrup and Gimingham 1969). As *Calluna* grows, it becomes highly branched and forms dense rounded canopies, often dominating the vegetation, the heathland enters what Gimingham termed the *building phase* (Barclay-Estrup and Gimingham 1969). This happens approximately 6 years after fire and lasts for about ten years. After 15-16 years, the heathland enters the *mature phase* where *Calluna* stands grow coarse with round to flat and increasingly open canopies (Kaland 2014). This increases light availability under the canopy and allows new species to establish, including trees from adjacent forests (Moen et al. 2006). If a new fire event is not introduced, the heathland will eventually become reforested via a transition phase often termed the *degenerative phase* by Gimingham. In this thesis, I base the description of post-fire successional phases on Gimingham's definitions, however, for consistency and to ease communication beyond specialised heathland ecologists, I term them *young* (pioneer), *intermediate* (building), and *old* (mature) successional phases in papers I, II, and IV, as well as in the synthesis, as this thesis is aimed at a broad ecological audience. 'Stage' and 'phase' are used synonymously.

Figure 4 (next page): The management cycle in coastal heathlands, showing the main post-fire successional phases or stages. Young, intermediate, and old successional stages in this thesis parallel the pioneer, building and mature phases in Gimingham (1988). Years are approximate, as post-fire succession time depends on several environmental factors, including grazing and climate. Instead of years since fire, the architecture of *Calluna* can be used to identify the successional stage. In the young post-fire phase, *Calluna* stands are present as fresh root shoots or seedlings. Over time, the *Calluna* canopy becomes more

branched and the heathland transitions into the intermediate stage. The *Calluna* stands become coarse and the canopy opens in the old stage. During this stage, a new prescribed fire is traditionally introduced. If management practices are abandoned, the heathland will eventually become reforested with deciduous forest, or sometimes invasive coniferous species such as *Picea sitchensis* and *Pinus mugo* (Saure 2012, Vikane 2020). Figure reproduced with permission from Velle et al. (2021).



The (not so) secret life of *Calluna vulgaris*

Calluna is a dominant species in northern coastal heathlands and can be described as a keystone species when considering the cultural aspect of the heathlands (Vandvik et al. 2014). *Calluna* is a light demanding evergreen dwarf-shrub, and a weak competitor in nutrient-rich environments. However, the shrub performs well on the nutrient poor soils along the European Atlantic coast if trees are prevented from dominating. The plant has a long life span (Gimingham 1985), produces a large number of seeds (Legg et al. 1992), which form a long-lived soil seed bank (Måren and Vandvik 2009). Shoots are evergreen and relatively nutritious, and the growth and productivity of *Calluna* can be promoted by human disturbances (Watt 1947). In addition to, or maybe because of, the important role *Calluna* plays in coastal heathlands, the species' ecology has

been of special interest for ecologists for more than a century (Rayner 1913, Knudson 1929, Whittaker and Gimingham 1962, Robinson 1972, Måren et al. 2010). Charles Gimingham demonstrated how *Calluna* is highly relevant for the two-way links between theoretical and applied ecology in his 1972 book “Ecology of heathlands” (Gimingham 1972). This book was published shortly after the paper by Mohamed and Gimingham (1970), which described in detail how cutting and burning alters the morphological growth form and productivity of *Calluna* shrubs. The resprouting from belowground organs after burning is an important trait in *Calluna* which ensures rapid regrowth. However, later studies discovered that this trait is not present north of $\sim 63^{\circ}\text{N}$, and consequently *Calluna* solely recovered from seeds here (Nilsen et al. 2005, Spindelböck et al. 2013). This has later been confirmed in a study exploring the post-fire variation in *Calluna* along a 340 km gradient on the Norwegian coast (Velle and Vandvik 2014).

The presence of humans in the coastal heathlands is not only evident from the vegetation and cultural landscape. Måren et al. (2010) and Vandvik et al. (2014) have demonstrated anthropogenic smoke adaptations in *Calluna*. Specifically, *Calluna* seeds from coastal heathland, where prescribed burning has been applied for centuries, germinate at higher rates when exposed to smoke molecules compared to a control group not exposed to smoke (Måren et al. 2010). This response was not found when the experiment was replicated on seeds from *Calluna* populations in forests or mountains in the same region, where prescribed burning had never been applied (Vandvik et al. 2014). These findings strongly suggest that *Calluna* has adapted to anthropogenic burning, a quite exceptional finding given how relatively short a time 6000 years is in an evolutionary perspective.

Even more recently, studies on the intraspecific genetic variation in *Calluna* have revealed high genetic diversity with clear geographical patterns. Preliminary results suggest that populations along the coast from Spain to southern Norway, including the British Isles have a common origin which is different from populations in central Europe, as well as from populations in northern and north-eastern Europe, including the north Norwegian west coast (Durka unpublished). Interestingly, the

smoke response demonstrated in Vandvik et al. (2014) was present across the two main genetic clusters in Norway, further strengthening the hypothesis that land-use legacies, and not climate, genetic origin, or post-glacial history, explain the observed smoke response of coastal heathland *Calluna* seeds. Yet it is not clear whether the absence of vegetative resprouting in northern *Calluna* populations is caused by climate or genetics. Consequently, more work is needed to disentangle land-use regime, climate, and genetics as drivers of *Calluna* ecology.



Figure 5: Flowering *Calluna* at Lygra, Alver, Norway in August 2017. *Calluna* is a long-lived dwarf-shrub which produces a high number of flowers annually. Each flower produces up to 50 seeds (Legg et al. 1992, Birkeli et al. 2021), providing a large contribution to the local seed bank. Seeds can survive for decades in the soil bank and germinate when the conditions are right. Germination of *Calluna* seeds in coastal heathlands is triggered by smoke (Måren and Vandvik 2009), a trait not found in populations outside of the anthropogenic fire regime (Vandvik et al. 2014). Photo: Siri V. Haugum.

The role of coastal heathlands today

Despite the once widespread distribution of coastal heathlands, this landscape type is currently red-listed throughout its distributional area (Janssen et al. 2016, Hovstad et al. 2018). Three factors have been important for the decline of coastal heathland

distribution. First, coastal heathlands are located where people settled along the coast and where people still live today. Thus, the coastal heathland landscape is present where human pressures are high. Cities, roads, industry, afforestation, and intensive farmland along the coast is often constructed on former heathlands. Second, land-use changes also indirectly affect the remaining heathlands negatively. For example, industry and intensive agriculture produce nitrogen pollution that reach heathlands through atmospheric deposition and run-off. Heathland vegetation is adapted to poor soils and have low critical load for nitrogen (Bobbink et al. 2003). Consequently, several heathland species are prone to being out-competed by other plant species adapted to greater nitrogen availability (Aarrestad 2009). In addition, *Calluna* shows higher susceptibility to drought stress when nitrogen loads increase (Meyer-Grünefeldt et al. 2015b). Third, abandonment of land-use management results in degraded heathlands and unmanaged secondary succession where species turnover drastically changes ecosystem functioning. Eventually, heathlands become reforested (Figure 4), either by native species, such as *Betula pubescens* and *Sorbus aucuparia*, or alien species, such as *Picea sitchensis* and *Pinus mugo* (Saure et al. 2013).

Coastal heathlands are valuable habitats for wildlife, despite being anthropogenic ecosystems. Before humans colonised Europe, open lowland ecosystems were abundant across the continent (Svenning and Sandel 2013). Megafauna herbivores, most of which no longer exist, created treeless grasslands, and plants and animals became adapted to these landscapes (Gill 2014). Some of these species found new habitats in the coastal heathlands when the naturally open landscapes disappeared. When the semi-natural open lowlands of Europe became increasingly altered by urban development and intensified agriculture over the last centuries, heathlands grew in importance as a refuge for species dependent on the open lowlands. Examples of such species are the Eurasian eagle-owl (*Bubo bubo*), marsh gentian (*Gentiana pneumonanthe*), grey scalloped bar (*Dyscia fagaria*), and orange waxcap mushroom (*Hygrocybe aurantiosplendens*). These species are now red-listed through most or all of their range, mainly because of loss of open lowland habitat, in particular heathlands (Henriksen et al. 2015).

In addition to the characteristic biodiversity and ecological values found in coastal heathlands, these ecosystems store large soil carbon pools. Studies quantifying soil carbon storage in coastal heathlands report stocks of 12-20 kgm⁻² carbon in the upper 20 cm of the soil (Bartlett et al. 2020, Friggens et al. 2020). The relatively cold and wet oceanic climate of coastal heathlands keep decomposition rates low, while a high abundance of root-associated fungi further limits decomposition (Averill et al. 2014). However, we know little about how land-use change impacts heathland carbon storage and the overall ecosystem carbon balance. Consequently, there is a knowledge gap on how the landscape should be managed in the future to conserve soil carbon storage, increase carbon sequestration, and help mitigate climate change.

Coastal heathlands in a changing climate

Before 2010, drought-induced diebacks of *Calluna* are described from the British Isles (Watson et al. 1966, Hancock 2008), the Netherlands (Britton et al. 2001), and at least once from Norway (Printz 1933), in addition to several diebacks caused by herbivorous heather beetles (*Lochmaea suturalis*) (Ladekarl et al. 2001, Pakeman et al. 2004). These diebacks are an important driver behind Arctic browning (Pakeman et al. 2004, Myers-Smith et al. 2020). Recently, diebacks of *Calluna* have occurred on the Norwegian coast with higher frequency and over a much greater spatial extent than previously observed (Bjerke et al. 2017, Parmentier et al. 2017, Treharne et al. 2020). These *Calluna* diebacks have been explained by a combination of low temperatures and dry weather in the weeks prior to the diebacks (Bjerke et al. 2017). In winter, soil freezing immobilizes soil water, putting evergreen species at risk of drying out. Evergreen species in cold and dry climates have strategies for limiting moisture loss, or they are protected from freezing by the insulating capabilities of snow through winter, such as continental populations of *Calluna* and *Vaccinium vitis-idaea*. The mild winter climate and high winter rainfall of coastal Norway means that winter droughts have been rare historically (Hanssen-Bauer et al. 2009), so plant populations along the coast are likely to be vulnerable should a drought occur during winter. For example, a large drought event in the winter of 2014 caused massive drought damage

and diebacks across Norwegian coastal landscapes (Figure 6), resulting in regional collapses in coastal heathland productivity (Parmentier et al. 2018). Additionally, the increased flammability of drought-damaged *Calluna* dramatically increases the risk of wildfire (Davies and Legg 2011, Log et al. 2017). The 2014 drought was followed by several wildfires in the subsequent weeks, threatening the lives of people and livestock, and destroying buildings and infrastructure (Log et al. 2017; Figure 7).



Figure 6: Dieback in *Calluna vulgaris* in Torsoya, Vega, Norway, approximately five months after the 2014 drought event. Large areas along the Norwegian coast had similar diebacks after the same drought event, especially at Helgelandskysten. Photo: Pål Thorvaldsen, published with permission.

Ecosystem resistance and resilience

How well an ecosystem tolerates a disturbance depends on the resistance and the resilience the ecosystem has to the disturbance (Box 1; Figure 8). In general, the ecological literature often uses the term *resistance* to describe the ability of an ecosystem to remain unchanged during and after subjection to the disturbance, and *resilience* to describe how well the ecosystem recovers after disturbance (Box 1;

Figure 8). If an ecosystem has high resistance and/or high resilience, it retains the ability to remain and perform ecosystem functions in a long-term perspective in the presence of disturbances.



Figure 7: Wildfire in Flatanger, 27th January 2014, during the 2014 drought event. The fire spread effectively in the recently drought-damaged heathland. Photo: Magne Ove Risskov/Flatangernytt, published with permission.

In this thesis, I refer to resistance and resilience by the commonly applied ecological definitions, yet multiple definitions exist (see Box 1). Specifically, I term the observation of no drought-induced changes as high resistance (Figure 8). Depending on context, I apply this definition to plant communities (**paper I**), carbon fluxes (**paper II**), and the survival and growth of the key-stone species *Calluna* (**paper I**). In **paper III**, we define resilience as the ability of plant communities and *Calluna* to recover to pre-drought condition and functioning, either without intervention or after burning (Figure 8). The work presented in this thesis is a part of the LandPress project (Box 2).

Box 1: Resistance and resilience in ecology

Ecological **resistance** is an ecosystem's ability to withstand a disturbance without changing or losing ecological functioning.

The concept of **resilience** in ecology was first introduced by Holling (1996) to describe non-linear changes in ecological systems. Holling defined two types of resilience: *Ecological resilience* - the ability of an ecosystem to absorb disturbance without changing its state, and

Engineering resilience - the ability of an ecosystem to return to its pre-disturbance state after being affected by the disturbance. This definition often includes a temporal aspect, where a short return time equals high resilience (Figure B1).

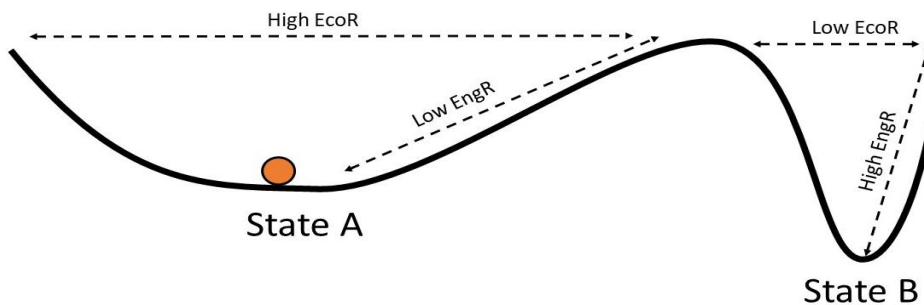


Figure B1: illustration of ecological resilience (EcoR) and Engineering resilience (EngR). The “ball and topography” model is often used to illustrate resilience. Here, the ball represents the ecosystem, valleys represent separate states of the ecosystem, and the topography represents different features of resilience when the ball is ‘pushed’ by a disturbance. The ecosystem can transition to a different stable state if ‘pushed’ past the threshold by a disturbance.

Holling’s *engineering resilience* has frequently been used to define the term resilience in later ecological literature (Westman 1978, Webster et al. 1983), whilst Holling’s *ecological*

Climate projections and extreme weather events

Extreme weather events similar to those that preceded the 2014 drought and *Calluna* die-back incidents are projected to increase in frequency in the future. Climate forecast models agree that the climate of the north European west coast is becoming increasingly warmer and wetter as a result of anthropogenic climate change (Hanssen-Bauer et al. 2009). In fact, the west coast of Norway already saw an increase in precipitation of 1.5-1.8% and an increase in temperature of 0.06-0.11 °C per decade between 1900 and 2014, with the largest changes happening in later decades and in spring and autumn (Hanssen-Bauer et al. 2009).

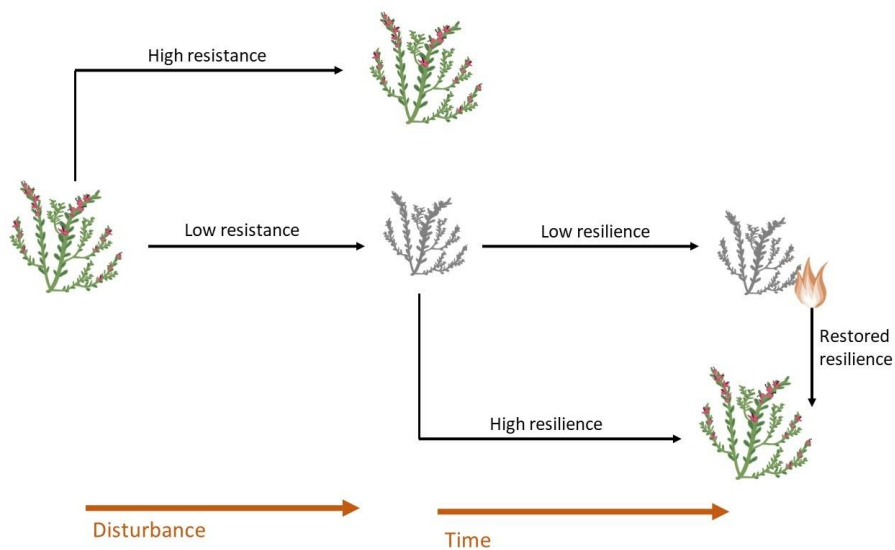


figure 8: Schematic overview of drought resistance and resilience in semi-natural coastal heathlands. The resistance of an ecosystem is its ability to stay unchanged when subjected to a disturbance. The resilience of an ecosystem is its ability to recover to the pre-disturbance state. Restoration practices, including burning, can be a tool to restore ecosystem functioning and resilience.

The regional future projection for temperature is an increase throughout the year, but with the largest warming from July to February, while almost all increase in precipitation is projected to take place between September and May. Despite the increase in precipitation, increasing climatic variability will lead both to more heavy rainfall events and to an increase of consecutive dry days (Hanssen-Bauer et al. 2009, Gutiérrez et al. 2021). This makes droughts more likely to occur, especially as the rainfall variability is accompanied by increased temperatures (IPCC 2021). These increasing amplitudes in weather result directly from increasing energy in the changing climate system, and the anthropogenic climate change driving these shifts is happening on temporal scales much shorter than those that plants can adapt to. A knowledge of the thresholds of disturbances that the system can withstand and how to restore the landscape after a major disturbance is important for mitigating the consequences of climate change in coastal heathlands.

Coastal heathlands are shaped and managed by people, and the key to preserving coastal heathlands and their ecosystem functions and services is to understand how they should be managed in a future with land-use changes and more extremes in climate. For the Norwegian heathlands, intensified droughts are of particular interest because drought is a rare disturbance historically but may become more frequent in the future, and because the vegetation has already shown severe diebacks in response to recent extreme drought incidents.

Box 2: The LandPress project

This PhD-thesis is part of the research project *Land use management to ensure ecosystem service delivery under new societal and environmental pressures in heathlands* (LandPress), funded by the Research Council of Norway over the MILJØFORSK programme (project number 255090) from 2016 to 2020.

LandPress is an interdisciplinary project focusing on the consequences of abandonment of traditional land-use practices such as grazing and prescribed burning, and how this interacts with climate change to cause significant ecological and societal changes. Marginalization and abandonment of land strongly affects ecosystems, causing large-scale successional changes and loss of habitats and ecosystem functions and services. These changes have negative societal impacts. Biomass build-up in successional landscapes result in increased risk of wildfires and associated societal costs related to fire control, mitigation of landscape fires, compensation for economic losses, and loss of safety. The role of land-use in ecosystem service provisioning may be especially relevant under future climate, where extreme climatic events are predicted to increase in frequency.

LandPress makes use of a rare opportunity, a 'natural experiment' created by extreme drought in the winter of 2014 that caused massive heather dieback, followed by large and costly landscape wildfires along the Norwegian coast. The project combines observational data on ecosystem responses and resilience after the 2014 drought event with field experiments to study impacts of drought across successional phases and bioclimatic gradients. We participate in the International Drought Experiment to embed our results and data in a larger international context.

LandPress interlaces five work packages, exploring the impact of land-use change in combination with extreme climatic events in terms of vegetation change, ecosystem resilience, ecosystem service provisioning, sustainability, and evidence-based management and fire-risk prevention. LandPress is a collaboration between The University of Bergen, Møreforskning, Norwegian Institute of Bioeconomy Research, Statistics Norway, Ohio State University and University of Copenhagen. The project has had an advisory board representing a broad set of stakeholders, including, policy makers, industry, regional and national management authorities.

Main objectives

The main objectives of this thesis are to:

i) quantify ecosystem responses to experimental drought in northern coastal heathlands,

and

ii) test how resilient these heathlands are after a major natural drought event, with and without fire,

as well as to

iii) contribute to the general understanding of ecological responses to increased frequency, duration, and intensity of drought in a precipitation-rich ecosystem, and how these responses interact with land-use.

Specifically, I ask the following research questions:

- a. Does heathland resistance to intensified drought vary over post-fire successional phases?
- b. Are coastal heathlands at the edge of their northern distribution range less resistant to intensified drought?
- c. Are northern coastal heathlands resilient to drought, and can this resilience be managed by fire?

Hypotheses and detailed research questions

Paper I – Coastal heathland vegetation responses to experimental drought

In paper I, we hypothesised that the coastal heathland plant community will be less resistant to intensified drought in H1) the northern region which is on the colder-climate brim of the coastal heathland distribution, and H2) early successional phases where plants have more acquisitive traits and shorter life cycles. In addition, we hypothesised that H3) *Calluna* growth would be most susceptible to drought in the young successional phase because of the relatively faster growth shortly after the fire, and especially in the north where all new plants originate from seedlings, increasing the shoot:root ratio relative to the vegetative resprouting observed further south (Nilsen et al. 2005, Velle and Vandvik 2014). Specifically, we expected to observe changes in plant community composition and reduced primary production as symptoms of low drought resistance.

Paper II – Impacts of experimental drought on carbon dynamics in coastal heathlands

In paper II, we focus on the two explicit research questions R1) How does prescribed burning management affect heathland carbon dynamics and storage? and R2) Does post-fire vegetation succession affect the resistance of heathland carbon balance to drought? Vegetation accumulation due to abandonment of land-use is often assumed to be a net sink of atmospheric carbon. Although vegetation accumulation increases the aboveground carbon pools, we expect the amplitude of both aboveground and belowground carbon fluxes to be higher with increasing post-fire succession, increasing the chances of old successional phases of becoming temporary net sources of atmospheric carbon.

Paper III – Recovery after severe drought in coastal heathlands with and without fire

In paper III, we hypothesised that i) heathland resistance to drought would be governed by both regional and microsite climate and would be higher in response to more extreme droughts and in less exposed microsities, ii) recovery in unburned plots

would be slow and affected by the extent of drought-damage, and iii) fire would effectively reset drought-damaged heathland, meaning that the rate of post-fire recovery depends on both climate and biotic habitat characteristics (Figure 9). Generally, we expected recovery to be slower towards the north because of lower temperatures and shorter growing season, but also because *Calluna* shrubs lack vegetative sprouting north of 63°N (Nilsen et al. 2005, Velle and Vandvik 2014). Also, we discussed how poor pre-conditions resulted in more severe damage.

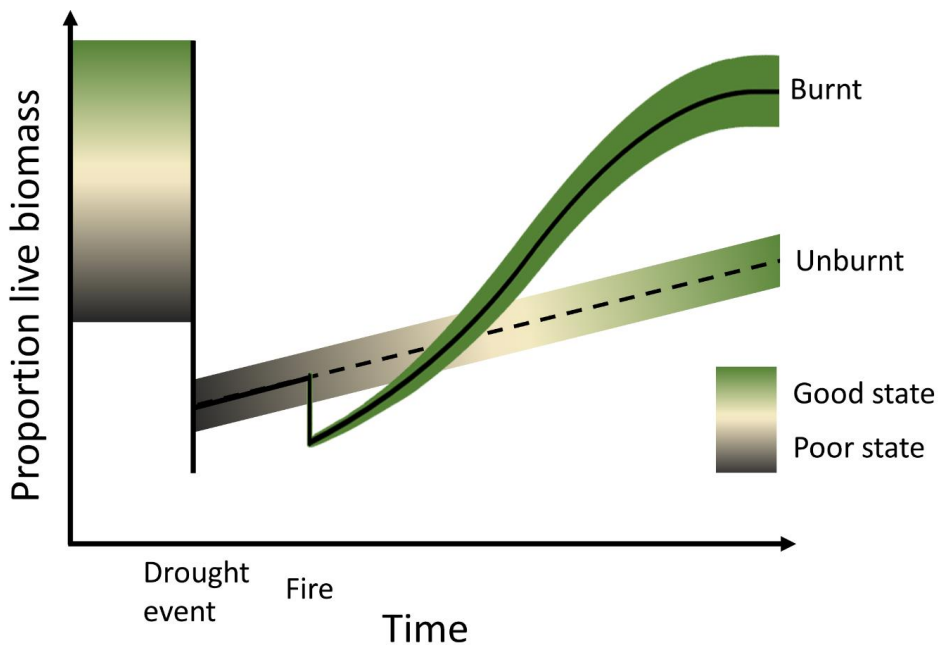


Figure 9: Conceptual diagram on recovery trajectories in the drought resilience experiment. The diagram shows how we predict the ecological state before the drought event to be closely correlated with the proportion of live biomass, and how we expect fire to immediately restore good ecological state. Heath in poor ecological state is likely to improve over time, but the uncertainty is high. Grey colours indicate poor ecological state and green colours indicate good ecological state.

Paper IV – Documented data

The last chapter in this thesis is a data descriptor outlining the motivation and methods for data collection, as well as providing an overview of the datasets produced as part of my PhD work. Although data documentation is still an unusual part of a doctoral thesis, it is a fundamental part of open and reproducible science,

supporting a growing expectation from the scientific community, funding agencies, and the society at large that research follows the FAIR principles (Findable, Accessible, Interoperable, Reproducible) (Wilkinson et al. 2016). Data papers are thus increasingly being published as stand-alone products or alongside standard research papers, and scientific journals are increasingly publishing data descriptors. My research was based on two large field experiments, where a large amount of data was collected. Publishing the data paper for the drought resistance project as part of the thesis allows me to document the data documentation process that ran parallel to data planning, collection, and validation. To enable datasets to be combined, all datasets followed the same rules for site, plot, and subplot identification, which I document in the paper.

Study sites and experimental designs

The overall objective of this thesis is to quantify the resistance and resilience of northern coastal heathlands to drought. In order to do so, we established two distinct in situ experiments. First, the *drought resistance experiment* experimentally manipulated a realistic increase in the frequency, duration, and intensity of drought periods for almost four years, allowing us to quantify the key drivers and responses of coastal heathlands to increased drought across three post-fire successional vegetation phases. Second, the *drought resilience experiment* made use of a naturally climatic gradient along the western coast of Norway to investigate how best to manage coastal heathlands following severe naturally-occurring drought spells.

Study sites and study habitats

The two experiments are located along the Norwegian coast, between 60 and 66 degrees north (Figure 10a). The climate is oceanic, with high precipitation (>1100 mm yr⁻¹; Table 1) and relatively low annual amplitude in temperature. Summers are cool, with a mean temperature of 12-15°C in July, whilst winters are mild with a mean temperature of 2-4°C in January. The growing season is relatively long (~ 250 days) but the duration declines from south to north.

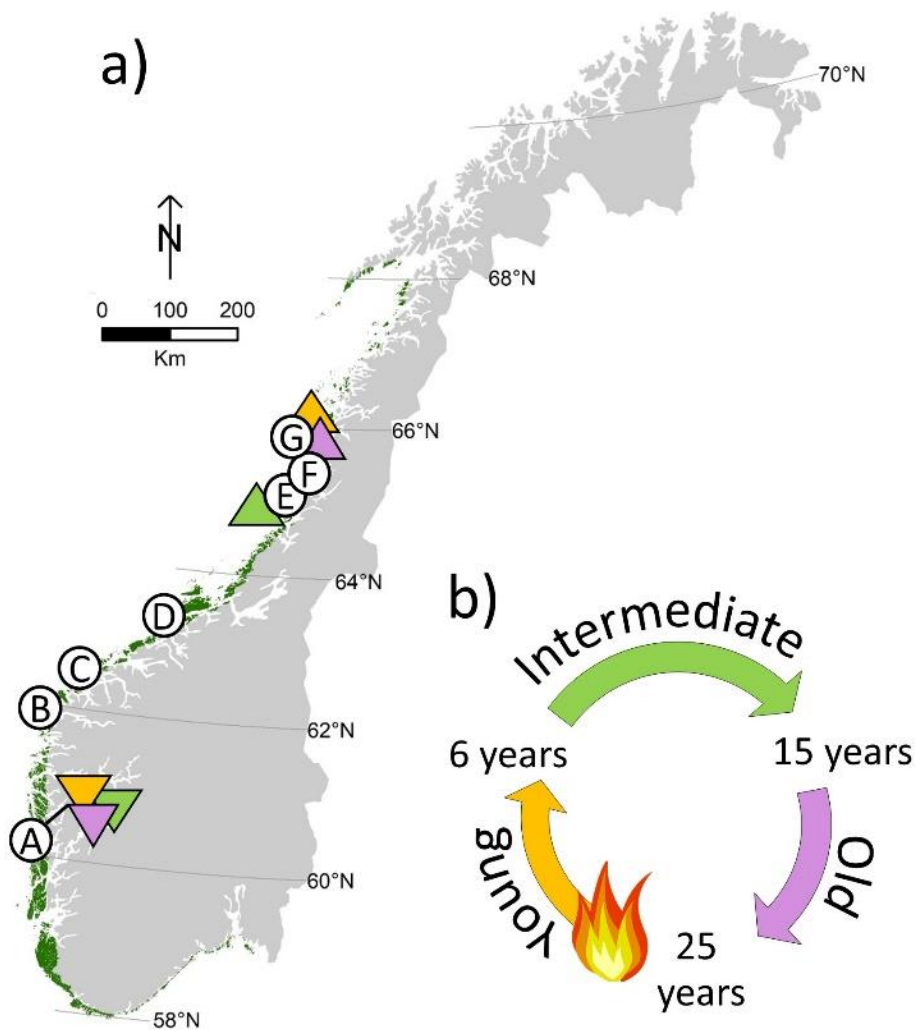


Figure 10 (next page): Study site locations for the drought resistance and resilience experiments. In panel a) dark green areas show the distribution of Atlantic heathlands in Norway with symbols representing sites belonging to the resistance or resilience experiments (coloured triangles and white circles, respectively). Note that the three resistance experiment sites located in southern Norway are spaced out for better readability. Upward pointing triangles show northern resistance sites and downward pointing triangles show southern resistance sites. In panels a) and b), symbol colours distinguish between heathland post-fire successional vegetation phases as described by Gimingham (1988). See Table 1 for site details.

Table 1: Climatic and ecological site information. Mean annual precipitation (MAP) is based on 1990-2019 data from the closest available climate station (North Young + Old, F: Vallsjø, North Intermediate: Liafoss (precipitation) and Nordøyen Fyr (temperature), South all phases: Myr (precipitation) and Fedje (temperature), A: Slåtterøy fyr, B: Ytterøyane, C: Svinøy fyr, D: Sandstad II, E: Rørvik Airport, G: Tjøtta). Length of growing season is defined as days with average temperature > 5°C (Moen 1998). Note that parts of sites A-G were experimentally burnt in 2017 to study post-fire successional development in drought-damaged heathlands (marked by *).

Region and successional phase	MAP (mm)	Latitude (°N)	Longitude (°E)	Growing season (days)	Burnt (year)	Island/ site name
North young	1254	65.83677	12.224506	197±4	2014	Store Buøya
North intermediate	1720	64.779	11.2193	205±9	2010	Haverøya
North old	1254	65.79602	12.22450	197±4	Before 1980	Skotsvær
South young	2020	60.70084	5.092566	258±11	2013	Lygra
South intermediate	2020	60.70084	5.092566	258±11	2004	Lygra
South old	2020	60.70084	5.092566	258±11	1996	Lygra
A	2080	60.220656	5.001823	264±5	Before 1990/ 2017*	Golta
B	2673	61.807887	4.922439	261±6	Before 1990/ 2017*	Novelandet
C	2560	62.359774	5.519645	266±5	Before 1990/ 2017*	Ytstevika
D	1136	63.304347	8.007803	214±20	Before 1990/ 2017*	Rossvolløya
E	1535	64.841056	10.848461	200±11	Before 1990/ 2017*	Bergsnova
F	1131	65.688430	12.067688	197±4	Before 1990/ 2017*	Torsøya
G	1309	65.796020	12.219299	207±4	Before 1990/ 2017*	Skotsvær

Experimental design - drought resistance (Papers I, II, and IV)

In order to identify thresholds for drought resistance in coastal heathland vegetation, and to investigate how threshold levels may depend on the ecological and/or climatic context (Knapp et al. 2015), we established a drought manipulation experiment in six heathland sites, representing each of the three main post-fire vegetation successional phases of coastal heathlands (young, intermediate and old post-fire succession), in southern Norway (approximately 60.5 °N) and in northern-Norway (approximately 65.8 °N) (Figure 9a). We constructed rain-out shelters following the International Drought Experiment (IDE) protocol by Drought-Net (<https://drought-net.colostate.edu>), which is based on the permanent rain-out shelter design from Yahdjian and Sala (2002) (Figure 11). Rain-out shelters increase the frequency, duration, and intensity of drought periods, and we specifically chose the IDE design as it yields efficient and reliable climate manipulations with relatively few side effects (Kreyling et al. 2017, Loik et al. 2019). As drought intensity is not expected to induce linear responses in vegetation (Hoover et al. 2018), we decided to establish two distinct levels of drought intensity at our sites, despite the IDE protocol using only one intensity level. We used the *precipitation trend* and *precipitation manipulation* tools created by Nathan Lemoine and available through <https://shiny-smith.biology.colostate.edu> to calculate the 1% quantile for 100 years of interpolated precipitation data, as recommended by the IDE protocol. Using Lemoine's tools, we calculated that a 45% roof cover was necessary to reduce precipitation to the 1% quantile. Nevertheless, we used a conservative approach to compensate for possible side effects by water entering the plots via strong winds and soil (we did not trench our plots), and thus we increased roof cover for our first drought level to 60%. For our second drought level, we chose to include an extreme drought treatment with 90% roof cover. The rainout shelters are made of a wooden frame with PVC lamellas (Figure 11). Each roof is 3x3 m, covering a 2x2 m plot (the area where we collect data) surrounded by a 0.5 m buffer zone. We replicated each drought treatment, and an ambient control, three times in each site, resulting in 54 plots (3 treatments × 3 replicates × 6 sites). All plots were fenced to deter herbivores, and all ambient control

plots were fitted with a similar physical construction as the drought treatment plots, that is, wooden frames surrounding the plot but without roof lamellas.



Figure 11: Photo of a rainout shelter with 90% roof cover, representing the extreme drought treatment. The shelter shown in the photo is installed on an intermediate successional phase plot in the south. *Calluna* dominates the vegetation and appears brown in the photo which was taken in spring. Nevertheless, these *Calluna* stands still have green shoots supporting livestock through winter. A moderate (60% roof cover) drought treatment plot is visible to the far left in the background. Photo: Siri V. Haugum.

Our rain-out shelters were constructed in spring 2017 and they were maintained until summer 2021. We installed sensors to quantify both intended drought-induced changes in microclimate (rain intercepted and soil moisture reduction) as well as potential unwanted side-effects (e.g., increased soil temperature and ground surface temperatures, reduced photosynthetically active radiation) (Table 2).

Table 2: Sensors and spatial and temporal coverage of microclimatic recording in the drought resistance experiment.

Microclimatic parameter	Sensor	Spatial measurement frequency	Temporal measurement frequency	Comments
Air temperature on site	ECT, Decagon Devices, Pullman, WA USA	One shared for all three sites in the south, installed in the young phase. One shared for the young and old phase in the north, installed in the young phase. One in the intermediate phase in the north (n=3)	Every 20 th minute between June 2017 and October 2020	Installed 150 cm above ground.
Precipitation on site	ECRN-100, Decagon Devices, Pullman, WA USA	One per site (n=6)	Every 20 th minute between June 2017 and October 2020	
Soil moisture	EC-5, Decagon Devices, Pullman, WA USA	One at 15 cm depth in each plot, and one at 5 cm depth in one replicate of each drought level (including ambient control) in each site (n=54+18)	Every 20 th minute between June 2017 and October 2020	
Soil moisture	SM300, Delta-T Devices, Cambridge, UK	Within 20 cm from soil respiration collar in each plot (paper II)	Measured in relation to soil respiration measurements (paper II)	
Soil temperature	TinyTag TGP-4510, Gemini, West Sussex, UK	One in each plot in the south (n=27)	Every hour between October 2018 and October 2019	
Soil temperature	Digital thermometer, Biltema, Åsane, Norway	Within 20 cm from soil respiration collar in each plot (paper II)	Measured in relation to soil respiration measurements (paper II)	
Lower canopy temperature	TinyTag TGP-4510, Gemini, West Sussex, UK	One in each plot in the south (n=27)	Every hour between October 2018 and October 2019	Installed 10 cm above ground. Sheltered against direct sunshine by a white plastic cover
Precipitation intercept	EC-5, Decagon Devices,	One replicate of the moderate drought treatment and one	Every 20 th minute between June 2017 and October 2020	Installed in the end of a gutter that

	Pullman, WA USA	replicate of the extreme drought treatment in the southern intermediate site (n=2)		collect run off from the roof lamellas
PAR	QSO-S, Apogee Instruments, Logan, USA	One replicate of each drought level (including ambient control) in the southern intermediate site (n=3)	Every 20 th minute between October 2018 and October 2020	Installed 50 cm above ground in the plots

The plots in the drought resistance experiment were not protected from lateral influx of soil water or rain. Consequently, water could potentially have entered the plots in several ways, reducing the efficiency of our rain-out shelter approach. Therefore, I calculated the Standard Precipitation Evapotranspiration Index (SPEI) on monthly intervals (Beguería and Vicente-Serrano 2017) to assess the effectiveness of our experimental drought manipulation at each site. The SPEI estimates a water balance based on precipitation and temperature, using historical data for the site to estimate when the site experiences rare water balance conditions (Vicente-Serrano et al. 2013). $SPEI > 0$ is a positive water balance, while $SPEI < 0$ is a negative water balance. $SPEI < -1$ is often set as the threshold for a site-specific moderate drought, and $SPEI < -2$ is commonly used as the threshold for extreme drought (Somorowska 2016, Slette et al. 2019). To calculate SPEI for the moderate and extreme drought treatments, I used rainfall intercept data from two roofs located in the intermediate site in the south as an intercept proxy for all sites, quantified as intercepted % of rainfall, combined with site-specific rainfall and air temperature at all sites (Table 2). The measured rainfall intercept was lower than what the initial calculations had estimated the roof cover reductions would amount to ($32.1 \pm 10.3\%$ and $43.5 \pm 20.3\%$ for the 60% and 90% roof cover treatments, respectively). This is possibly an underestimation of interception, and can be caused by for example wind, evaporation, or flooding of the precipitation gauge. However, using SPEI calculations can be considered a conservative approach for assessing drought severity compared to using the roof cover (60% and 90%). Consequently, to investigate ecological drought as it is directly experienced by plants, I also measured soil moisture at 15 cm depth in all plots (Table 2; Box 3).

We recorded vegetation composition within a permanent 1x1 m subplot at peak growing season annually, that is, early to mid-August, by visually estimating the cover of each plant species present within the subplot (**Paper I**). Here, we also monitored new shoot growth on ten permanently marked *Calluna* plants in each plot annually. In the remaining three square metres of the plot, we measured a broad suite of processes directly relating to ecosystem function. For example, we quantified i) soil respiration rates throughout the entire year using a closed chamber system and an infrared gas analyser, ii) total plant and soil carbon stocks using biomass harvests and via the loss-on-ignition methodologies, iii) seasonal decomposition rates using two standardised tea types, and iv) annual biomass accumulation using new shoot and root growth as proxies (**Paper II** and **Paper IV**). Details of the data collection are described in their respective papers.

Table 3: Observed precipitation and temperature across study sites during the study period, and the 1961-1990 (Mean I) and 1991-2020 (Mean II) climate normals. Data are reported seasonally: JJA = summer (June-August), SON = autumn (September-November), DJF = winter (December-February)*, MAM = spring (March-May). Precipitation is reported as the accumulated precipitation in the month interval (Acc precip), and as the ratio of days with precipitation (days with precipitation/total days in period, Days of precip). *December data from the previous year. See Table 1 for names of the climate stations.

Sites	Season	Year	Acc precip (mm)	Days of precip	Max temp (°C)	Mean temp (°C)	Min temp (°C)	Growth degree days (0°C)	Growth degree days (5°C)
North Y+O	JJA	Mean I	NA	NA	NA	NA	NA	NA	NA
		Mean II	214.8	0.65	26.5	12.6	3.6	1144.5	689.7
		2017	290.7	0.67	23.8	12.8	3.6	1178.8	718.8
		2018	286.7	0.77	30.5	12.5	3.1	1154.9	694.9
		2019	193.9	0.58	31.7	12.9	3.1	1191.3	731.3
	SON	Mean I	NA	NA	NA	NA	NA	NA	NA
		Mean II	381.6	0.73	19.9	7.0	-6.3	646.4	270.5
		2017	373.4	0.67	19.4	7.6	-7.3	712.9	322
		2018	504.8	0.79	21.9	7.9	-4.8	721.8	318.8
		2019	279.1	0.58	20.8	5.2	-10.1	506.8	169.6
	DJF	Mean I	NA	NA	NA	NA	NA	NA	NA
		Mean II	377.7	0.76	9.7	1.0	-12.7	188.5	15.8
		2017	485.8*	0.84	9.4	2.6	-11.4	279.5	28.8
		2018	188.4	0.52	9.2	-0.2	-12.6	106.9	4.8
		2019	312.2	0.69	10.6	0.9	-11.2	186.3	16.8
	MAM	Mean I	NA	NA	NA	NA	NA	NA	NA

		Mean II	254.6	0.69	20.2	4.6	-9.0	432.2	124.2
		2017	245.7	0.59	16.1	3.8	-9.9	366.0	63
		2018	148.3	0.57	25	4.2	-12.7	459.0	184.9
		2019	161.9	0.54	22.9	4.8	-12.2	471.5	163.8
North I	JJA	Mean I	407.3	0.67	NA	NA	NA	NA	NA
		Mean II	404.6	0.65	23.6	12.5	5.2	1020.1	616.4
		2017	594.7	0.70	NA	12.8	NA	1177.6	795
		2018	491.1	0.65	NA	12.3	NA	1136.4	676.4
		2019	373.8	0.58	26.8	12.8	6.1	1180.9	720.9
	SON	Mean I	648.5	0.75	16.2	7.0	-3.0	647.5	253.1
		Mean II	620.0	0.65	17.6	7.9	-2.1	719.8	313.2
		2017	553.4	0.59	NA	9.0	NA	819.0	393.7
		2018	801	0.66	21.2*	7.7*	-5.7*	763.7	355.3
		2019	579	0.52	17.5	6.7	-3.9	613.8	228.1
	DJF	Mean I	534.6	0.65	8.5	0.9	-9.8	179.4	13.3
		Mean II	603.5	0.65	9.0	2.2	-7.9	246.6	21.6
		2017	905.5	0.79	9.5	3.6	-5.9	345	44.3
		2018	366	0.52	NA	2.7	NA	226.4	10.4
		2019	637.6	0.66	NA	NA	NA	NA	NA
	MAM	Mean I	378.2	0.57	NA	NA	NA	NA	NA
		Mean II	442.2	0.60	17.7	4.9	-4.4	428.7	99.8
		2017	596.9	0.54	14.6	4.5	-3.1	425.2	75.6
		2018	306.1	0.41	NA	4.5	NA	446.7	140.8
		2019	365.1	0.47	19.4	5.1	-5.2	483.4	143.9
South	JJA	Mean I	435.9	0.69	NA	NA	NA	NA	NA
		Mean II	482.9	0.66	24.8	13.6	6.7	1165.5	735.9
		2017	687.2	0.76	22.1	13.4	7.5	1234.9	774.9
		2018	431.2	0.60	28.7	13.9	7.7	1133.8	723.8
		2019	651.2	0.67	30.4	14.1	7.2	1298	838
	SON	Mean I	847.4	0.84	NA	NA	NA	NA	NA
		Mean II	756.9	0.74	19.4	9.9	-0.1	871.1	442.0
		2017	687.2	0.80	20.8	10.2	-0.3	925.2	488.6
		2018	1138.9	0.75	22.3	9.8	-0.1	889.5	456.1
		2019	565.4	0.64	18.5	8.7	-0.8	795.5	364.6
	DJF	Mean I	586.4	0.67	NA	NA	NA	NA	NA
		Mean II	740.4	0.72	10.0	3.9	-3.6	341.7	54.9
		2017	820.6	0.78	11.0	5.2	-3.3	474.2	99.1
		2018	749.3	0.66	9.9	3.5	-1.5	327.2	34.7
		2019	521.1	0.72	9.4	4.7	-2.5	424.7	60.7
	MAM	Mean I	350.3	0.59	NA	NA	NA	NA	NA
		Mean II	436.2	0.60	19.7	6.4	1.9	588.6	184.9
		2017	489.4	0.67	22.7	6.8	-1.8	627.1	198.8
		2018	230	0.49	25.5	6.3	3.4	590.9	247
		2019	339.6	0.53	22.3	7.0	-1.2	641.2	236.1

Statistical approaches

Paper I: Plant community dynamics are explored using non-metric multidimensional scaling (Oksanen et al. 2019), and linear mixed effects models (Bates et al. 2015) with species richness, analysis of similarity (anosim, 999 permutations, Bray Curtis distance), and evenness (Hallett et al. 2020) at the plot level as response variables, and using experimental drought, successional phase, region, and their interactions as explanatory variables. All experimental treatment variables are crossed factors. Likewise, harvested biomass and *Calluna* growth are assessed parametrically with linear mixed-effects models with restricted maximum likelihood, following the same general dataset and predictor variable structure. The models are based on the data collected in the fourth year of the drought resistance experiment, except for the variables Bray Curtis Distance, *Calluna* height, and stem diameter, which are quantified as the difference between the first and the fourth year. To reduce model complexity, regions and successional phases are tested in separate models instead of full models. For *Calluna* models, plot was specified as a random factor.

Paper II: Repeated measures mixed effects models (Bates et al. 2015, Kuznetsova et al. 2017) are used to test for changes in vegetation and soil carbon stocks, soil respiration rates, and litter decomposition rates as responses to post-fire successional phase and experimental drought intensity, and the interaction between them, with plot as a random factor. Sampling time is specified as a fixed factor for litter decomposition, and month of measurement is specified as a fixed factor for soil respiration. Soil respiration fluxes are calculated with nonlinear regression to avoid underestimation of absolute flux rates (Pedersen 2020). Annual soil respiration per plot is modelled following a classic Arrhenius relationship, using plot and time averages of soil temperature. Rate of litter decomposition is calculated using Weibull distributions of litter mass loss (Cornwell and Weedon 2014), which allow litter decay rates to decrease over the course of decomposition.

Box 3: Effects and side effects of the rainout shelters on microclimate.

Annual precipitation during the study period (2016-2020) was between 77% and 98% of the annual mean for the 1981-2016 climate normal (Figure 12). A few natural droughts occurred during the study period, with SPEI values for the ambient treatments reaching $\text{SPEI} < -1$ several times and $\text{SPEI} < -2$ once or twice (Figure 13). Soil moisture data demonstrated that during periods with high rainfall, the difference between the ambient control and the moderate drought treatment was negligible, and there were only small differences between the ambient control and the extreme drought treatment. However, during drier periods, the difference in soil moisture between both drought treatments and the ambient control increased. The greatest difference in soil moisture between drought treatments and ambient controls coincided with the lowest soil moisture recorded in the ambient control plots (Figure 14). For most sites, this took place in summer 2018 where an extreme drought spell occurred throughout Norway (Buras et al. 2020). There were only small differences in photosynthetically active radiation (PAR) between the drought treatments, while the extreme drought treatment had slightly lower PAR in late summer and autumn (Figure 15). We found few indications of a greenhouse effect on temperature in the drought treatments. Temperature in the lower canopy (10 cm above ground) isolated between 12 am and 3 pm in summer (May-August) increased slightly in the extreme drought treatment in the intermediate successional phase, and in the moderate drought treatment in the old successional phase (Figure 16a). Soil temperature (2 cm belowground) measured between 12 am and 3 pm in May and June increased in the extreme drought treatment in the young successional phase, and in both the moderate and extreme drought treatment in the intermediate and old successional phases (Figure 16b). Note that there is a large variation in observed temperatures, and that the significant differences disappears when the observed period is extended to the whole growing season. Also note that temperature was only measured in the three sites in the south, and PAR was only measured in one replicate of each drought treatment and only in the intermediate phase in the south (Table 2).

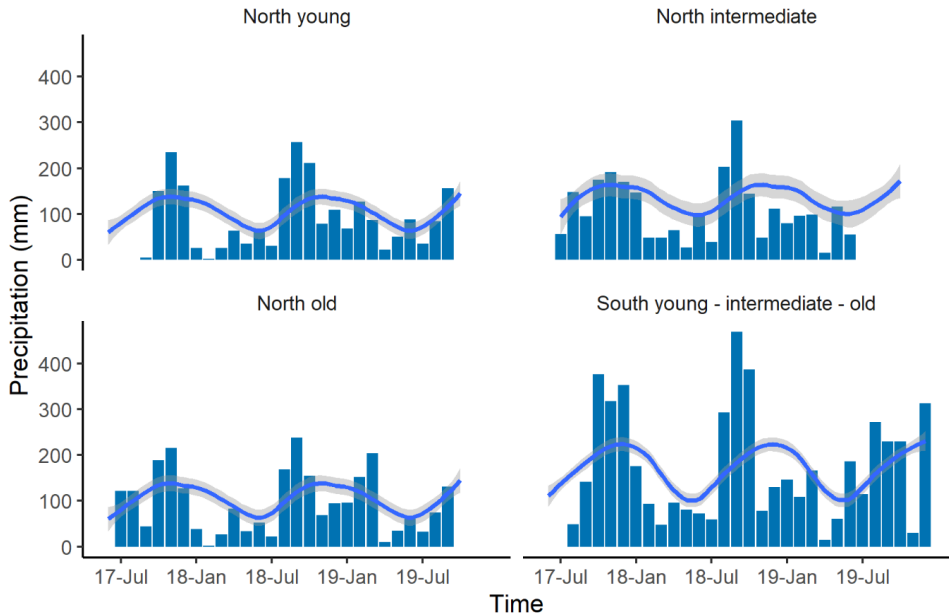
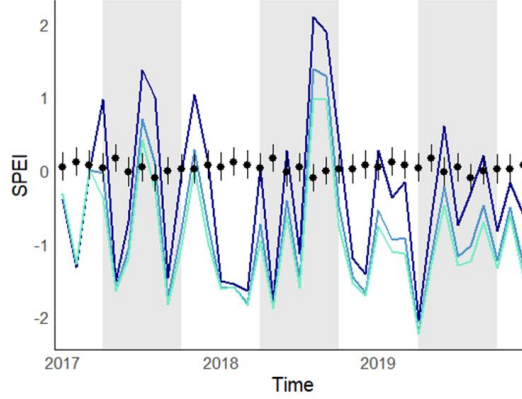


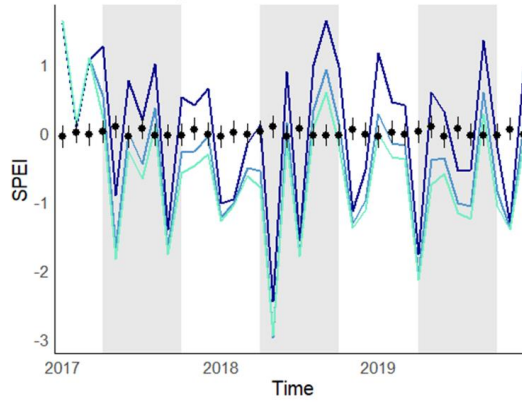
Figure 12: Precipitation in the drought resistance experiment sites during the study period. Measured on-site precipitation during the study period (bars), and daily mean precipitation from 1990 to 2019 using data from the closest available weather station (lines with 95% confidence interval). Note that the young and old phases in the north are located on separate islands approximately 5 km apart. They therefore receive very similar amounts of precipitation, and they share the same weather station for historical precipitation records. The three successional phases in the south are located only a few hundred metres apart on the same island, and hence they share both measured precipitation and the climate station for historical precipitation.

Figure 13 (next page): Standardised Precipitation Evapotranspiration Index for the drought resistance experiment across study sites and experimental drought treatments. Average Standardised Precipitation Evapotranspiration Index (SPEI) in the three drought treatments (dark blue = ambient; pale blue = moderate drought, 60% roof cover; turquoise = extreme drought, 90% roof cover) over the study period 2017–2019 compared to long-term monthly averages (black symbols \pm 1 standard error (SE)) from 1981–2019 in the south and 1991–2019 in the north.

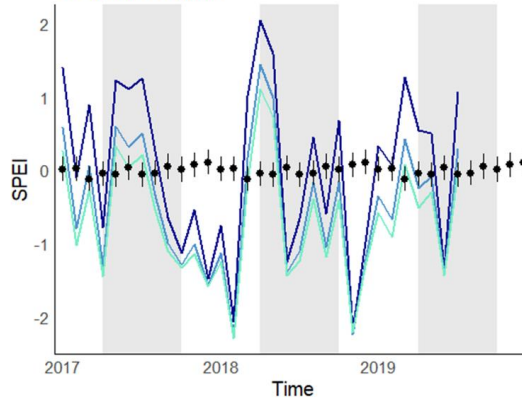
Northern region - young and old



Northern region - intermediate



Southern region



Drought intensity — Ambient — Moderate — Extreme

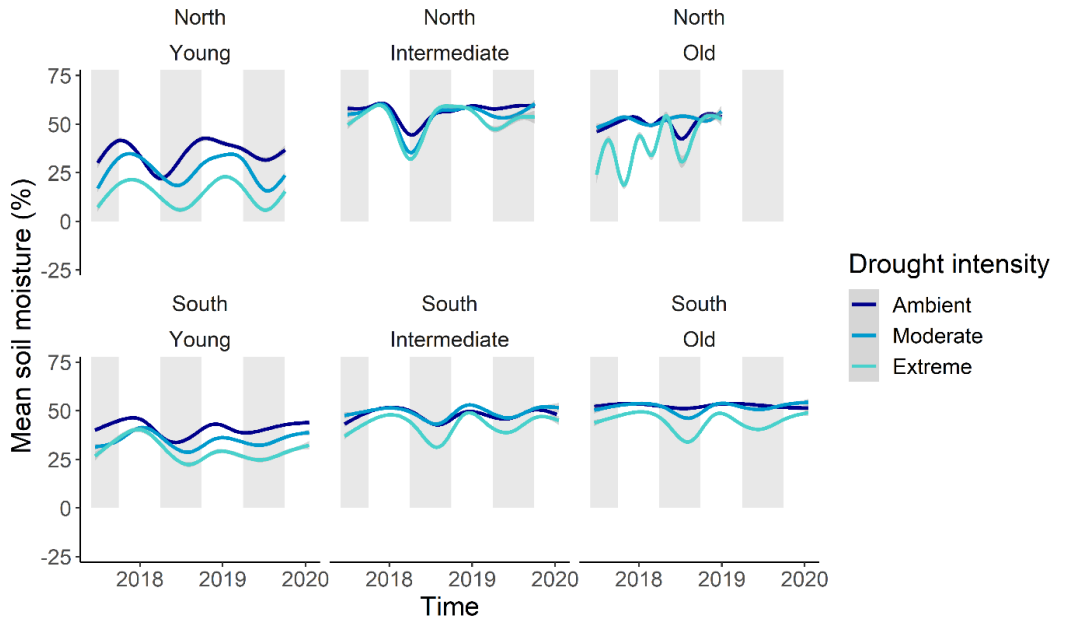


Figure 14: Mean soil moisture in the three drought treatments in each site across the study period. Soil moisture was recorded at 15 cm depth every 20th minute. Grey areas indicate the extent of the growing season (April–September). The extreme natural drought that hit much of Norway in 2018 (Buras et al. 2020) can be seen as a decline in ambient soil moisture.

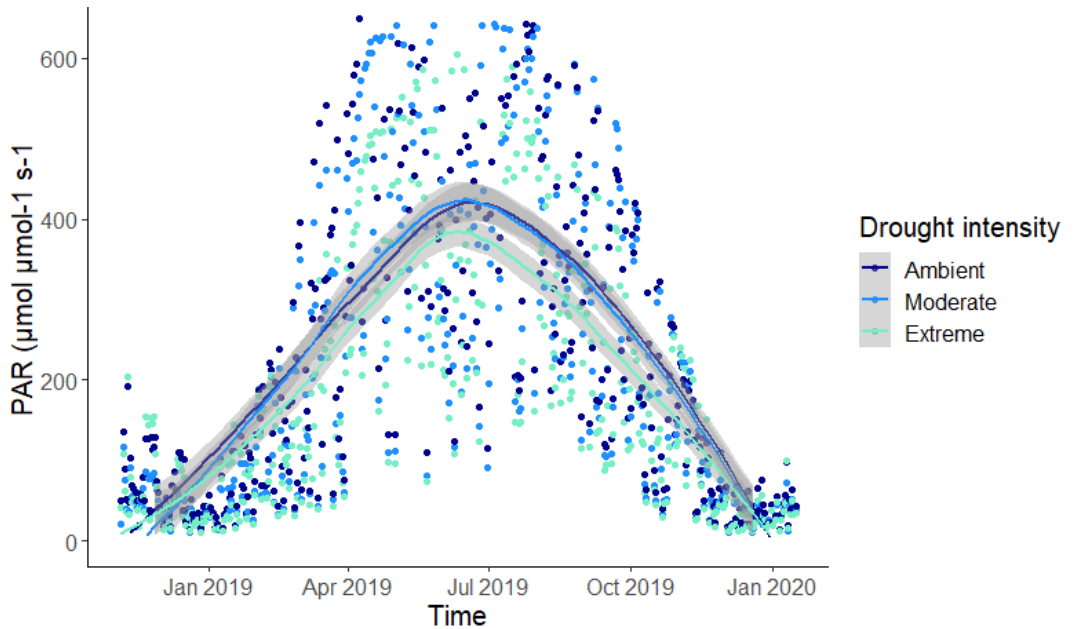
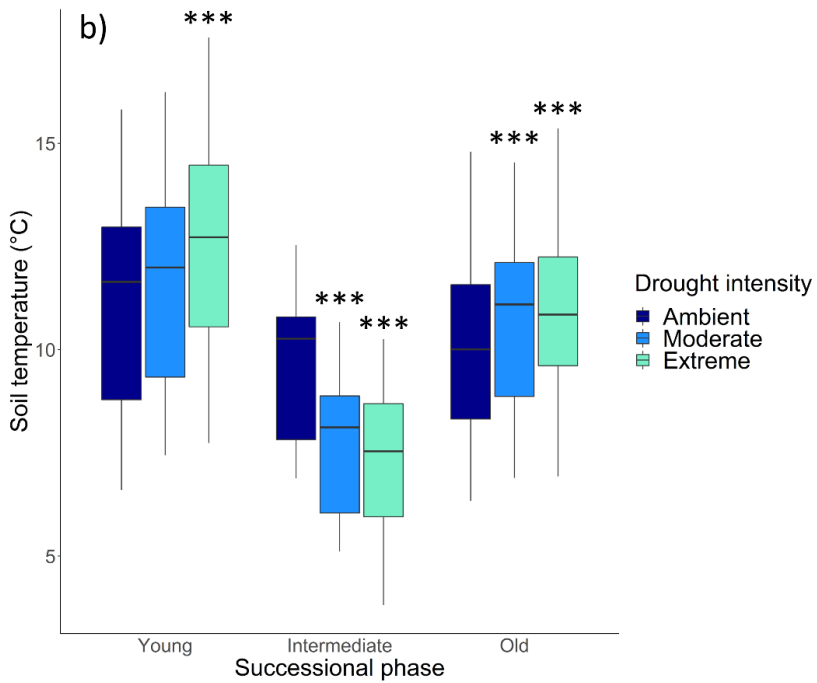
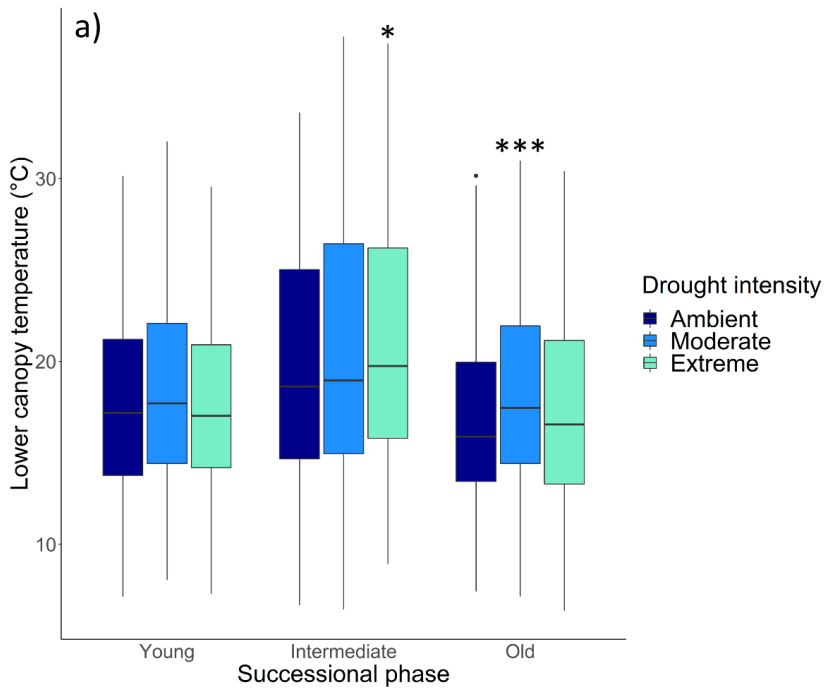


Figure 15 (previous page): Mean daily Photosynthetic Active Radiation (PAR). PAR was measured in three plots in the intermediate post-fire phase in the southern site from October 2018 to January 2020, with 95% confidence interval. The three plots were all facing directly south on the same slope, and represented one drought treatment level each. PAR values were filtered for values $> 10 \mu\text{mol}\mu\text{mol}^{-1}\text{s}^{-1}$ to exclude nighttime measurements.

Figure 16 (next page): Observed temperatures across successional phases and experimental drought treatments in the southern part of the drought resistance experiment. a) Lower canopy (10 cm above surface) temperature between 12 am and 3 pm in summer 2019 (May–August) measured hourly in all plots in the south ($n=27$). b) Soil temperature (5 cm depth) between 12 am and 3 pm in summer 2019 (May–June) measured hourly in all plots in the south ($n=27$). July and August are not included for soil moisture due to failure on several loggers, resulting in sparse and scattered data for the last part of summer. Asterisks show significant differences in mid-day summer temperature between a drought treatment level and the respective ambient control. Lower canopy temperature was 2.3°C higher in the ambient controls in the intermediate phase compared to the ambient controls in the young successional phase ($p<0.001$). Soil temperature was significantly lower ($p<0.001$) in the ambient controls in the intermediate successional phase (1.6°C difference) and in the successional old phase (1.3°C difference) compared to the young successional phase.



Experimental design - drought resilience (Paper III)

To investigate how resilient heathlands were after crossing their drought resistance threshold, we selected seven geographically distinct coastal heathlands containing substantial *Calluna* dieback (20-100% of *Calluna* cover) caused by the 2014 winter drought event. The sites were located along the Norwegian coast from 60.2°N to 65.8°N (Figure 10a). All sites had been managed with prescribed burning in the past but at the start of the study were in the mature (old) successional phase. All sites were extensively grazed by Old Norse sheep both prior to and during the experiment. We placed ten plots of 1x1 m in homogeneous terrain and vegetation cover in 2016 (in total 70 plots) and burned a continuous fire in a part of the site containing half of the plots (n=5) in each site in late winter or early spring of 2017 (Figure 17). We recorded vegetation composition within the permanent 1x1 m plot at peak growing season annually, that is, early to mid-August, from 2016 to 2019, similar to our drought resistance experiment.



Figure 17: Prescribed fire with an approximately 20 years return interval is one of the most important tools in traditional management of northern coastal heathlands.

Prescribed fire takes place on frozen or water saturated ground, leaving roots, seed banks and soil organic matter protected from flames and high temperatures, whilst most of the aboveground vegetation combusts. The photo shows prescribed burning on Smøla, site D in the heathland resilience experiment, on 8th March 2017. Photo: Siri V. Haugum.

Post-fire regeneration is well described for the study region (Nilsen et al. 2005, Velle and Vandvik 2014, Måren et al. 2018), and this literature allowed us to compare whether secondary succession in our burned plots followed the commonly observed trajectories despite the pre-fire drought event. Moreover, the unburned controls plots allowed us to monitor whether drought alters the successional pathway over the course of 3-6 years in later successional phases, and whether *Calluna* could regenerate from a dieback without the use of fire.

Statistical approaches

Paper III: The meteorological severity of the 2014 drought was explored by comparing relative humidity, temperature, and precipitation for January 2014 with a time series of 17 to 98 years of January data extracted from the closest available climate station. We calculated and compared the cumulative cover and proportions of the main functional groups across sites and times. For *Calluna* specifically, we did the same for vital, damaged, and dead stands. We used mixed effects models to test whether relative humidity in January 2014, soil depth, or aspect explained the proportion of dead *Calluna* in 2016, and the same approach was applied to test *Calluna* recovery after fire in response to time and latitude and *Calluna* seedlings in response to latitude. The trajectories of plant community assemblies through the study period are visualised by a principal components analysis.

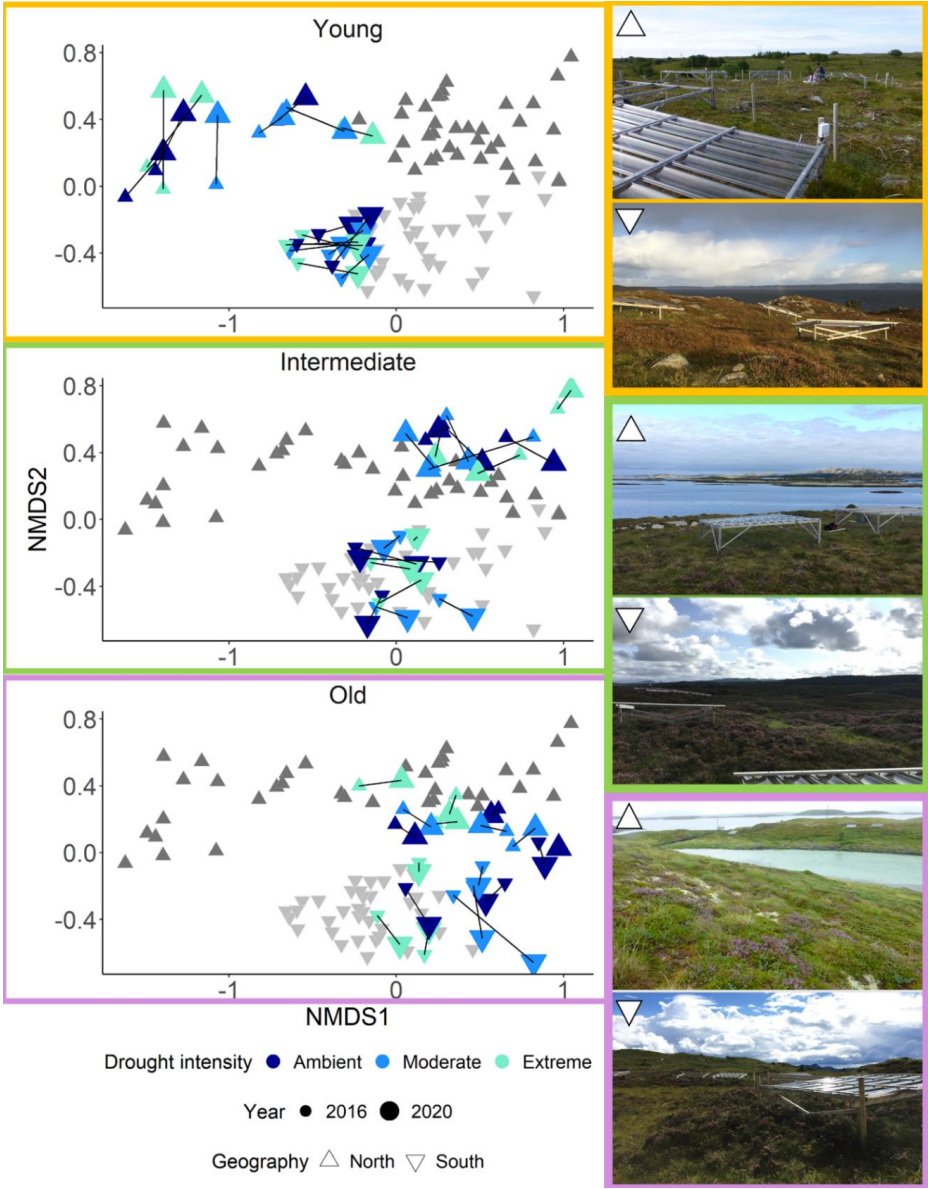
Summary of main findings and general discussion

In the following, I present and discuss the main findings from the drought resistance and resilience experiments in the light of existing literature. Please note that further details and discussion of results are presented in the individual papers. I end this section by discussing future implications for coastal heathland management and their associated ecosystem functions, based on the new knowledge that we gained from my PhD research.

Coastal heathland resistance to experimental drought

The six study sites in the drought resistance experiment were chosen to reflect plant communities typical of coastal heathlands in the respective post-fire successional phases and at their respective latitudes. **Paper I** shows that, overall, the plant community assemblages have high drought resistance as their successional and regional vegetation fingerprints remained throughout the four-year study period, irrespectively of drought treatments (Figure 18). Aboveground biomass accumulated with increasing time post-fire, and this accumulation was faster in the south than in the north (as seen in Velle and Vandvik (2014) and in Figure 19). However, similar to plant community composition, aboveground biomass also remained unaffected by the experimental drought treatments on the timescales of this experiment (Figure 19).

Figure 18 (next page): Non-metric multidimensional scaling of vegetation composition in the drought resistance experiment between 2016 and 2020. Years are distinguishable by the size of the symbols for the focal successional stage in each panel. Plots in the north are marked with upward-pointing triangles, and plots in the south are marked with downward-pointing triangles. The different shades of blue represent each drought treatment. All plots are shown in each of the three panels, but only plots belonging to the focal successional stage within each panel are highlighted in colour. Plots belonging to other successional stages are shown as grey shades (dark grey for the north and pale grey for the south) and they are included to ease the comparison between successional stages. Stress = 0.12. A photo of each site is included on the right-hand side. Yellow frames show the young successional stages, green frames show the intermediate successional stages, and purple frames show the old successional stages.



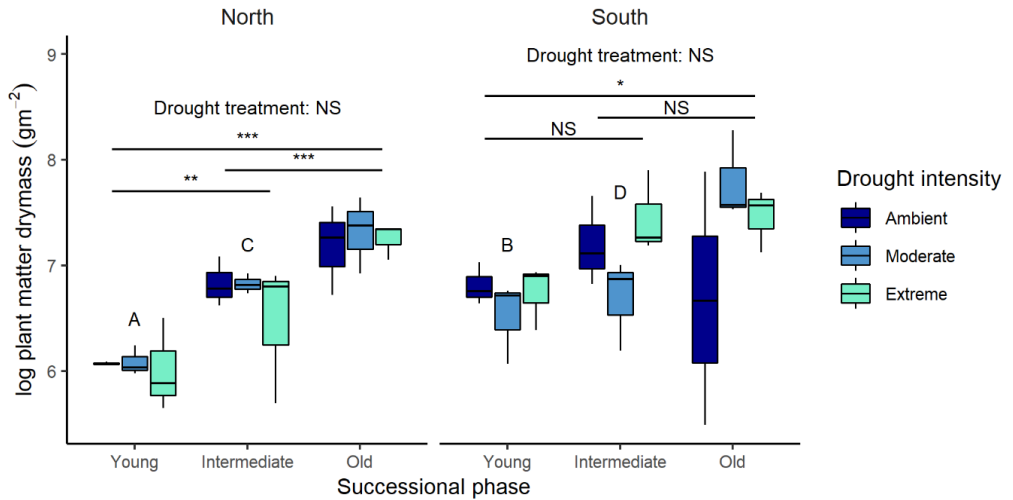


Figure 19: Aboveground biomass harvested in the drought resistance experiment in the third growing season after the onset of experimental drought. Three squares of 25x25 cm were harvested as one collated sample from each plot. Horizontal lines indicate differences between successional stages within regions (* significant at $p < .05$; ** significant at $p < .01$; *** significant at $p < .001$; NS non-significant). Significant differences are found between the two regions for the young (A:B) and intermediate (C:D) successional stages but not for the two old successional stages. There was no significant effect of experimental drought on harvested aboveground biomass.

Calluna increases in abundance over time and species richness as well as evenness decline in the two oldest successional stages relatively to the young successional stage (Table 2 in **Paper I**). The growth of the monitored *Calluna* stands exhibited a higher growth rate in the southern relative to the northern sites, as well as some difference between successional stages within regions, but there was no response to experimental drought except for increased annual shoot growth in the extreme drought treatment in the old successional stage in the north (Figure 5 in **Paper I**).

The lack of drought responses observed in plant community assemblies, primary production, and *Calluna* growth can lead to the conclusion that heathlands have high resistance to experimental drought. It is well established that arid ecosystems are more drought sensitive than mesic ecosystems (Huxman et al. 2004,

Peñuelas et al. 2004, Knapp et al. 2015), yet our finding is surprising, given the massive *Calluna* dieback following the natural winter drought in 2014 (Bjerke et al. 2017). However, in **Paper II**, where I quantify drought-effects on ecosystem carbon dynamics in the southern part of the drought resistance experiment, I find several lines of evidence that suggest heathlands might not be as resistant to experimental drought as the many non-significant responses in **Paper I** suggest. Specifically, I find that while both aboveground and belowground accumulation of biomass is determined by successional vegetation phases, belowground biomass accumulation in the old successional phase significantly increases in response to the extreme drought treatment (Figure 20). Additionally, I also find non-significant tendencies of experimental drought having opposite effects on soil respiration, specifically inducing a decline in the young and intermediate successional phases, and an increase in the old successional phase (Figure 4 in **Paper II**).

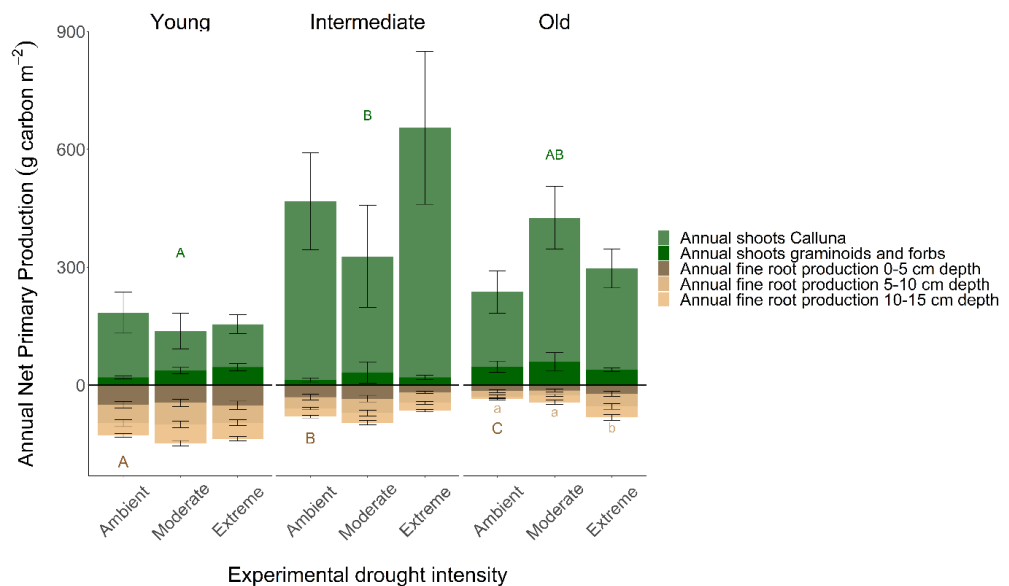


Figure 20: Annual net primary production across experimental drought treatment and post-fire successional phases. Aboveground biomass accumulation is estimated from harvested annual shoots of graminoids and forbs and counts of *Calluna* shoot tips. Belowground biomass accumulation is estimated from root production in root ingrowth cores.

Few climate change experiments combine multiple response parameters, which some would argue reduce their use as realistic proxies for future climate change (Rosenblatt and Schmitz 2014). However, Jentsch et al. (2011) is one of the noteworthy exceptions. They found no significant response of above- and belowground primary production to severe drought events in a five-year drought experiment in German grasslands. In contrast, soil biota activity, leaf traits, plant phenology, and plant-plant interactions all responded to the drought manipulation, with effect sizes large enough to cause changes in ecosystem function. The work by Jentsch et al. (2011) shows the importance of considering the spatial and temporal hierarchy and resolution of ecosystem responses when interpreting results from climate-change experiments. For example, Kröel-Dulay et al. (2015) found plant communities to be relatively resistant to experimental drought and warming across seven heathland sites in Europe. Nevertheless, they found that within individual sites, experimental drought reduced total plant cover, lowered species richness and induced changes in vegetation composition after 7 to 14 years. When only considering effect sizes from the first 2 to 5 years, these responses were either not significantly different from controls, or only marginally different. Together, these studies suggest that the seemingly high resistance of the plant community in our drought resistance experiment might not be indicative of longer, decadal time scales. This hypothesis is further strengthened by observations of short-term vegetation browning in the north in the third and fourth year of the drought resistance experiment. The browning, shown in Figure 21, emerged during summer, but was largely reversed in the autumn. The browning was not severe enough to significantly affect standing biomass or plant community assemblies, and the browning is therefore not reflected in our data. However, short-term browning might be early warnings of a temporally limited resistance to experimental drought on plant fitness. We plan to continue the study to uncover long-term impacts on vegetation from drought.

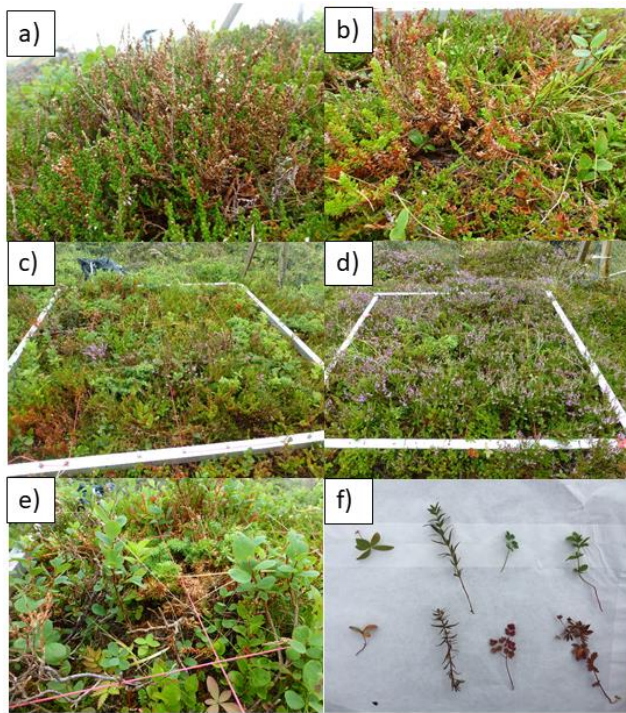


Figure 21: Observed temporary browning in the drought treatments of the resistance experiment in the north. a) partial browning of *Calluna vulgaris*, b) partial browning of *Empetrum nigrum*, c) plot with drought damage, d) plot without drought damage, e) partial browning of *Juniperus communis*, f) forbs from a plot without drought damage (upper row) and with drought damage (lower row), from left: *Lysimachia europaea*, *Galium boreale*, *Thalictrum alpinum*, *Potentilla erecta*. Photos: Liv Guri Velle and Siri V. Haugum.

The ecological and statistical reliability of the drought resistance experiment

Our drought manipulation experiment successfully prolonged and increased the severity of natural dry periods, resulting in increased drought frequency and intensity. The surprisingly few ecological responses to our experimental drought treatments can have multiple explanations, spanning from a high ecological resistance in the plant community, to study designs that do not successfully monitor the parameters of change, including too short a monitoring time. Thus, two important limitations of the drought resistance experiment should be discussed.

First, experimental drought offers more control over environmental conditions and can be performed at much shorter temporal and spatial scales than observational field studies. However, a manipulation experiment will rarely mimic the natural world perfectly. Whilst our drought resistance experiment successfully created only very small side-effects on radiation and temperature, we were not able to control

vapour pressure deficit, that is, the difference between the actual moisture content in air and the amount of moisture the air can hold when saturated. High vapour pressure deficit is characteristic of naturally occurring droughts and is a critical driver of plant moisture loss (Grossiord et al. 2020) as shown in **Paper III**. In most studies, including ours, experimental drought is created by reducing liquid water input to the system, thereby reducing available soil water for plants. If vapour pressure deficit is low during a period with reduced moisture input, we might overestimate the actual additional drought stress imposed by our treatments because the plants lose less water than they would during a natural drought. Our drought experiment mainly induced intensified drought in naturally dry periods, which reduces the potential mismatch between soil water input and vapour pressure deficit, which to some extent could counteract this experimental side-effect. Still, relative humidity or vapor pressure deficit is rarely included in drought experiments (Grossiord et al. 2020, Aguirre et al. 2021), including in our study. I would recommend future studies to include at least one of these parameters to reduce the possible experiment artifact bias in drought experiments.

Second, the drought experiment has relatively low replication as it contains only three replicates per treatment, succession, and region, combining to a total of 54 plots. This limits the power of the study, especially in detecting site- and stage-specific drought effects. Installing and running field-based experiments are notoriously cost and labour intensive. We opted for including two regions, three drought treatments, and three successional stages at the cost of fewer replicates. We exploited the relatively large experimental investment by measuring as many response variables as possible. In this way, we cover more of the spatial and temporal variation in northern coastal heathlands and gain a better understanding of hierarchical ecosystem responses to experimental drought. Moreover, the study design and our statistical approaches were tailored to compensate for the reduction in statistical power given the few replicates. Specifically, the gradient design itself, including the replication in two regions, adds to the ecological reliability of the experiment (Kreyling et al. 2018). Also, several of the response variables are causally linked, such as the well-replicated *Calluna* growth which drives less replicated

functional group biomass. These linkages provide several response variables reflecting the same underlying processes. Additionally, we ran the mixed effects models for plant community dynamics in **Paper I** as reduced models – in addition to the full models of the hypotheses testing – to assess whether reduced model complexity would allow more effects to attain significance.

Box 4: Common ways to report drought in ecological climate change experiments.

High natural rainfall variability complicates planning of exact rainfall manipulation experiments. Consequently, well-documented measurements of site climate and microclimate are important to enable comparison between experiments, regions and years (Slette et al. 2019). Some experimental drought studies report on-site rainfall and assume that the percentage roof cover equals percentage rainfall reduction on a 1:1 basis (Blum et al. 1989, Hannusch et al. 2020). While this may seem an intuitive approach to describe an experimental climate manipulation treatment, it provides little information about the context of the rainfall reduction, that is, the extent to which rainfall reduction and roof artifacts actually influenced microclimatic conditions *in situ*, how unusual the experimental rainfall reduction was in a historical perspective, or how much the ambient rainfall diverges from mean annual precipitation. In parallel with better and more affordable microsite climate sensors on the market, more studies report microclimate data (Gilgen and Buchmann 2009, Carlyle et al. 2011, Bütof et al. 2012), and quantify roof artifacts (Vogel et al. 2013, Phillips et al. 2018, Loik et al. 2019). Whilst these measurements increase our understanding of realised versus estimated drought manipulation effect, caution should be taken when interpreting microclimate variables with high spatial variability (Graham et al. 2012, le Roux et al. 2013), especially when the replication rate is low. More recently, it has also become increasingly common to report precipitation metrics such as Palmer Drought Severity Index (Palmer 1965) or Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2013) in order to provide a historical context for the rainfall reduction, thereby alleviating some of the shortcomings mentioned above. In this thesis, I report the

effect of the drought experiment as fixed roof cover, rainfall intercept from roofs, reduction in soil moisture, and estimates of SPEI. Replicating the drought resistance experiment across a combined post-fire succession and climate gradient, adding an extreme drought treatment level, measuring multiple ecological responses, and linking our findings to observations from a naturally-occurring drought event adds to a strong combined approach in understanding the effect of intensified drought in coastal heathlands.

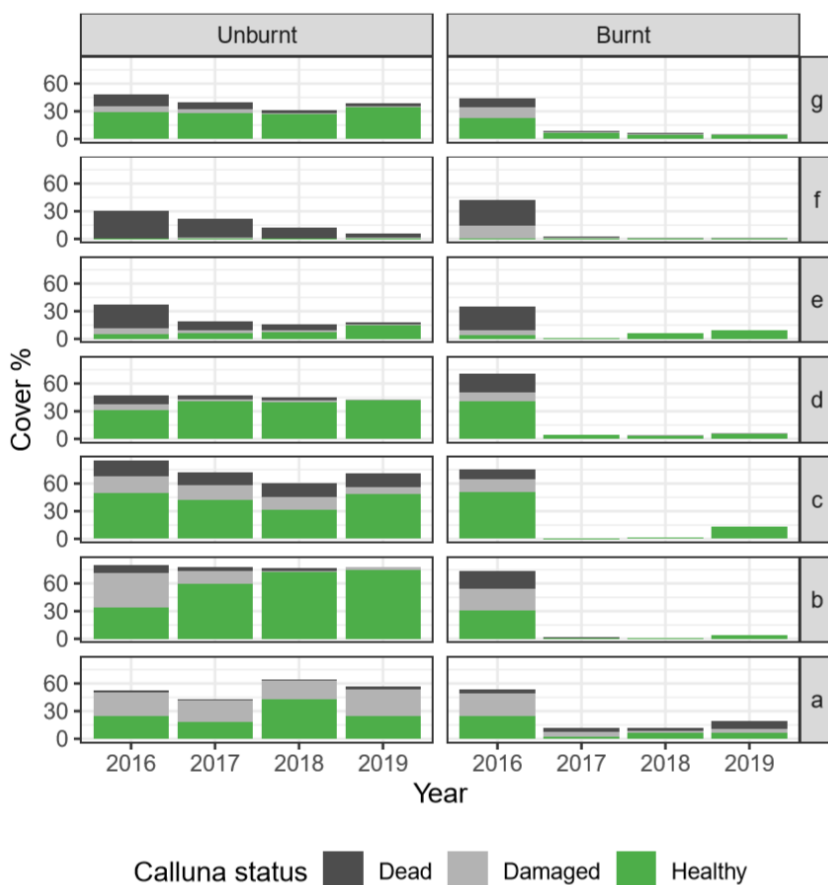
Drought resilience of northern coastal heathlands

The proportions of damaged and dead *Calluna* varied across sites, but overall, there was less vital *Calluna* in the northernmost sites. The unburnt plots in the drought resistance experiment followed two different trajectories (**Paper III**). In sites B, D, and E, the amount of drought-damaged plant tissue in *Calluna* declined during the study period, either because of recovery or replacement of damaged tissue (Figure 22). In the remaining sites, we observed little to no recovery during the study period. The seven study sites were selected in summer 2016, which was approximately two and a half years after the extreme drought event of winter 2014. Consequently, it is possible that at least some plants underwent a limited recovery in that first period after the drought but prior to our study began. Similarly, we cannot know whether heathlands that we perceived to be without substantial drought damage in 2016, and which we therefore excluded as suitable field sites because they looked healthy, were affected minimally by the drought event, or if they had already undergone some form of rapid recovery in the time before summer 2016. Nevertheless, we visited several potential field sites in each region before settling on the seven sites used in this study, and it is our clear impression that plant damage occurring in these sites is representative of each site's respective region.

The two trajectories of drought-damaged *Calluna* suggest the existence of a threshold where plants with damage below a certain extent will recover within a few years – see site B (Figure 22) as an example – whilst plants with damage that exceeds the threshold do not recover, such as site F (Figure 22). In our analyses, we

distinguished between *dead* and *damaged* plant tissue, in other words whether the whole plant was dead or if the stand had only partial browning occurring. In general, we saw more dead tissue in northern Norway, and relatively more damaged tissue in southern Norway in 2016. During the study period, it seemed as if the dead tissue disappeared, resulting in reduced *Calluna* cover, whilst the damaged tissue recovered or was replaced by new, live tissue. This was perhaps a similar effect as we observed in the drought resistance experiment, where partial browning emerged in several plots in the north during summer, but the browning was no longer visible when we returned to the study plots in autumn. Our findings in the drought resilience experiment (**Paper III**) have many parallels to Hancock (2008) who observed severe *Calluna* dieback following a winter drought with exceptional low air humidity, with minimal *Calluna* recovery after three years, similar to our observations in site F. In our study, we observed more dead *Calluna* stands in the northernmost sites, which overlaps with the most drought exposed weather conditions (Figure 4 in **Paper III**). This correlation makes it difficult to distinguish whether the high proportion of dead *Calluna* in the north was a response to a greater drought exposure, relative to southern Norway, or whether northern *Calluna* provenances had lower (winter) drought resistance. Whilst the first explanation is plausible, it is interesting that we did not observe any drought damage on *Empetrum nigrum* L. which was abundant in several of the northern sites – especially sites E and G – and which is considered vulnerable to winter droughts (Watson et al. 1966, Bell and Tallis 1973, Bokhorst et al. 2009). However, it is possible that *Empetrum nigrum* had a faster recovery compared to *Calluna* and therefore had restored vital tissue by summer 2016.

Figure 22 (next page): Mean cover of *Calluna* across sites and time. We report the status of *Calluna* stands in the drought resilience experiment as vital (green), damaged (grey), or dead (dark grey) across the study period. For site locations, see Figure 10a.



Fire can restore resilience in northern coastal heathlands

Whilst unburnt plots in some sites in the drought resilience experiment showed partial or nearly full recovery during the five-year study period (**Paper III**), we were unable to identify the factors determining a successful recovery. In contrast, all sites showed recovery of healthy *Calluna* after prescribed fire (Figure 22). All sites in the drought resistance experiment were in a late successional phase prior to the experimental fire, and the post-fire recovery rate of *Calluna* is comparable to recovery after fire in the late mature (old) successional phase reported in Velle et al. (2012). In the sites north of 63°N (sites D to G), *Calluna* recovers solely from seeds (Nilsen et al. 2005).

Figure 9 in **Paper III** shows that we found relatively fewer *Calluna* seedlings in sites D to G than in sites A to C, where *Calluna* recovers from both seeds and vegetative

shoots. Spindelböck et al. (2013) demonstrate lower germination rates of *Calluna* seeds from northern Norway compared to southern Norway; however, local drought events might also increase mortality of seedlings (Meyer-Grünefeldt et al. 2015a). Our data do not inform about the causes for the low number of seedlings in the north, yet they illustrate the conservation challenge of depending on recruitment from drought-sensitive seedlings in a time where droughts are increasing in frequency. Overall, whilst prescribed fire is a more reliable tool to restore northern coastal heathland vegetation after a major drought than time alone, the risk of drought events in the vulnerable recovery phase highlights the benefit of preventing drought impacts in the first place. Moreover, the results in **Paper II** show that droughts can affect carbon dynamics in the old successional phase at a lower drought exposure than the aboveground vegetation respond to (**Paper I**). Our observations of little or no drought damage in heathlands in the young and intermediate successional phase suggest that keeping large and continuous areas of heathland from moving into the late successional phase where it is more prone to drought damages can prevent landscape-scale dieback.

Are these findings restricted to northern coastal heathlands?

Our *Calluna* populations were located on the central north and northern margins of their European distribution area, and, consequently, these *Calluna* populations should likely be less drought-adapted than *Calluna* vegetation further south in mainland Europe. Nevertheless, we did not observe any significant growth responses to drought on *Calluna* in our experiment. This was surprising because drought tolerance generally differs between provenances of the same plant species (Eilmann et al. 2013). For example, Meyer-Grünefeldt et al. (2016) found that *Calluna* populations at the southern and eastern range margins had lower shoot:root ratios and lower tissue ^{13}C values than populations in the central range distribution area. A low shoot:root ratio often indicates plant preferential growth allocation towards reduced leaf evaporation loss of water, and improved soil water uptake. Moreover, leaf ^{13}C values can in some instances be used as a proxy for water use efficiency (Farquhar and

Richards 1984, Seibt et al. 2008, Roussel et al. 2009). Why would our *Calluna* stands not show similar growth responses when exposed to drought?

First, the cold and wet climate in our study areas hampers microbial decomposition of dead plant remains, resulting in build-up of organic matter in the soils (Andrieux et al. 2018). These organic-rich, peaty soils have a relatively high water holding capacity (Robinson et al. 2016), which can buffer or slow declines in soil moisture during drought periods.

Second, several studies have shown that *Calluna* and other heathland plants are more susceptible to drought under higher nitrogen loads. This happens as a result of an increased shoot:root ratio, and consequently greater evaporation rates and therefore greater water demands (Pitcairn et al. 1995, Southon et al. 2012, Meyer-Grünefeldt et al. 2015a). That said, Norway has relatively low atmospheric nitrogen deposition loads and little agricultural run-off relative to central and southern Europe. In fact, our study areas all have annual nitrogen deposition rates less than 11 kg ha⁻¹ (NILU 2018), which is close to or below the limit for increased drought-sensitivity in *Calluna* and other heathland species (Bobbink et al. 2003, Stevens et al. 2011).

Third, the combination of a cold and wet climate and low nitrogen inputs, favours bryophyte growth. Consequently, bryophyte cover in all our heathland sites forms a continuous surface layer, which further buffers against soil moisture declines (Bates 1998). The cold and wet climate also stimulates plant-mycorrhizal fungi interactions, specifically Ericales-ericoid mycorrhizae in coastal heathlands (Johnson et al. 2017). While ericoid mycorrhizae remain poorly explored and understood ecologically, we know that these fungi have proven to be highly resistant to a number of environmental stressors, including drought (Read 1983, Cairney and Meharg 2003, Mitchell and Gibson 2006). In our study sites, *Calluna* and other Ericales, such as *Erica tetralix*, *Vaccinium* spp. and *Empetrum nigrum* dominate the plant communities. It is therefore possible that a high drought resistance in Ericales, at least partly due to mycorrhizal associations, could strongly influence the drought resistance of the whole plant community.

Last, almost all plant species in this study are perennials with relatively long lifespans. Therefore, reduced fitness might not necessarily lead to species turnover within the community or lead to significant biomass reductions on the relatively short temporal scale covered by this experiment. Regarding the dominant Ericales, these shrubs contain a large amount of woody biomass, which remains conserved over multiple years, and observational changes are therefore not likely to manifest in the short-term, even if the plants were indeed drought-stressed.

Do the results from this thesis call for new management practices?

Our data suggest that once past the critical seedling stage, increasing post-fire age makes *Calluna* stands (**Paper III**) and ecosystem functioning (**Paper II**) more vulnerable to drought. This confirms the impression we got when selecting sites for the drought resilience experiment. When we travelled the coast to find suitable study sites, it became clear that *Calluna* dieback occurred almost exclusively in heathlands that had not been burned for more than 20 years, that is, they were in the old successional phase. This observation was further validated through personal communication with multiple landowners, and when looking through unpublished data for a related study (Thorvaldsen, pers. comm.). Our results therefore imply that the old successional phase is less resistant to drought than the young and intermediate successional phases. This is an interesting observation as *Calluna* is generally considered to be more drought resistant with increasing age as roots are more developed (Meyer-Grünefeldt et al. 2015a). However, that young stands are more vulnerable to drought because of small root biomass is not a valid argument for stands that regenerate vegetatively from belowground roots. In contrast, old and large stands have more shoot biomass, and hence more evapotranspiration. But, if soil water is immobilised by frost, high root biomass is of little help. We do not know what the soil conditions were like during the 2014 drought event, but it is possible that not the entire soil column penetrated by roots was frozen, hence making liquid water available for deep roots.

Today, disproportionately large parts of the northern coastal heathlands are in the old successional phase because of management cessation and abandonment. Consequently, droughts and other disturbances that only affect the old successional phase, or which affect this phase relatively more than the younger phases, will impact the majority of northern coastal heathlands. Following the 2014 winter drought, several large wildfires took place and consumed large areas of heathlands and threatened thousands of people and multiple infrastructure installations (Log et al. 2017). Drought-damaged biomass fuelled these wildfires in near-zero temperatures, and the widespread lack of heathland management made it possible for the fire to effectively spread across a relatively homogeneous landscape (Log et al. 2017). More recently, numerous similar wildfires occurred in the warm and dry summer of 2018 (The Norwegian Directorate of Civil Protection 2019), and again during summer 2021 (NRK.no 2021). Concerningly, because these fires followed a prolonged drought period, the fires were able to penetrate into the soil and combust roots, seed banks and soil organic matter (Grau-Andrés et al. 2019). Considering the vast amount of carbon stored in the upper heathland soil layers (Bartlett et al. 2020, Friggens et al. 2020; Figure 23, **Paper II**), these summer fires undoubtedly resulted in large carbon releases into the atmosphere. Such carbon losses are less likely during a winter fire due to frozen or wet soils. Moreover, the loss of seed banks may slow heathland regeneration rates post fire (Måren and Vandvik 2009). As reduced heathland management already negatively affects biodiversity and ecosystem services in these ecosystems it is one of the main reasons why coastal heathlands are now red-listed. Continuing a traditional management of heathlands not only maintains habitat heterogeneity that is important for biodiversity (Velle et al. 2014), but it also conserves ecosystem functions and thereby increases the resistance and resilience of heathlands to intensified drought and wildfire. This thesis demonstrates the importance of management to maintain the conservation values in coastal heathland and to buffer ecosystem functioning against intensified drought following climate change.

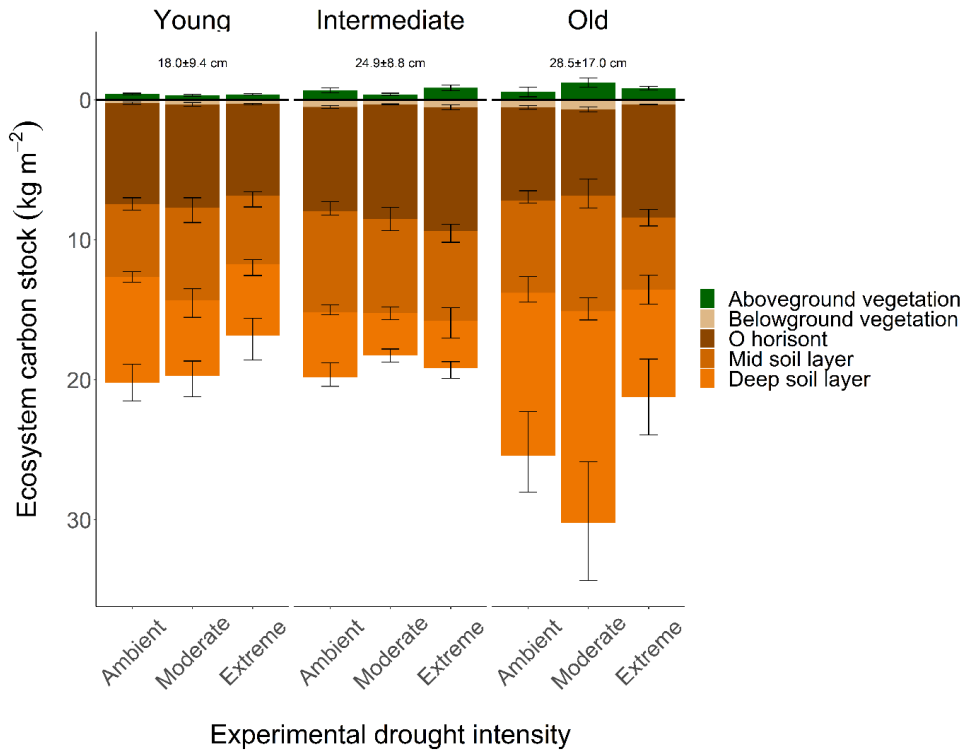


Figure 23: Carbon pools across the three successional phases and experimental drought treatment in the southern part of the drought resistance experiment. Soil is by far the largest carbon pool, and the amount of carbon stored belowground make coastal heathlands one of the most carbon rich landscapes in Norway, despite sparse aboveground biomass (Bartlett et al. 2020). Numbers display the difference in soil depths across sites.

Conclusions and further perspectives

The findings in this thesis show that whilst the drought resistance of northern coastal heathlands can be challenging to predict, prescribed fire remains a key tool in restoring and maintaining ecosystem functioning. Although plant community dynamics and primary production show relatively high resistance to experimental drought, we do see a change in ecosystem functioning as a response to experimental drought in the old successional phase. Increased frequency and intensity of drought periods due to climate change is already affecting Norwegian coastal heathlands, resulting in loss of ecosystem services and increased wildfire risk, with drought

impacts undoubtedly continuing to increase in severity throughout this century. The traditional management of coastal heathlands can mitigate these negative effects from climate change and can be efficiently applied on short timescales.

Further research should aim at a closer monitoring of environmental conditions during natural and experimental droughts. This thesis also illustrates the importance of including multiple response variables with causal linkages across hierarchical spatial and temporal resolutions when performing ecological climate change experiments.

Afterword

My doctoral programme included two and a half years for scientific work, half a year of coursework, and one year of teaching as duty work. One of my first teaching experiences as a PhD student was to participate in the International Plant Functional Traits Course in Peru. Here, a group of 29 students and instructors collectively collected research-grade plant functional trait and ecosystem data (Geange et al. 2021). As part of the process, they learnt reproducible data collection and management practices. Early on, I decided to build on this experience to engage undergraduate and graduate (BSc and MSc level) students in my research. The aim of student engagement was to provide students with hands-on experience in research early on in their studies (Lawless and Rock 1998), along with me getting helping hands in the lab and field. This aligns with the growing trend of students as partners (Matthews et al. 2018) and course-based research (Thompson et al. 2016, Geange et al. 2021) in higher education. The aim is not to place students in the same role as professionals, but to acknowledge that students can contribute in developing and producing outcomes to a research project, a course, or the conceptualisation of a theory (Cook-Sather et al. 2014). A growing body of evidence also show that students that actively engage in research experience increased understanding of scientific concepts (Russell et al. 2007), higher motivation (Olimpo et al. 2016), and are more likely to graduate with a scientific degree (Rodenbusch et al. 2016). Moreover, universities are research institutions with a mandate to not only transfer formal knowledge to students, but to also equip students with transferable ‘soft skills’, such as critical and creative thinking, communication and storytelling skills, and exploratory and investigation skills (Karimi and Pina 2021). These are core skills in research, and a major learning outcome from research engagement.

The students participated in my research activities for a minimum of two months, and up to two years. Not all datasets with student contribution have been manifested in a research paper as yet. The remaining datasets are presented in **Paper IV** (Figure 24), and whilst not presented in **Papers I-III**, they have an important role in making follow-up studies motivated by the results in this thesis possible, as well as

being a resource for meta-analyses of common response variables across study systems. However, these benefits of student involvement cannot be justified if it compromises data quality. Research on data quality produced by undergraduate students is limited, although several studies find that citizen science projects commonly produce data of comparable quality to data collected by professionals. Moreover, these studies show that the more knowledge the participants have in the field, and the more self-confidence they have on the methods, the less likely is the quality of the data to diverge from that collected by professionals. Students have specialised knowledge from higher education in the specific scientific field and receive a much closer training and follow-up than participants in citizen science projects. As with any studies, structured data collection protocols and data validation are essential steps in conducting good science.

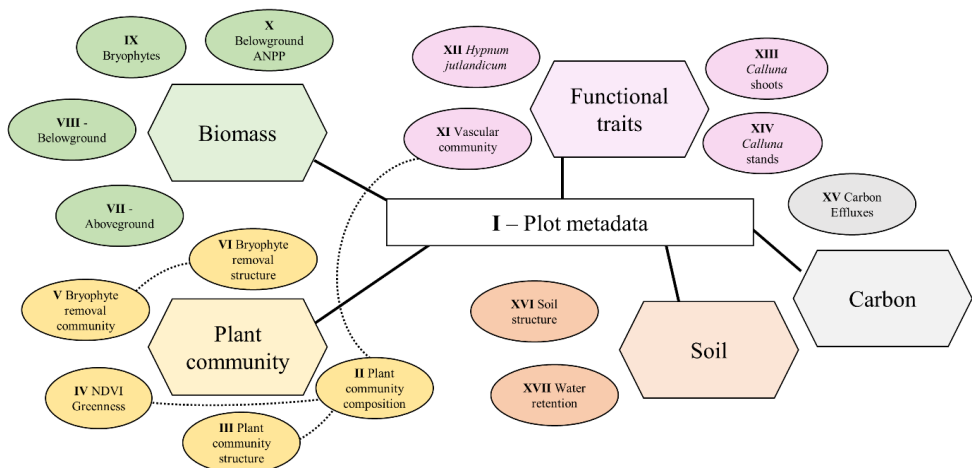


Figure 24: Overview of the 17 datasets presented in **Paper IV**. See Paper IV for details.

The data validation steps are determined by the specific dataset. Data validation includes manual proof reading of species names, visualising cover of species across time to check for signs of misidentifications, checking for logical impossibilities, manual evaluation of outliers and missing data, testing for observer bias, etc.

I would also like to point out that whilst student involvement can be a valuable resource in data collection, the involvement should also benefit the student, providing for instance, salary, study credits, network opportunities, participation at conferences, and – when contributing substantially to data collection – offer of co-authorship, following the standards of the ‘Vancouver protocol’ (International Committee of Medical Journal 2018). These guidelines were followed for my students, several of whom earned credits, salaries, and co-authorships on the data paper and other project outcomes.

To assess student outcomes and learn from their experiences, I invited the 13 students who participated in data collection through the 10 ECTS course ‘BIO299 – Research Project in Biology’ for some of the datasets presented in this thesis to anonymously answer a survey on their perceived learning outcomes. Overall, students reported a higher interest and wider understanding of research after participating in the course and they would recommend the course research participation to other students (Table 4, Figure 25).

Table 4: Questions for survey on students’ perspectives of contribution to data collection in an actual research project. Ranking questions on a scale from 1 (Not true at all) to 5 (Very true) was mandatory, whilst free-text comments could be added to all questions voluntarily. All responders were anonymous.

- 1 Participating in the project made me LESS motivated to continuing my studies**
A1: I think the project was great at all levels. When I finished it I wanted to learn more new things, experience more things and even analyze more data in R!
A2: It's good to be part of something that actually matters
A3: As I found the investigation exciting, it helped me decide to study a master degree! It also encouraged me to read books and bibliography (more than necessary) and feel more curious about mosses!
- 2 Participating in the project made me MORE motivated to continuing my studies**
A1: I feel that I am ACTUALLY contributing to ACTUAL science, and that's very motivating :)
A2: At the moment. And some moments after. Lets say a year. :-) However, after finishing my thesis back at home university I was out of energy and also out of topics to continue with (as it seems at the time), so I have not continued further.
A3: Thought me that it is possible to combine research and conservation
- 3 I am more interested in research after participating in the project**
- 4 By participating in the project I learned things that were not covered otherwise in my studies**

A1: Haven't participated that long in the project so far, but I assume that i will learn thing that's not covered in my studies.

A2: Set a heathland on fire! Ability to determine a bryophyte from a very small piece of it :-) And tricks in R

A3: Learned alot of how actual research work

A4: I believe that participating in a project helps learning how university research works, and it gives you the opportunity to learn scientific knowledge, the scientific method and the way to move around a department (with its external contacts too)

5 Participating in the project improved my professional network

6 I find it easier to read and understand scientific papers after participating in the project

7 Participating in the project helped me decide on my post-study career goals

8 I got more responsibility than I could handle

9 I was not trusted with the responsibility I could handle

10 I was listened to if I had suggestions or objections about the research methods

11 I was sometimes being exploited as free labour

A1: I spent a lot of time working on the project, but I am quite used to that your work on thesis is your work (at my home university, technicians belong mostly to funded projects). There was a moment when a girl working in a lab told me, what she earns by hour and I laught "haha, if I did this for money, I would be loaded!", however I have not felt exploited at all. Also, I think that someone might have paid for "my amazing house on Lygra", while I was there doing fieldwork :-)

12 I got fair credit for my contribution to the project

13 I would recommend other students to participate in similar research projects

A1: It's a great opportunity to jump in the professional scientific world!

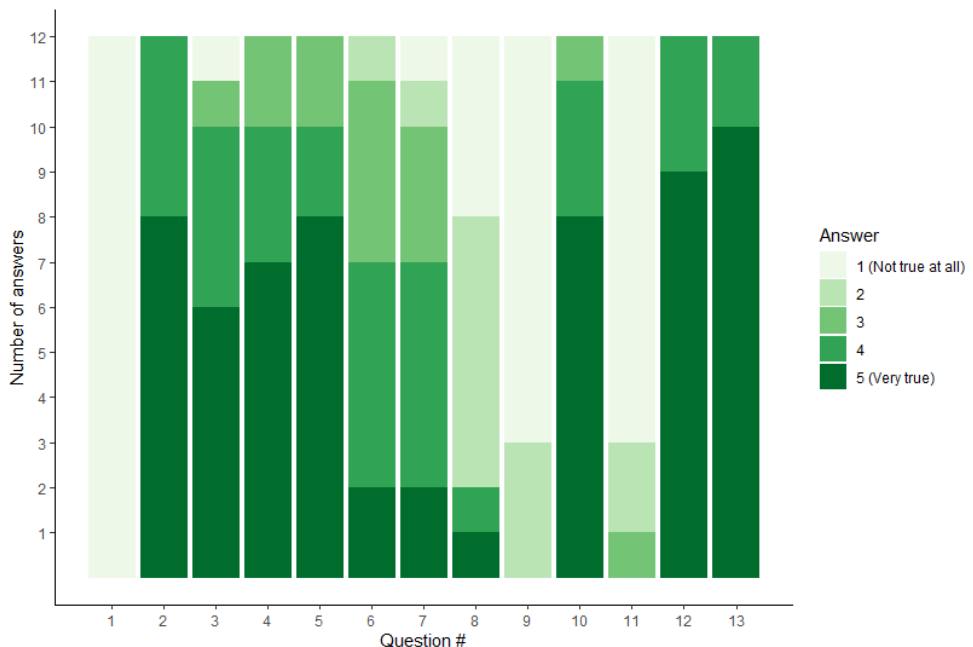


Figure 25 (previous page): Responses in the survey on student perspectives of contributing to data collection in a research project. The students were involved in research for one or two semesters between 2017 and 2020 and worked on the ongoing activities in the project, which varied across the period. Three of the 13 invited students were exchange students from European countries, and 12 of the invited students answered the survey.

The survey presented here has a small sample size, but still show some interesting responses, although most of them align with studies on students' perception on research engagement during their studies. For example, Russell et al. (2007) show that undergraduate research experiences generally increase students' interest in STEM (Science, Technology, Engineering, and Mathematics) careers, whilst some are unaffected or even have a decreased interest. All students that responded to the survey (Figure 25) reported increased motivation to continue their studies (question two) but did not necessarily gain increased interest in research (question three). This highlights the value of hands-on experience in self-development, and aiding students in career choices, although the answers to question seven show that some students are still uncertain about career goals after course-engaged research. I find the responses to questions 8, 9, and 11 to be of particular interest. Two students responded that they were given more responsibility than they could handle (score 4 and 5 out of 5), and one student implied that they were somewhat exploited for labour (score 3 out of 5). This suggests that a two-way communication on expectations before and during the student engagement could be improved.

Acknowledgements

Thanks to Vigdis Vandvik, Liv Guri Velle, Beate Zein, Ragnhild Gya, Inger E. Måren, Anne E. Bjune, and Casper Tai Christiansen for feedback on the synthesis, and to Cathy Jenks and patiently proofreading the synthesis. Thanks to Lisa Simonsen who made the illustrations of *Calluna vulgaris* in Figure 8.

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Paper I



Coastal heathland in the young successional stage at Lygra, Alver. Photo: Siri V. Haugum

Research

Coastal heathland vegetation is surprisingly resistant to experimental drought across successional stages and latitude

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Oikos

00: 1–13, 2021

doi: 10.1111/oik.08098

Subject Editor: John Parker
Editor-in-Chief: Dries Bonte
Accepted 20 August 2021



In the last decade, several major dwarf-shrub dieback events have occurred in northern European coastal heathlands. These dieback events occur after extended periods with sub-zero temperatures under snow-free conditions and clear skies, suggesting that coastal heathlands have low resistance to winter drought. As climate projections forecast increased drought frequency, intensity, and duration, coastal heathlands are likely to experience more such diebacks in the future. There are, however, few empirical studies of drought impacts and responses on plant communities in humid oceanic ecosystems. We established a drought experiment with two distinct levels of intensified drought to identify responses and thresholds of drought resistance in coastal heathland vegetation. We repeated the experiment in two regions, separated by five degrees latitude, to represent different bioclimatic conditions within the coastal heathlands' wide latitudinal range in Europe. As coastal heathlands are semi-natural habitats managed by prescribed fire, and we repeated the experiment across three post-fire successional phases within each region. Plant community structure, annual primary production, and primary and secondary growth of the dominant dwarf-shrub *Calluna vulgaris* varied between climate regions. To our surprise, these wide-ranging vegetation- and plant-level response variables were largely unaffected by the drought treatments. Consequently, our results suggest that northern, coastal heathland vegetation is relatively resistant to substantial intensification in drought. This experiment represents the world's wettest (2200 mm year⁻¹) and northernmost (65°8'N) drought experiment to date, thus filling important knowledge gaps on ecological drought responses in high-precipitation and high-latitude ecosystems across multiple phases of plant community succession.

Keywords: arctic browning, Atlantic heathlands, climate change, fire, International Drought Experiment (IDE), rain-out shelter

Introduction

Drought is projected to increase in frequency, intensity, and duration in most terrestrial biomes under current and future anthropogenic climate changes (Dai 2013, Shukla et al. 2019), but ecological responses to drought are intrinsically hard to predict



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(Marshall et al. 2008, Zhang et al. 2019). Because of increased temporal and spatial heterogeneity in precipitation patterns with climate change (Knapp et al. 2008, Butcher et al. 2014), intensified drought is projected also in regions with high and increasing mean annual precipitation (Mishra and Singh 2010, Dai et al. 2018). Northern-European coastal heathlands are located in oceanic coastal regions with high annual precipitation (1000–2200 mm annually) and low seasonal amplitude in temperature compared to adjacent inland regions. During the last decade, this heathland region has been subjected to increased precipitation, but also extreme and prolonged winter droughts, the latter of which has been implicated in severe dieback events of the dominant species *Calluna vulgaris* (hereafter *Calluna*) (Hancock 2008, Phoenix and Bjerke 2016, Parmentier et al. 2018). These dieback events have raised considerable concern about how this landscape and its associated ecosystem services will persist in a future climate with increased drought risk.

In recent decades, land-use changes have transformed large tracts of European semi-natural and natural open lowland habitats into either urban developments or arable land (Desender et al. 2010, Exeler et al. 2010), or afforested or naturally reforested habitats (Velle et al. 2014, Wehn and Johansen 2015). As a result of this widespread heathland habitat loss and degradation, coastal heathlands are now considered endangered on both the Norwegian and EU red lists of habitats (EC Habitats Directive 1992, Hovstad et al. 2018). Because of the abandonment of traditional management, current heathlands are disproportionately dominated by old and degenerative successional phases (Moen et al. 2006). The post-fire successional phases differ in community composition, structure and biomass, and hence also in ecosystem functioning (Smith and Knapp 2003, Garnier et al. 2004, Winfree et al. 2015). If different successional phases also differ in resistance and resilience to drought, the cessation of heathland management will have additional implications for conservation and ecosystem functioning. Identifying patterns and thresholds of drought resistance in heathland ecosystems is therefore of key interest for regional economics and culture, nature conservation and climate change mitigation.

During the past two decades, numerous drought experiments attempted to quantify responses and resistance of plant communities and ecosystem functioning to temporary reduction or exclusion of precipitation (Hoover et al. 2018). Recurring responses to intensified experimental drought include reduced plant species richness and primary production (Prieto et al. 2009, Lanta et al. 2012). However, diverging ecological responses to drought between similar ecosystems suggest context-dependencies resulting from e.g. different dominant vegetation types (Cherwin and Knapp 2012, Kimball et al. 2016), land-use legacies (Foster et al. 2003, Bürgi et al. 2017, Karlowisky et al. 2018, Legay et al. 2018) or variation in baseline climatic conditions (Knapp et al. 2017, Slette et al. 2019, Korell et al. 2021). The observed climatic context-dependencies in vegetation responses to drought remain particularly problematic as existing drought experiments are clustered in temperate and relatively

low-precipitation regions in the United States and in central and Mediterranean Europe, and therefore cover limited geographical, ecological, and climatic extent (Hoover et al. 2018, Stuart-Haëntjens et al. 2018). In contrast, few experiments have so far investigated drought impacts in 1) high latitudes, 2) ecosystems with high annual precipitation, and 3) along secondary successional gradients (Prieto et al. 2009, Bretfeld et al. 2018, Hoover et al. 2018), which are all key characteristics of north-European heathlands. Consequently, our current knowledge from existing drought experiments is poorly suited for predicting drought resistance in northern coastal heathlands.

Because of the nature of drought, with high variation in frequency and duration (Mishra and Singh 2010), and because of time-lagged ecological responses, especially in systems dominated by long-lived species (Svenning and Sandel 2013), reports of ‘no effect’ in short-term ecological drought experiments might hide emerging but delayed responses (Magurran et al. 2010, Knapp et al. 2012, Wolkovich et al. 2012). One way to increase the sensitivity of ecological measurements is to focus on demographic parameters and plastic responses in growth or functional traits at different stages in a species life cycle, as these respond to drivers on relatively short timescales (Kimball et al. 2016). Traits related to growth, survival or reproduction of the whole plant community, or of keystone or indicator species, can reveal short-term responses to drought, and thereby predict longer-term community outcomes (Smith and Knapp 2003), even when species abundances remain unaltered during the course of the study (Kimball et al. 2016).

Here, we present vegetation responses in a four-year intensified drought experiment in Norwegian coastal heathlands. We use rainout shelters (Yahdjian and Sala 2002) to create two levels of drought (60% and 90% shelter cover) in addition to an ambient control treatment, which we repeated within each of the three main post-fire successional phases of coastal heathlands (Gimingham 1988; Fig. 1b) and in two regions – in southern Norway, where coastal heathlands are highly abundant, and in northern Norway, close to the northern range-edge of coastal heathlands. From this experiment we report effects of experimental drought on 1) plant community composition, specifically richness, evenness and Bray–Curtis dissimilarity, 2) aboveground primary production, and 3) annual primary and secondary growth on >400 specimens of the dominant species *Calluna*. We replicated each drought treatment three times. We hypothesized that the coastal heathland plant community will be less resistant to intensified drought in H1) the northern region which is on the colder-climate brim of the coastal heathland distribution, and H2) early successional phases where plants have more acquisitive traits and shorter life cycles. In addition, we hypothesized that H3) *Calluna* growth would be most susceptible to drought in the young successional phase because of the relatively faster growth shortly after the fire, and especially in the north where all new plants originate from seedlings, increasing the shoot : root ratio relative to the vegetative sprouting observed further south (Nilsen et al. 2005,

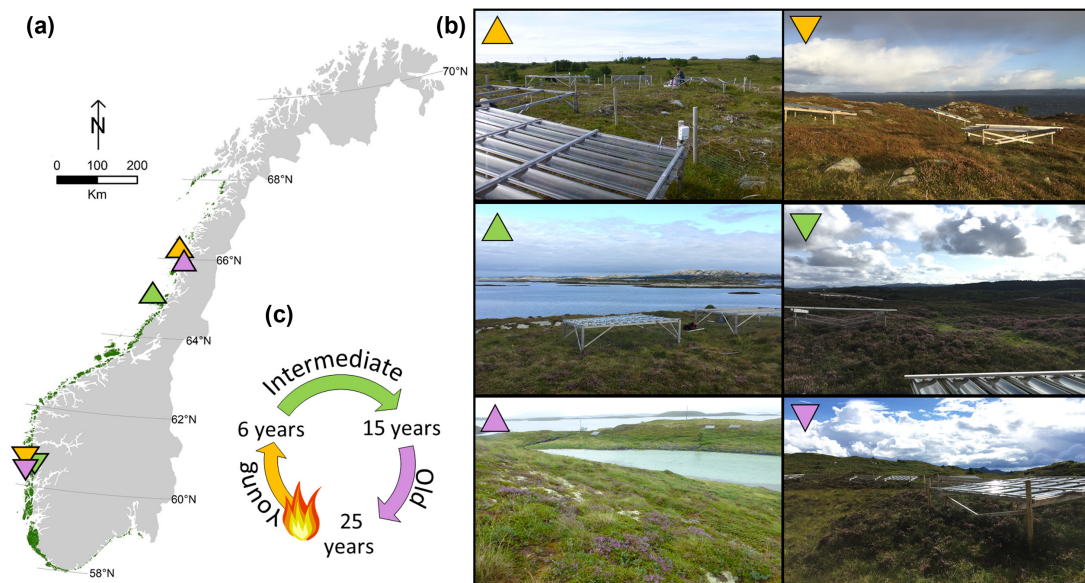


Figure 1. Study system, study sites, and experimental setup. (a) The geographical distribution of coastal heathlands in Norway (dark green area), with the six study sites indicated. Shapes indicate regions (\blacktriangle = north, \blacktriangledown = south), colours indicate the post-fire successional phase of each site, based on (b) the traditional heathland management cycle (Watt 1947, Gimingham 1988, Velle et al. 2021). (c) The six study sites, representing the successional phases from young (top) to old (bottom) in the north (left-hand photos) and south (right-hand). Table 1 for site details. Within each site, we implemented a DroughtNet rainfall exclusion experiment (using 3×3 m roofs) with three treatments (ambient, moderate = 60% roof cover, extreme drought = 90% roof cover) replicated three times, for a total of 54 plots (see text for details). Southern sites are spaced out slightly for visibility.

Velle and Vandvik 2014). Specifically, we expected to observe changes in plant community composition and reduced primary production as symptoms of low drought resistance.

Material and methods

Study system

Northern-European coastal heathlands constitute semi-natural landscapes, managed by prescribed fire and low-intensity grazing for millennia (Vandvik et al. 2005, Måren et al. 2010), and they are valued for their ecological and cultural history (Gimingham 1987, Hjelle et al. 2018). *Calluna* is present across the whole post-fire successional gradient but changes morphology from long apex growth in the early post-fire years, to a bushier growth after 6–15 years, before stands grow coarser with reduced canopy density after 15 years. The morphology of *Calluna* is often used to identify the successional phase of the management cycle displayed in Fig. 1b (Gimingham 1988, Velle et al. 2021). This growth pattern is consistent for *Calluna* across its geographical range, but populations show region-specific traits (Vandvik et al. 2014, Meyer-Grünefeldt et al. 2016). For example, whilst *Calluna* frequently resprouts from belowground organs after

fire, only seed germination is observed north of 63 degrees north (Nilsen et al. 2005, Velle and Vandvik 2014). Today, the landscape heterogeneity shaped by post-fire succession supports important habitats have become increasingly important for a range of species, including red-listed birds, plants, invertebrates and fungi (e.g. Eurasian eagle-owl *Bubo bubo*, marsh gentian *Gentiana pneumonanthe*, grey scalloped bar *Dyscia fagaria* and orange waxcap mushroom *Hygrocybe aurantiosplendens*). More recently, coastal heathlands are also acknowledged for their role as a large terrestrial carbon pool (Marrs et al. 2019, Bartlett et al. 2020, Friggens et al. 2020).

Study sites

The study is conducted in six coastal heath vegetation sites in Norway. The study sites were selected to represent three successional phases separated by time since last fire each sampled in two distinct geographical regions, at ca 60°N and near the northern brim of the Atlantic heathland distribution at ca 65°N (Fig. 1a). All sites are representative for their post-fire successional phase and the geographical region (Velle and Vandvik 2014). Specifically, the young successional phases have high cover of graminoids (e.g. *Agrostis* spp., *Festuca rubra*) and forbs (*Potentilla erecta*, *Trientalis europea*, *Galium saxatile*), while the cover of dwarf shrubs

Calluna vulgaris is initially low but increases with time since fire. The intermediate successional phases have denser cover of dwarf shrubs (*Calluna vulgaris*, *Erica tetralix*, *Vaccinium* spp.) and a few sedges *Carex* spp.. Last, the old successional phases are dominated by taller and coarser *Calluna vulgaris* stands. The bryophyte ground cover (dominated by *Hypnum* spp., *Hylocomium splendens*, *Pleurozium schreiberi*) recovers gradually after fire. In general, the northern sites have more boreal species than the southern sites (e.g. *Trichophorum cespitosum*, *Arctous alpinus* and *Arctostaphylos uva-ursi*). The climatic differences between regions are reflected in higher precipitation and a longer duration of the growing season in the southern region, whereas mean summer and winter temperatures are similar between regions (Table 1). All sites are rich in soil organic matter (30–40% dry weight in the upper 30 cm), acidic (pH 3.8–4.9, except for the young site in the north where pH ranged from 4.4 to 6.3), with a soil depth of 20–30 cm, and high soil water holding capacity ($-0.7 \text{ g}_w \text{ g}_s^{-1}$) (Haugum 2021).

Experimental design

We installed nine $2 \times 2 \text{ m}$ permanent plots at each of the six sites in 2016, following the Drought-Net protocol for short-stature vegetation (Drought-Net 2017). In spring 2017, we randomly allocated plots to either moderate drought, extreme drought or ambient controls, resulting in three replicate plots per treatment, successional stage and region, for a total of 54 plots (Fig. 1c). The three levels of drought were implemented by fixed rainout shelters (modified from Yahdjian and Sala 2002) with 60, 90 and 0% roof cover (Icopal Fastlock Uni Clear), respectively. All plots were fenced in spring 2017, except on the northern intermediate site located on a small island, with no large herbivores present during the first two years of the experiment. Here, the plots were fenced in spring 2018.

Microclimate

Local climate stations with a temperature sensor and precipitation gauge were installed in each site to monitor microclimate and drought effects. Soil moisture sensors were installed at 15 cm depth in all plots from summer 2017. From October 2018 to January 2020, we measured temperature sensors at 8 cm soil depth and at ground level at all sites in the south to

quantify potential warming side effects from the plastic roofs. Moreover, we set up local climate stations to measure quantified photosynthetic active radiation (PAR) inside the plot, and rainwater intercepted by the roof, in one moderate and one extreme drought treatment in the intermediate phase in the south for the same period (Haugum 2021).

Plant communities

We surveyed vegetation composition in all plots annually from 2016 (pre-treatment year) to 2020. These measurements were made in a permanently marked $1 \times 1 \text{ m}$ plot. At peak growing season, mid-July to late August, we visually determined the ground cover of all vascular plants and bryophytes on species level, except for liverworts which we registered collectively as one taxon. We followed the nomenclature of (Lid and Lid 2013) for vascular plants and (British Ecological Society 2010) for bryophytes. Because of canopy layering the sum of coverages was frequently $>100\%$.

Calluna traits

In each plot, we selected 10 individuals of *Calluna*, targeting five of the shortest individuals and five of the tallest individuals in each plot to maximise variation in size. On each individual, we measured primary growth as stand height in mm (one replicate), current year's growth on three random shoots in mm following (Mohamed and Gimingham 1970), and secondary growth as stem diameter in mm (three replicates). These measurements were made annually in October, which is at the end of the growth season, from 2016 to 2019. Some individuals in the young successional phases in both north and south were lost to grazing in the winter 2016/2017 when the plots were not fenced. In addition, the individual markings on several individuals in the young successional phase in northern Norway were torn off (likely by sheep or birds) to such an extent that we excluded the *Calluna* measurements from this site from the analysis due to low replicate numbers.

Biomass harvest

We measured standing aboveground biomass by destructively harvesting three randomly placed $25 \times 25 \text{ cm}$ squares within each $2 \times 2 \text{ m}$ plot, avoiding the permanent $1 \times 1 \text{ m}$ plot, in August 2019. All vascular plants rooted inside the square

Table 1. Climatic and ecological site information. Mean annual precipitation (MAP) is based on data from 1990 to 2019, whilst mean summer temperature (MST) and mean winter temperature (MWT) is based on data from 1980 to 2019. Length of growth season (GS) are based on data from 2019. Supporting information for climate data sources (Supporting information). Time since last fire is provided by the local land-owners (Haugum 2021).

Region and successional phase	MAP (mm)	MST (°C)	MWT (°C)	GS (days)	Latitude	Burned (year)
North young	1254 ± 184	13.4 ± 1.3	0.7 ± 1.6	147	65°50'12.4"	2014
North intermediate	1720 ± 461	13.3 ± 1.4	1.5 ± 1.9	150	64°46'44.4"	2010
North old	1254 ± 184	13.4 ± 1.3	0.7 ± 1.6	147	65°47'45.7"	Before 1980
South young	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	214	60°42'03.0"	2013
South intermediate	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	214	60°42'03.0"	2004
South old	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	214	60°42'03.0"	1996

were harvested, in addition to bryophytes, lichens and litter within the square. Vascular plants were sorted into Ericales, graminoids, forbs and bryophytes. Standing dead plant matter, including yellow graminoid leaves, were sorted as 'dead'. Each biomass fraction per square was dried at 65°C for minimum 48 h, before weighing at 0.01 g precision.

Data analysis

All data analyses were performed in R ver. 4.0.2 (<www.r-project.org>). To assess the drought effect of the rain-out shelters, we quantified both meteorological and ecological drought. Meteorological drought was calculated using standardized precipitation evapotranspiration indices, using the package SPEI (Beguería and Vicente-Serrano 2017). First, historic precipitation and temperature data were retrieved from the nearest public meteorological station (available from Norwegian Centre for Climate Services (NCCS), Supporting information for details). These data were available from approximately 1980 to 2019. To estimate the drought effect of the rain-out shelters, we calculated SPEI values for the moderate and extreme drought intensities by reducing the precipitation data by the amount of rainwater intercepted by the 60% and 90% cover rainout shelters, using measurements of rain interception from the local climate stations. Ecological drought was quantified using the soil moisture measurements.

The variation in species composition within and between sites was visualised as a non-metric dimension scaling plot using the *metaMDS* function in the *vegan* package (Oksanen et al. 2019). The *anosim* function was used to test for differences in species composition between regions and successional stages (999 permutations, Bray–Curtis dissimilarity). Evenness (E_{var}) was calculated for the fourth year of the drought treatment (2020) using the *community_structure* function in the *codyn* package (Hallett et al. 2020).

The effects of drought, successional phase, region and their interactions on plot-level plant community structure, plot-level standing biomass and individual-level *Calluna* growth were assessed parametrically with linear mixed-effects models with restricted maximum likelihood in the *lme4* package (Bates et al. 2015). We based these models on the data collected in the fourth year, except for Bray–Curtis distance and *Calluna* height and stem diameter, which were quantified as the difference between the first and the fourth year. To reduce model complexity, we analysed regions and successional phases individually instead of building full models with nested designs. Specifically, two-way interactions between drought and successional phases as fixed factors were explored within regions (north versus south; $n=27$ per region), and interactions between drought and region as fixed factors were explored within successional phases (young, intermediate and old; $n=18$ per successional stage). For *Calluna* models, plot was specified as a random factor. We ran all models as full-factorial hypothesis tests without model optimization. To explore to what extent non-significant results were due to low power, we also ran a stepwise backwards model selection to explore if other factors were significant if higher-order terms

were dropped. Biomass for individual functional groups was Log_{10} or square root transformed to achieve normality and homogeneity of variances.

Results

Experimental drought effects on microclimate

The rainfall interception by the roofs were $32.1 \pm 10.3\%$ and $43.5 \pm 20.3\%$ for the moderate and extreme drought treatment, respectively. This increased frequency and intensity of meteorological drought in two distinguishable levels below the ambient (control) level (Fig 2a). Specifically, the extreme drought treatments incurred meteorological drought ($\text{SPEI} < -1$) and extreme drought ($\text{SPEI} < -2$) both more frequently and with longer duration than the controls. Overall, the annual precipitation during the study period was between 77% and 98% of the normal rainfall based on the 1981–2016 climate normal (Supporting information), with high annual and interannual variability, where winter and early growth season tended to be drier than the climate normal, especially in the northernmost sites.

The roof cover also reduced soil moisture, but with considerable variation between sites and over time (Fig. 2b). The effect was more pronounced in dry than wet periods, indicating that the treatments resulted in increased drought intensity and frequency, rather than in lower mean soil moisture overall. Specifically, the moderate and extreme drought treatment reduced daily mean soil moisture during summer (June–August) with $2.3 \pm 3.9\%$ ($p < 0.001$) and $26.5 \pm 4.2\%$ ($p < 0.001$), respectively, across sites and successional phases. However, in July 2018, when a natural drought occurred, soil moisture was $14.2 \pm 36.9\%$ and $32.0 \pm 26.2\%$ lower in the moderate and extreme drought, respectively. In contrast, no significant effect of the drought treatments was observed on mean soil moisture through winter (December–February) (Fig. 2b).

Plant community composition and structure

Species composition varied between regions and successional stages in accordance with the overall study design (Fig. 3; $R=0.72$, $p=0.001$). Specifically, the post-fire successional phases clustered chronologically with post-fire time from low to high axis 1 score, whereas the two regions were separated on axis 2 (Fig. 3). The NMDS successfully captured the main compositional variation in the vegetation (stress=0.12). The species composition within sites was more variable over both space and time in the north, and in the younger successional stages within each region (Supporting information, Table 2). In contrast, plant community composition was not affected by drought treatments, as reflected in the relatively minor shifts overtime of the drought treatments in the NMDS plot (Fig. 3) and in the minor and non-significant changes in Bray–Curtis dissimilarity over time in response to drought treatments (Table 2).

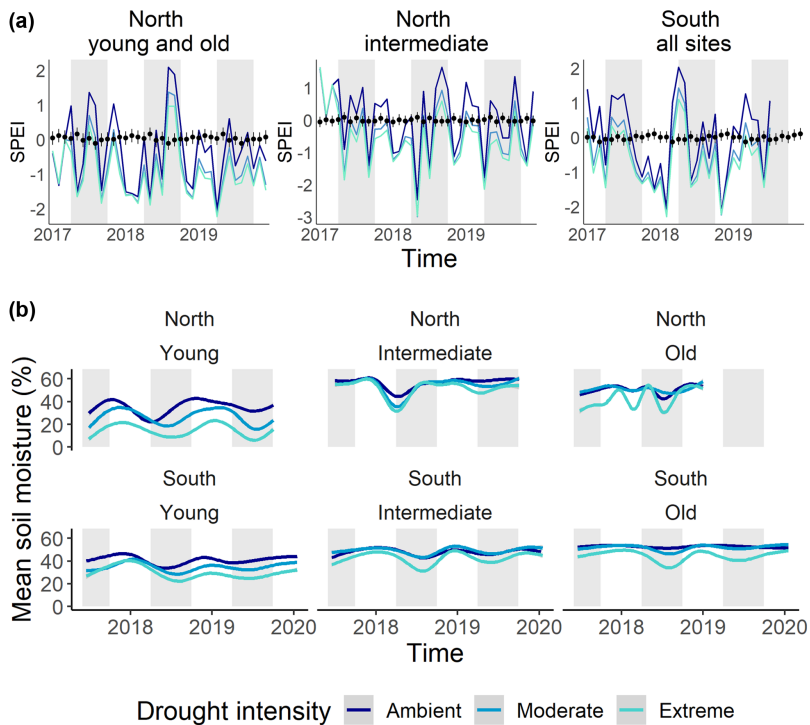


Figure 2. Drought treatment effects on precipitation and soil moisture. (a) Average standardized precipitation evapotranspiration index (SPEI) in the three drought treatments (dark blue = ambient; pale blue = moderate drought, 60% roof cover; turquoise = extreme drought, 90% roof cover) over the study period 2017–2019 compared to long-term monthly averages (black symbols \pm 1 SE) from 1981 to 2019 in the south and 1991 to 2019 in the north. (b) Mean soil moisture in the three drought treatments in each site across the study period. Values are means of replicates ($n=3$) of the same drought treatment and successional phase combination. Soil moisture is recorded at 15 cm depth every 20th minute. Grey shades indicate the growing season (April–September).

Plant community structure also differed between regions, and between successional phases within regions. Specifically, the northern region had greater species richness than the southern region, and species richness and evenness decreased with time since fire within both regions (Table 2). Experimental drought generally did not affect the community structural parameters, however, except for the intermediate successional phase in the southern region, where evenness decreased in response to the extreme drought treatment (Table 2).

Biomass

Total biomass increased with post-fire age ($p < 0.001$ in the north and $p=0.02$ in the south; Fig. 4), and was also higher in the south than the north for the young successional phase ($p < 0.001$) and the intermediate successional phase ($p=0.041$). Generally, the biomass harvested in 2019, three years after the start of drought manipulation, was not affected by the drought treatment. Litter increased with drought in the old successional phase in the south. Supporting information for details on responses for each functional group.

Calluna traits

Calluna stands in the old successional phase in the north responded to the extreme drought treatment by increasing annual shoot length growth by 76% and 83% compared to the moderate drought treatment and the ambient control, respectively (Fig. 5a). We did not observe any other responses to drought on *Calluna* primary or secondary growth. Height and stem diameter growth over the 2016–2019 period declined from the intermediate successional phase to the old successional phase in the north (Fig. 5b–c), while stem diameter growth showed the opposite response in the south. Primary growth was much higher in the south than in the north. Specifically, annual shoot increment was 83% ($p < 0.001$) and 226% ($p < 0.001$) higher in the intermediate and old successional phase, respectively, and increase in stand height was 75% ($p=0.040$) and 624% ($p < 0.001$) higher, respectively. However, the increase in stem diameter was 296% higher in the north than in the south in the intermediate phase ($p=0.003$), and 227% higher in the south than in the north in the old successional phase ($p=0.002$).

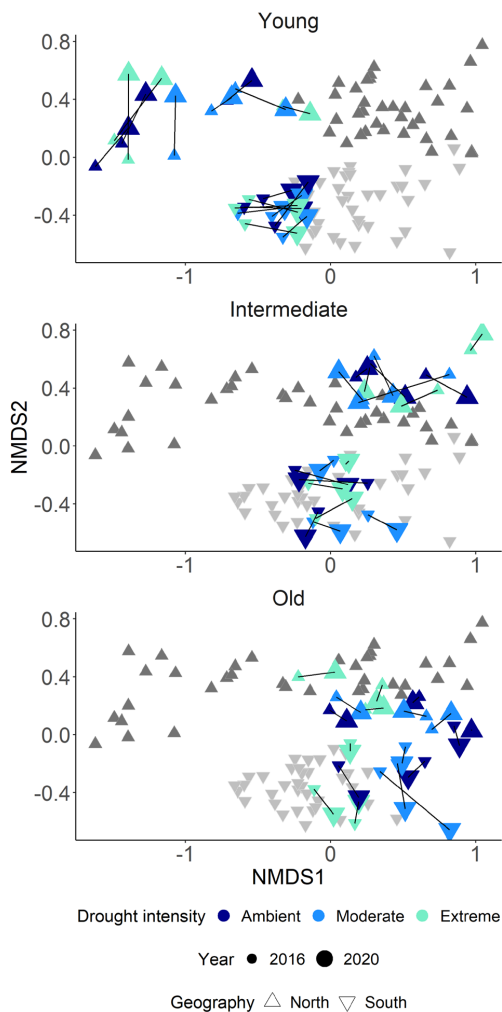


Figure 3. Changes in species composition across all sites and treatments over time, based on a non-metric dimensional scaling (NMDS) of the vascular and non-vascular plant community composition across all sites, treatments and years. For clarity, the NMDS is displayed three times, highlighting patterns in the (a) young, (b) intermediate and (c) old successional phases, with only first and last years are shown. Within each plot, the drought treatments of the highlighted phase are represented by the blue scale (dark blue = ambient; pale blue = moderate drought, 60% roof cover; turquoise = extreme drought, 90% roof cover) and the last year is indicated using larger shapes. On all plots, shapes indicate regions (\blacktriangle = north, \blacktriangledown = south), grey shading displays non-focal site plots; pale grey for the south, dark grey for the north. Stress = 0.12.

Discussion

Here we report on plant community responses to experimental drought; specifically on changes in the species composition, richness and evenness of the heathland vegetation, and biomass and species-specific growth of the dominant dwarfshrub *Calluna* over four growing seasons. The experiment successfully induced two distinct levels of drought across three post-fire successional phases in two climatic different regions. However, we found surprisingly few ecological responses to experimental drought. Moreover, we did not find support for the hypotheses that resistance to experimental drought is lower in H1) heathland plant communities on the northern brim of the coastal heathland distribution, and H2) plant communities in early post-fire successional phases. This experiment represents the world's wettest (2200 mm year⁻¹) and northernmost (65°8'N) drought experiment to date (Korell et al. 2021), and it therefore adds knowledge about drought responses in understudied climatic and ecological space. Below we discuss the microclimatic changes caused by the drought experiment, our observed responses, and how this study contributes to an improved understanding of ecological drought responses in general.

Experimental drought conditions

The fixed rainout shelters (following the design in Yahdjian and Sala 2002) successfully imposed two distinct levels of drought in addition to the ambient control, as assessed by our climatic and soil moisture data, but with large intra- and interannual variation. The largest difference in soil moisture between the experimental drought levels was observed during dry periods. Consequently, the drought experiment did not impose one drought lasting four years, but increased the frequency, intensity and duration of droughts. Quantitatively, the reduction in soil moisture in the drought plots relative to ambient controls were comparable to or exceeded the magnitude of the natural drought that occurred in summer 2018 (Skaland et al. 2019, Buras et al. 2020), suggesting that the experimentally imposed drought regimes were climatologically and ecologically realistic. During the study period, droughts occurred primarily in spring and summer and we did not encounter a prolonged drought in sub-zero temperatures.

We did not observe non-drought side-effects from the roofs on soil or ground temperature, and reduction in photosynthetic active radiation (PAR) was negligible (Haugum 2021), paralleling reports of no significant side-effects from a similar rain-out infrastructure in California (Kreyling et al. 2017, Loik et al. 2019). Other studies have found slight changes in air and soil temperature, but also here these changes did not affect primary production (Vogel et al. 2013).

Comparison to other studies

As studies experimentally manipulating drought conditions via rain-out shelters accumulate, it is becoming increasingly

Table 2. Linear model estimates for community structural variables in the fourth study year as a response to drought, post-fire time and regions. Models with p-value below 0.05 are considered significant and highlighted in bold. Evenness= E_{var} , BCD=Bray-Curtis dissimilarity between first and last year. *=significant only in the reduced model.

	Hypothesis	Model term	Evenness	Richness	BCD	
North n=27		Intercept	0.74	41.67	0.55	
	Drought	Moderate	-0.06	-5.00	0.02	
		Extreme	-0.02	-5.67	-0.05	
		Intermediate	-0.16	-20.33	-0.04	
	Succession	Old	-0.36	-21.00	-0.22	
		Drought × Succession	Moderate × Intermediate	0.07	6.33	-0.02
			Extreme × Intermediate	-0.07	5.00	0.04
	Moderate × Old		0.10	4.00	-0.05	
	South n=27	Drought	Extreme × Old	0.15	7.00	-0.17
Intercept			0.57	24.67	0.55	
Moderate			0.03	1.67	-0.07	
Succession		Extreme	0.05	1.67	-0.07	
		Intermediate	-0.11*	-1.33	-0.10	
		Old	-0.09*	-5.67	-0.25	
Drought × Succession		Moderate × Intermediate	-0.02	-4.33	-0.02	
		Extreme × Intermediate	-0.01	-3.67	0.04	
		Moderate × Old	0.01	-3.33	0.13	
Young n=18	Region	Extreme × Old	-0.04	-2.67	0.11	
		Intercept	0.74	41.67	0.55	
		South	-0.17	-17.00	0.00	
	Drought	Moderate	-0.05	-5.00	0.02	
		Extreme	-0.02	-5.67	-0.05	
		Intermediate	0.08	6.67	-0.09	
	Region × Drought	South × Intermediate	0.07	7.33	-0.02	
		South × Extreme	0.07	7.33	-0.02	
		Intercept	0.59	21.33	0.51	
Intermediate n=18	Region	South	-0.12	2.00	-0.06	
		Moderate	0.01	1.33	0.00	
		Extreme	-0.10	-0.67	-0.01	
	Region × Drought	South × Intermediate	-0.01	-4.00	-0.09	
		South × Extreme	0.14	-1.33	-0.02	
		Intercept	0.39	20.67	0.32	
	Old n=18	Region	South	0.10	-1.67	-0.03
			Moderate	0.04	-1.00	-0.02
			Extreme	-0.13	1.33	0.12
Region × Drought		South × Intermediate	-0.00	-0.67	0.09	
		South × Extreme	-0.12	-2.33	-0.08	

clear that responses to drought are not consistent (Cherwin and Knapp 2012, Knapp et al. 2017, Karlowky et al. 2018, Legay et al. 2018, Korell et al. 2021). Yet, most studies find that reduced soil moisture leads to reduced aboveground primary production (Peñuelas et al. 2004, Kongstad et al. 2012, Vogel et al. 2013, Alon and Sternberg 2019, Hannusch et al. 2020, Zhang et al. 2020). Some studies also observe changes in the plant community, often driven by a decrease in abundance of dominant species (Hoover et al. 2014, Alon and Sternberg 2019). Most studies are short-term and single-site, which hampers comparison between studies and synthesis of general responses to drought. A few replicated experiments exist, however, and Peñuelas et al. (2004) found that heathland primary production responded most negatively to drought in the most arid site, but found no response in the least arid site, demonstrating context-dependencies in response to drought along a gradient of increasing ambient precipitation. Moreover, a study by Kröel-Dulay et al. (2015), building on Peñuelas et al. (2004), demonstrates

that more responses to experimental drought emerged in the experiments after 7–14 years. The weak responses to drought in our high ambient precipitation systems are consistent with the trend towards weaker responses in wetter climates and on shorter time-scale in these two previous studies as suggested in Bachmair et al. (2018) and Korell et al. (2021).

The overwhelmingly non-significant results in our study beg the question of whether we lack the statistical power to detect biologically meaningful results. Several lines of evidence suggest that this is not the case (Schweiger et al. 2016). The ecological reliability of the experiment is enhanced by including gradient designs (three successional phases, three drought treatments) and by replicating the experiment in two regions. Our response variables are also causally linked reflecting the same underlying processes, which gives clear expectations about linkages between the resulting variables. We also note that the absolute effect sizes of the drought treatments in all cases are much lower than the successional effects, and the drought-related parameter estimates tend to

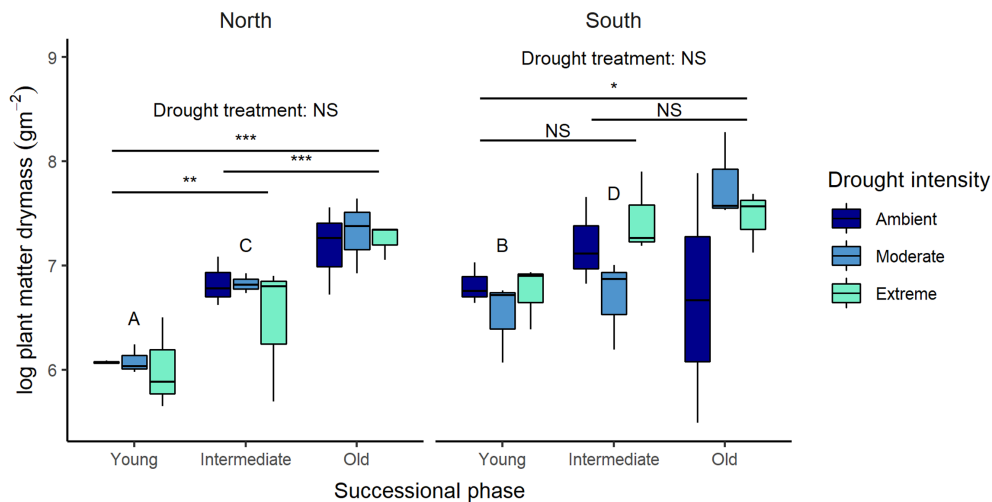


Figure 4. Harvested biomass across drought treatments and post-fire successional phases in the two study regions. We found no significant responses to drought treatments, either as main effects or as interactions with regions or successional phases. Asterisks indicate significant differences between successional phases within regions. Letters annotate significant differences between regions within the young (A:B) or intermediate (C:D) successional phases. Note the log-scaled Y-axis.

cancel each other out, suggesting that the drought effects are not prominent in this system.

Furthermore, the characteristics of northern European coastal heathlands ecosystems may render them relatively resistant to drought. First, the high soil organic content of boreal coastal heaths combined with dense vegetation and bryophyte carpets may provide a mechanistic explanation, as organic soils (Robinson et al. 2016) and dense bryophyte mats (Bates 1998) generally have high water holding capacity. Second, *Ericales* form mutualistic relationships with ericoid mycorrhiza (Read 1983, Mitchell and Gibson 2006), which have high ability to withstand and adapt to environmental stress, and therefore also reduce stress effects on their host plants (Cairney and Meharg 2003). As *Ericales*, including *Calluna*, are dominant in the plant community, the symbiotic relationship with ericoid mycorrhiza might buffer community level stress responses (Diaz et al. 2006). Third, experimental drought treatments may be less effective in moist climates. Rain-out shelters reduce or exclude precipitation, which is a key-driver of drought. However, natural drought typically co-occurs with high temperatures and high vapor-pressure deficit (Ibe et al. 2020). These conditions do not necessarily co-occur with the experimental reduction of precipitation, especially in otherwise moist climates, which may partly explain the surprisingly weak effects of drought in our study. Fourth, atmospheric nitrogen deposition is a threat to heathlands (Heil and Diemont 1983, Maskell et al. 2010), partly through lowering drought resistance in heathland plants (Meyer-Grünefeldt et al. 2016). As our study takes place in a part of Europe with relatively low nitrogen deposition (5–8 kg ha⁻¹ year⁻¹) (NILU 2018) compared to the rest of Europe (CCE IMPACT Database, 2004), this

may explain the relatively high drought resistance of our study system. Lastly, we assess drought responses in terms of differences in responses between roofed plots and controls. However, the controls were subjected to the ambient weather through the study period, which may not be representative of the long-term local climate. This is an important, and often underacknowledged shortcoming of many climate manipulation experiments. In fact, Langley et al. (2018) found that species frequently changed their abundance more in the ambient controls than in the treatment plots during long term (>10 years) climate manipulation experiments. Plants in northern-European heathlands are expected to be adapted to consistently wet conditions, rather than droughts (Meyer-Grünefeldt et al. 2016), and their resilience to our quite severe experimental droughts merits further and more detailed investigations into the underlying processes.

Discussion of hypotheses

We hypothesised that heathlands on the northern brim of the coastal heathland distribution (at 65°8'N) would be less resistant to drought than the populations in the centre of the distribution further south (at 60°7'N). We also hypothesised that the young successional phases would have lower resistance to drought than older phases because species abundant in this phase and younger *Calluna* plants have more resource acquisitive functional traits and can respond sooner to environmental changes than later-successional plant communities and older plants (Grime 1977, Prach et al. 1997). We expected this to be especially evident in the north where *Calluna* is only recruited from seeds, and not vegetative sprouting (Nilsen et al. 2005,

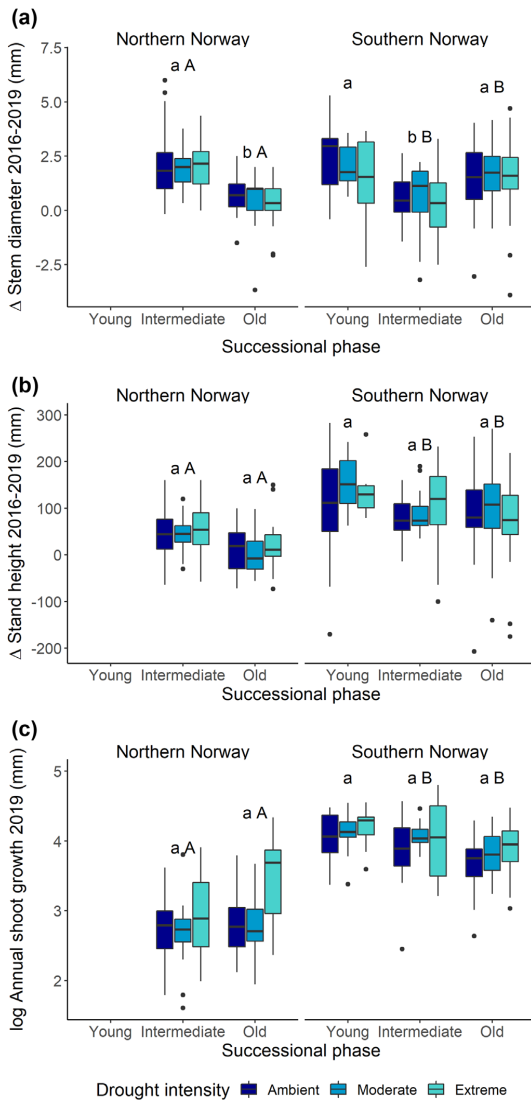


Figure 5. Primary and secondary *Calluna* growth as response to experimental drought across post-fire succession in two regions. (a) Length of growth increment in 2019, (b) change in stand height of 10 tagged *Calluna* specimens per plot from 2016 to 2019 and (c) change in stem diameter of 10 tagged *Calluna* specimens per plot from 2016 to 2019. Annual growth increments were significantly higher in the extreme drought treatment in the north compared to the moderate drought treatment (Tukey HSD $p < 0.001$) and ambient control (Tukey HSD $p < 0.001$). All other drought responses were non-significant. Non-capitalized letters annotate significant differences between successional phases within the same region. Capitalized letters annotate significant differences between regions of sites in the same successional phase.

Velle and Vandvik 2014), and hence have a larger shoot : root ratio (Meyer-Grünefeldt et al. 2015, Ibe et al. 2020). Our data did not support these hypotheses. In contrast, we found increased litter in the moderate and extreme drought treatment compared to the ambient control in the old successional phase in the south, suggesting that old-growth stands of *Calluna* may have lower resistance to experimental drought. Despite having, in general, more extensive roots which facilitate water uptake, old stands also have a large and open canopy that promote evaporation (Gimingham 1988) and lower wood density (Marrs 1986) which increase the risk of cavitation (Hacke et al. 2000, Willson and Jackson 2006).

However, we also note that in the third and fourth year of the experiment, after the onset of the rain exclusion (i.e. 2019 and 2020), we did observe short term browning during summer that was often no longer visible in fall, reflecting low resistance, but high resilience to experimental drought. Photos of the browning are presented in the Supporting information. This temporary browning did not affect the biomass or abundance of species on the timescales covered in this study and was therefore not reflected in our data. We speculate that this could be an early warning of a longer-term drought response which may restore support to H1 in following with other studies that observe ecological drought responses on longer time scales than covered by this study (Peñuelas et al. 2004, Kröel-Dulay et al. 2015). Accordingly, we plan to maintain the experiment to enable follow-up studies to test these hypotheses.

Understanding the study system

While we found only weak evidence of drought responses across successional phases and latitudes, some general attributes of northern coastal heathlands are apparent. For example, our results add to a series of other studies showing that the heathland plant community composition and structure is changing in predictable ways over the post-fire succession (Mallik and Gimingham 1983, Vandvik et al. 2005, Velle et al. 2014, Måren et al. 2018), but with distinguishable regional patterns (Webb 1998, Moen et al. 2006, Velle and Vandvik 2014). There is a general trend for *Calluna* abundance and biomass accumulation rate increase over succession, and diversity to peak in the young successional phase, but with generally slower dynamics, less resource-acquisitive traits and lower peak biomass in the north (Velle and Vandvik 2014). Because of this heterogeneity, coastal heathlands might respond differently to environmental drivers, even over relatively small spatial scales.

Conclusions

This study is an important contribution to filling the knowledge gap on ecological drought responses in high-precipitation and high-latitude ecosystems, and the role of secondary plant community succession on these responses. We report

high resistance to four years of experimental drought across six coastal heathland sites. Moreover, the variation in plant community composition and succession between sites demonstrates the role of local climate, as well as land-use history, in shaping vegetation structure and potentially longer-term responses. Upholding landscape heterogeneity of heathlands through management with prescribed fire is therefore not only a means to conserve heathland vegetation and habitat diversity, but also a means to increase drought resistance on the landscape level. More knowledge on the effects of different kinds and intensities of droughts, and over different time-scales, is needed to bridge the gap between these experimental findings and the observations of large-scale dieback on the landscape scale.

Acknowledgements – We are grateful to many colleagues and students for help with setting up the infrastructure, harvesting and sorting biomass, measuring *Calluna* growth, and recording plant community structure: Kristine Birkeli, Sigmund Alsaker, Astrid Bjørnsen, Lucely V. Bustamante, Casper T. Christiansen, Romane Collin, Amy E. Eycott, Ivar Fineid, Kjetil F. Fosheim, Sonya Geange, Victoria H. Grape, Hannah Guthu, June V. Haugum, Siri A. Hestad, Kristine H. Holm, Elisabeth Nesheim-Hauge, Ingvild S. Joys, Daiki Koga, Betsabe M. Kuan, Lea Mouton, Sára Nagy, Jenny Neuhaus, Jonas S. Nilssen, Christine Pötsch, R. M. Prathibha Nilakshi Ranasinghe, Kris K. Sevaldsen, Silje Stornes, Philippine Surer, Ida T. Vangdal, Vincent Zimmerman, Hedda V. B. Ørbæk and Didrik Aamold. We thank Casper Tai Christensen and Amy E. Eycott for critically reading the manuscript. Last, we thank the land-owners for allowing us to set up the experiments on their land. *Funding* – This work was funded by the Research Council of Norway (MILJØFORSK project 255090, INTPART project 274831) and L. Meltzers Høyskolefond.

Author contributions

Siri V. Haugum: Conceptualization (supporting); Methodology (equal); Validation (lead); Visualization (lead); Writing – original draft (lead). **Pål Thorvaldsen:** Conceptualization (equal); Methodology (equal); Supervision (supporting); Writing – original draft (supporting). **Vigdis Vandvik:** Conceptualization (equal); Methodology (equal); Supervision (lead); Writing – original draft (supporting). **Liv G. Velle:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (supporting); Writing – original draft (supporting).

Data availability statement

Data are available from the Open Science Framework (<<https://osf.io/mv84d/>>) (Vandvik et al. 2021).

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Supplementary information

1. Climate and weather recordings

Table S1: Public meteorological stations used for historical precipitation and temperature

Station name	Lat	Lon	Data	Time	Site
Eikanger-Myr	60.669735	5.337034	Precipitation	1980-2019	South young, intermediate and old
Liafoss	64.839602	11.953654	Precipitation	1990-2019	North intermediate
Vega-Vallsjø	65.699904	11.851126	Precipitation and temperature, growth season	1991-2019	North young and old
Hellisøy fyr	60.752104	4.711070	Temperature	1980-2004	South young, intermediate and old
Fedje	60.752104	4.711070	Temperature, growth season	2004-2019	South young, intermediate and old
Nordøyan fyr	64.8044715	10.5349912	Temperature	1980-2019	North intermediate
Rørвик lufthavn	64.838968	11.145201	Growth season	2019	North intermediate

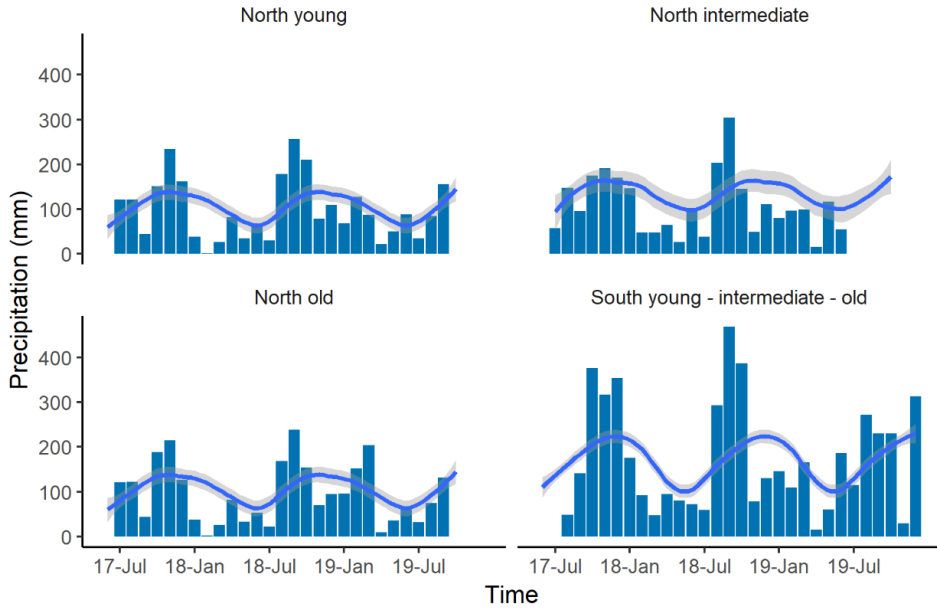


Figure S1. Observed on-site precipitation during the study period shown as bars, and mean precipitation from 1990 to 2019 from the closest public weather station shown as graph with 95% confidence level.

2. Plant community dynamics

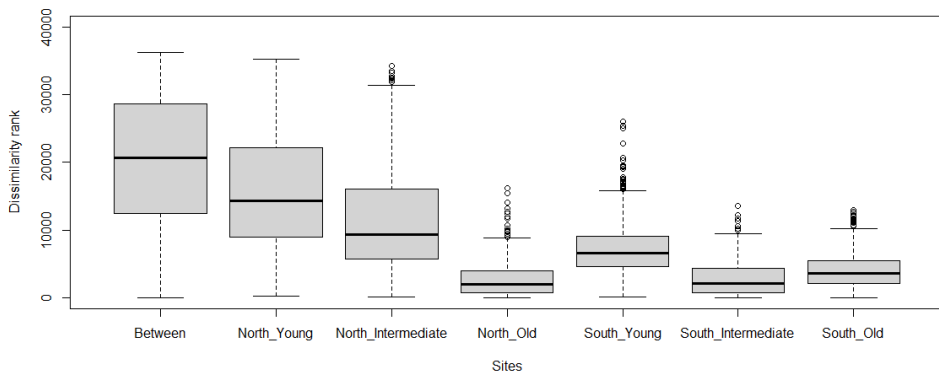


Figure S2: Within-group and between-group dissimilarities for the six study sites.

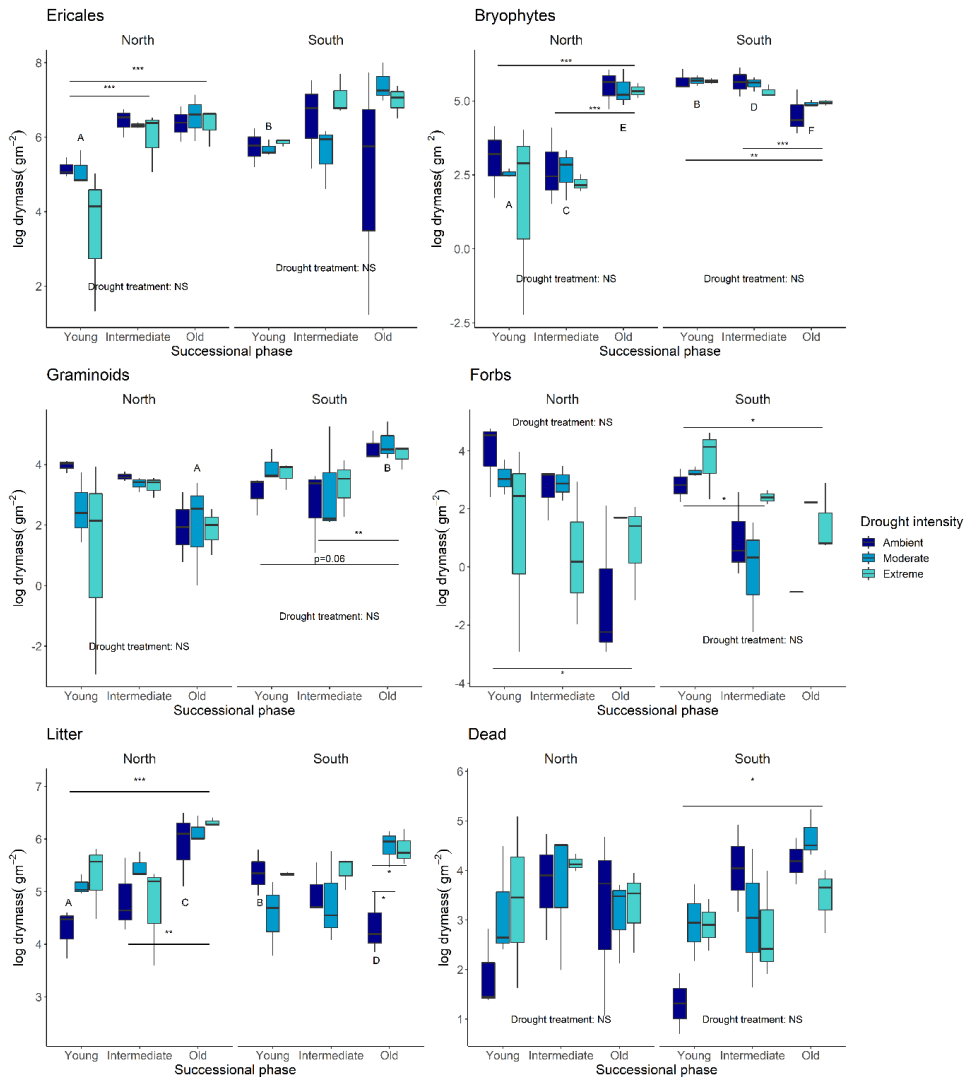


Figure S3: Harvested biomass for individual functional groups for all drought treatments and post-fire succession in the two regions. Asterisks show differences between phases with regions, and letters annotate difference between regions within successional phases. We observed no significant responses to drought treatments within regions or successional phases, and neither in interaction with regions nor successional phases. Note the log-scaled Y-axes.

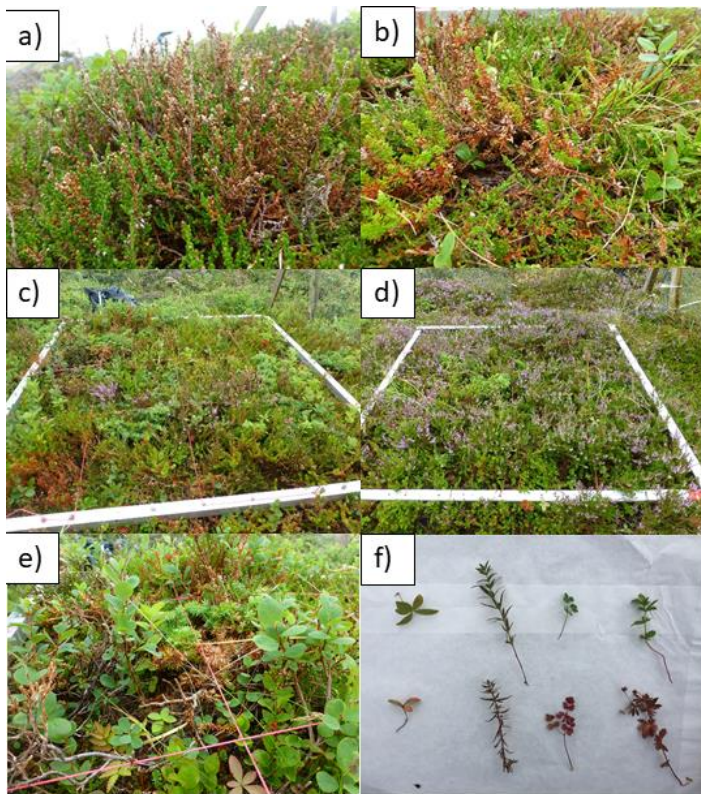


Figure S4: Observations of browning in field: a) *Calluna vulgaris*, b) *Empetrum nigrum*, c) plot with drought damage, d) plot without drought damage, e) *Juniperus communis*, f) forbs from plot without drought damage (upper) and with drought damage (lower), from left: *Lysimachia europaea*, *Galium boreale*, *Thalictrum alpinum*, *Potentilla erecta*.

Paper II



A teabag containing green tea installed aboveground in a plot in order to measure decomposition rates. Photo: Siri V. Haugum

Paper III



Prescribed burning in Nerlandsøy, Sunnmøre, February 9th 2017. Photo: Siri V. Haugum.

Paper IV



Two BSc students measuring vegetation height in an extreme drought treatment plot in the young successional phase in the south, August 2019. Photo: Siri V. Haugum.



Graphic design: Communication Division, UIB / Print: Skjipes Kommunikasjon AS



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ISBN: 9788230867082 (print)
9788230853481 (PDF)